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Positive affects in lambs: appeasing effects of stroking
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Sophie Hild, Marjorie M. Coulon, Delphine Briand, Raymond Nowak, Xavier Boivin. Positive affects in lambs: appeasing effects of stroking. Joint meeting of the 33rd International Ethological Conference (IEC) & the Association for the Study of Animal Behaviour (ASAB), International Council of Ethologists (ICE).; Association for the Study of Animal Behaviour (ASAB)., Aug 2013, Newcastle, United Kingdom. 242 p. hal-02744787

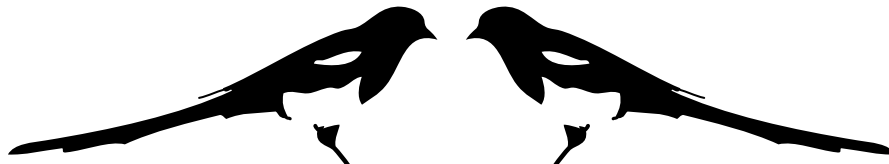
HAL Id: hal-02744787

<https://hal.inrae.fr/hal-02744787>

Submitted on 3 Jun 2020

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BEHAVIOUR 2013

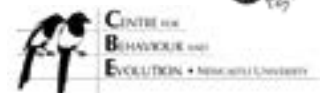
Joint meeting of the 33rd International Ethological Conference (IEC) & the Association for the Study of Animal Behaviour (ASAB)



Abstract Book

4th - 8th August 2013

The Sage, Newcastle-Gateshead UK



BEHAVIOUR 2013

Symposia Abstracts

Symposium 1 Behavioural changes with advancing age: strategies and constraints

S1.1 Social careers in Jackdaws - a longitudinal study

Simon Verhulst, University Of Groningen
Moniek Geerdink, Jelle Boonekamp, Martijn Salomons

Social dominance in Jackdaws is related to life history components such as number and quality of fledglings and their sex ratio. It is therefore of interest what determines an individual's dominance and how it is modified during life. We present the results of a longitudinal study of social dominance in a colony of free-living Jackdaws and show that: (1) dominance rank of individuals within a cohort was highly repeatable, (2) this was in part due to body size: larger individuals were more dominant and size does not change with age, (3) individual birds became more dominant as they aged, (4) more dominant individuals died at a younger age, (5) dominance decreased the last year an individual was alive. The latter mirrors our recent finding in the same colony that telomere length shortened faster during the last year of life. These results indicate that senescence near the end of life is not a gradual process, as often assumed, but a deterioration process that is much accelerated when death comes near.

S1.2 Early environmental effects on the rate of behavioural senescence

Neil Metcalfe, University Of Glasgow
Who-Seung Lee, Pat Monaghan

It is increasingly recognised that the environment experienced in early life can have significant long-term effects - including on behaviour - that may only become apparent in old age. One potential effect is that stressors encountered in early life could influence the time of onset or rate of senescence, which may influence traits such as locomotor performance, social status and reproductive success. In this talk we explore these concepts in studies of the three-spined stickleback (*Gasterosteus aculeatus*), an ideal species for such studies due to its short lifespan and well-documented behavioural repertoire. We will show that environmental conditions that influence juvenile growth trajectories have long-term effects: accelerated growth causes accelerated senescence across a broad spectrum of behaviours, ranging from swimming endurance through nest building to courtship vigour. However, compensatory growth increases both the chance of surviving to reproductive age and early reproductive success. The fitness consequences of different growth trajectories thus depend on the relative importance of early reproductive success

versus reproductive lifespan, and so are predicted to differ between populations and environments.

S1.3 Prudent and constrained parents: successful strategies at golden ages

Alberto Velando, Universidade De Vigo
Roxana Torres

Recent studies in wild populations provide compelling evidence that reproduction decrease at advanced ages. This pattern of senescence in long-lived animals may be attributed to a decline in functional capacities, but also to a prudent investment strategy at older ages to slow down the rate of decline and hence increase the time for reproduction. Interestingly, current evidence also suggests that reproductive investment by old animals is likely to be influenced by expected current success but also by future prospects. Here, we reviewed some evidence supporting constrained reproduction and strategic investment of old animals. Additionally, we show some results in the blue-footed booby, a long-lived seabird, suggesting that old animals can rest to mitigate the negative effects of senescence or strategically do the utmost when future prospects are limited.

S1.4 Sexually extravagant males age more rapidly

Gabriele Sorci, CNRS
Michel Saint Jalme, Yves Hingrat, Frederic Lacroix, Brian Preston

Evolutionary theories of ageing posit that increased reproductive investment occurs at the expense of physiological declines in later life. Males typically invest heavily in costly sexual ornaments and behaviour, but evidence that the expression of these traits can cause senescence is lacking. Long-lived houbara bustards (*Chlamydotis undulata*) engage in extravagant sexual displays to attract mates. We showed that males investing most in these displays experience a rapid senescent deterioration of spermatogenic function at a younger age. This effect is sufficiently large that the expected links between male showiness and fertility reverse in later life. Our results cannot be explained by the selective disappearance of competitive phenotypes; they are instead consistent with an early vs. late life trade-off in male reproductive competence, highlighting the potential significance of sexual selection in explaining rates of ageing.

S1.5 What explains for negligible and accelerated senescence in castes of the eusocial honey bee (*Apis mellifera*)?

Daniel Munch, Norwegian University Of Life Sciences
Gro V. Amdam

The honey bee represents an alternative aging model that features an extreme diversity of longevity patterns among siblings. As in other highly social species, colony-organization emerges through a structured division of labor between essentially sterile workers. Workers pass through a sequence of caste specific sib care behaviors such as nursing the brood and foraging for food. Gerontology research centers around the dramatic consequences of social caste differentiation for an individual's lifespan: accelerated aging in forager bees is contrasted by a slowed progression of aging symptoms in nursing workers, and by the absence of detectable senescence (negligible senescence), when bees postpone resource transfers during winter. By manipulating the social environment of bees we show how individuals with short and extremely long lifespan can be transformed into one another. Our behavioral, anatomical, proteomic and epigenomic screening data exemplify the significant effects of social caste on aging. We argue that the alternative utilization of a common yolk precursor protein (vitellogenin) in nursing and somatic maintenance can link social resource transfers with slowed aging in nurse and winter bees. In contrast, forager bees with lowest vitellogenin levels become frail within days, which may facilitate the removal of disease-prone individuals from the colony.

Symposium 2 The Galton Symposium: Sexual selection and variability in preferences in humans

S2.1 Visual cues to pathogens change mate preferences

Anthony Little, University Of Stirling
Ben Jones, Lisa DeBruine

Evolutionary approaches to human attractiveness have documented several traits that are proposed to be attractive across individuals and cultures, although both cross-individual and cross-cultural variation are also often found. Previous studies show that parasite prevalence and mortality/health are related to cultural variation in preferences for attractive traits. We examined whether visual experience of pathogen cues may mediate such variable preferences by showing individuals slideshows of images with cues to low and high pathogen prevalence and measuring their visual preferences for face traits both before and after exposure.

We found that both men and women moderated their preferences for facial masculinity and symmetry

according to recent experience of visual cues to environmental pathogens. Change in preferences was seen mainly for opposite-sex faces with individuals preferring more sex-typical and more symmetric faces after exposure to pathogen cues than when not exposed to such cues.

Overall, our data demonstrate that preferences can be strategically flexible according to recent visual experience with pathogen cues. Given that cues to pathogens may signal an increase in contagion/mortality risk, it may be adaptive to shift visual preferences in favour of proposed good-gene markers in environments where such cues are more evident.

S2.2 Systematic variation in men's dominance perceptions

Benedict Jones, University Of Glasgow
Christopher Watkins

Most research on potentially adaptive systematic variation in face perception has focused on individual differences and/or facultative responses in women's mate preferences. By contrast with this focus on the effects of intersexual selection on attractiveness judgments, here we describe a series of correlational studies and priming experiments that suggest intrasexual competition has shaped both individual differences and facultative responses in men's perceptions of other men's dominance. In particular, we show that cues of other men's dominance, such as masculine facial structures, are more salient to subordinate men than they are to dominant men and that men's perceptions of other men's dominance are sensitive to the outcome of recent confrontations. Together, these results reveal a high degree of flexibility in men's dominance perceptions, which may function to optimize the strategies they employ in intrasexual competition.

S2.3 Opposite-sex siblings decrease attraction, but not prosocial attributions, to self-resembling opposite-sex faces

Lisa DeBruine, University Of Glasgow

Contextual cues of genetic relatedness to familiar individuals, such as co-socialization and maternal-perinatal association, modulate prosocial and inbreeding avoidance behaviours towards specific potential siblings. These findings have been interpreted as evidence that contextual cues of kinship indirectly influence social behaviour by affecting the perceived probability of genetic relatedness to familiar individuals. Here we test a more general alternative model, in which contextual cues of kinship can influence the kin recognition system more directly,

changing how the mechanisms that regulate social behavior respond to cues of kinship, even in unfamiliar individuals. We show that possessing opposite-sex siblings influences inbreeding-relevant perceptions of facial resemblance, but not prosocial perceptions. Women with brothers were less attracted to self-resembling, unfamiliar male faces than were women without brothers, while both groups found self-resemblance to be equally trustworthy for the same faces. Further analyses suggest this effect is driven by younger, rather than older, brothers, consistent with the proposal that only younger siblings exhibit the strong kinship cue of maternal-perinatal association. Our findings provide evidence that experience with opposite-sex siblings can directly influence inbreeding avoidance mechanisms and demonstrate a functional dissociation between the mechanisms that regulate inbreeding and those that regulate prosocial behaviour towards kin.

S2.4 Women's self-perceived health and attractiveness predict their male vocal masculinity preferences in different directions across short- and long-term relationship contexts

David Feinberg, McMaster University
Lisa DeBruine, Benedict Jones, Anthony Little, Jillian O'Connor, Cara Tighe

Research has revealed that women's self-perceived attractiveness positively predicts preferences for male facial and vocal masculinity. Other research has demonstrated that women who perceive themselves to be less healthy prefer male masculinity more than do women who may be healthier. As self-perceived health may predict self-perceived attractiveness, previous findings may appear to be contradictory. Therefore, we compared the effects of self-perceived attractiveness and health on vocal masculinity preferences in long- and short-term contexts.

We found that although self-perceived health and attractiveness were positively correlated, self-rated attractiveness positively predicted long-term vocal masculinity preferences, whereas self-rated health negatively predicted short-term vocal masculinity preferences. While health and attractiveness may share a common basis, we show independent relationships with preferences based on relationship context. Such preferences are potentially adaptive as masculine men may pass on immunity to infection to their offspring, which may be a relatively greater benefit for women in poor health and masculine men may be more likely to invest in relationships/offspring with relatively attractive women, decreasing the cost of choosing a masculine long-term partner for attractive women.

These data resolve a potential conflict between health and attractiveness influences on the attractiveness of masculinity and highlight sophisticated individual

differences in preferences.

S2.5 Does MHC dissimilarity among partners drive mate choice, or result from inbreeding avoidance based on alternative cues? Insights from a ten-year study in a wild solitary lemur

Elise Huchard, University Of Cambridge
Alice Baniel, Susanne Schliehe-Diecks, Peter. M. Kappeler

Female choice for partners carrying dissimilar genes at the Major Histocompatibility Complex (MHC) may contribute to limit inbreeding or to improve the immunity of future offspring. It is however often difficult to establish whether observed MHC dissimilarity among mates drives mate choice, or represents a by-product of inbreeding avoidance based on MHC-independent cues using correlative studies in wild populations.

Here we used 454-sequencing and a 10-year study of wild grey mouse lemurs (*Microcebus murinus*), small, solitary primates from western Madagascar to (1) compare the relative importance on mate choice of two MHC class II genes, DRB and DQB, that are equally variable but display contrasting patterns of selection at the molecular level, with DRB under stronger diversifying selection and (2) assess the effect of variable degrees of genetic relatedness among candidate mates on the detection of MHC-dependent mate choice.

Our results reveal disassortative mate choice at DRB, but not at DQB, and that DRB-disassortative mate choice remains detectable after excluding all related dyads (characterized by a relatedness coefficient $r > 0$). These findings suggest that observed deviations from random mate choice at MHC are driven by functionally important MHC genes (like DRB) rather than passively resulting from inbreeding avoidance.

Symposium 3 Exploring the role of networks in animal social behaviour

S3.1 Having it all? Trade-offs in Multi-dimensional Behavioural Networks among Female Baboons social dynamics of female baboons

Derek Murphy, University Of Aberdeen

Recent research on the sociality of chacma baboons has sparked debate as to whether female baboons sustain long-lasting social bonds with particular other individuals or whether the social dynamics of female baboons are better described as a series of short-term relationships with different partners in response to local contingencies.

Here, using social network analysis, I investigate the social dynamics of female chacma baboons in response

to local ecological, social and demographic contingencies over a ten-year period. Results suggest that the social interaction patterns of baboons are influenced not only by seasonal effects, but also by social and demographic factors such as troop size, rank, the number of infants in the troop, and whether or not a female is the mother of an infant.

S 3.2 Personality and Social Networks in Brown Capuchin Monkeys (*Sapajus apella*)

Blake Morton, University Of Stirling
Mark Tranmer, Hannah M. Buchanan-Smith, Phyllis C. Lee

Understanding the social organisation of animals is a primary goal within the field of behavioural ecology. While animals typically form relationships on the basis of kinship, age-sex, and dominance rank, exceptions to these rules exist yet remain largely unexplored. Measures of "personality" in animals typically reflect consistent individual differences in behaviour, including sociality, motivation, attention, learning, cognitive performance, risk-taking, general well-being, and coping strategies. An interesting question, therefore, is to what extent individual differences in personality explain the social organisation of animals, particularly beyond that of simpler social rules (i.e. kinship, age-sex, and rank).

In this study, we examine the relative contribution of personality, social rank, age-sex, and maternal relatedness to the social structure of two groups of brown capuchin monkeys (*Sapajus apella*).

Results are discussed in light of the role that individuals play within social networks, and the various factors that may underlie sociality in animals.

S3.3 Elephant networks and the power of leadership

Vicki Fishlock, Amboseli Trust For Elephants & University Of Stirling
Cynthia Moss, Phyllis Lee

African savannah elephants have multi-tiered social networks where individual relationships persist over decades, affecting survival and reproductive success. In this complex and flexible system experienced individuals act as repositories of social and ecological knowledge, particularly in the context of threats or seasonal movement decisions.

We explore the network positions that these experienced females occupy in a well-studied population in Amboseli, Kenya, investigating family position in relation to female age and family properties (size, cohesiveness, matriarch experience) at different tiers of organization.

We use cohesiveness - the propensity for family members to be together - to explore how social decision making may be disseminated through experienced females in a family, rather than simply restricted to a matriarch - the oldest female, who forms an attractive nucleus for her own family, and her bond group.

S3.4 The spatial and temporal dynamics of elephant social networks

Shermin Silva, Colorado State University
Sergey Kryazhimskiy, George Wittemyer, Jonathan Dushoff

In order to understand the social and ecological factors that structure animal societies, it is necessary to study the dynamics of social networks from a comparative perspective. Asian and African elephant species have diverged by approximately 6 million years, but occupy similar niches in their respective environments as mega herbivores. Both African savannah elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) occupy seasonal habitats which nevertheless differ in terms of absolute rainfall and hence productivity. Comparison of social dynamics within and between these populations highlights the ecological variables influencing social structure. Current paradigms for studying social structure use association indices in conjunction with general statistical tools (permutation tests and clustering algorithms) in defining social networks. While the study of animal social networks has expanded in recent years, they have essentially ignored an important variable governing all interaction: space.

Here I show how incorporating space explicitly can shed new insights on the factors that drive contact structures and differentiate truly social affiliations from those which are primarily resource-driven.

S3.5 Social transmission and the establishment of traditions in wild Great tit networks

Lucy Aplin, University Of Oxford & Australian National University

Animal culture plays a potentially important role in adaptive behavioural plasticity. However, cultural transmission takes place in specific social contexts; group dynamics and social networks will determine the pattern and persistence of traditions. Our understanding of the interaction between social dynamics and animal culture has been seriously limited by a lack of experimental data from natural systems. We experimentally seeded a novel behaviour into a wild population of great tits (*Parus major*). Using a two-action & control design, puzzle-boxes were installed in isolated subpopulations, with one individual in each

population trained to one of two alternative solutions. Behaviour was then data-logged using PIT-tag antennae and electronic sensors. Social networks were separately measured using a grid of feeders recording temporal feeding associations. Overall, 88% of individuals in each treatment solved with 29,816 solves by 267 individuals; only 5 individuals solved in the control population. Task acquisition followed a classic sigmoidal curve and solution was heavily biased towards that originally demonstrated, suggesting that local arbitrary traditions were being established through social learning. Network-based diffusion analysis was used to show the importance of associations for diffusion dynamics. Finally, we identified interactions between individual learning strategies and the spread and maintenance of traditions

Symposium 4 How horses see the world: cognition and welfare

S4.1 Do horses with poor welfare show ‘pessimistic’ cognitive biases?

Severine Henry, Umr 6552 Ethos- Universite Rennes 1
Martine Hausberger, Melissa Bateson

Negative affect is known to cause individuals to interpret ambiguous stimuli ‘pessimistically’, exhibiting an increased expectation of punishment. Here, we hypothesised that horses suffering from poor welfare conditions would show more pessimistic judgement biases compared to horses with a better welfare state.

We compared 36 horses living either in either restricted, riding school conditions (two sites) or in more naturalistic conditions (one site). The welfare of the horses was assessed by recording health-related and behavioural measures. All horses were also trained on a spatial judgment task during which they learnt to expect edible food in one location and unpalatable food in another. Judgement bias was tested using three ambiguous locations intermediate between the trained locations.

A strong site effect was found: the horses living in the site characterized by the highest levels of behavioural and health-related problems exhibited a clear pessimistic bias when judging ambiguous stimuli, whereas the horses living in more natural conditions, associated with a good welfare state, showed an optimistic bias.

This study is the first to reveal a link between poor welfare and pessimistic judgement biases in domestic horses, and reinforces existing data suggesting that horses in some riding schools may suffer from poor welfare.

S4.2 Basal Ganglia Dysfunction and Equine Learning Ability

Linda Greening, Hartpury College
Laura Douglas

Differences in learning ability and performance of domestic *Equus caballus* have been studied in relation to age, breed, and gender groups, however few studies report controlling for the effects of horses displaying stereotypic behaviours.

Compared with non-stereotypic horses, crib-biters are less likely to show the desired response within a given time frame but more likely to persist during the extinction phase of a positively reinforced operant task. Crib-biting horses also appear to display quicker learning ability and performance, compared to pair matched control horses, when using both local and distal cues during preferential place learning.

These and other findings indicate altered neuro-physiology linked to basal ganglia dysfunction in the stereotypic horse population, which has been associated with sub-optimal living conditions and impaired learning ability in a number of species. Crib-biting horses therefore appear; to display greater visual and spatial awareness making them faster to learn using stimulus-response learning strategies and, show increased motivation to engage in the performance of a learnt task involving a food reward making them less prone to extinction. In combination these findings may influence equine training regimes, however differences between learning ability of horses displaying locomotor compared with oral stereotypies has yet to be determined.

S4.3 Behavioural plasticity of horses in detour task

Paolo Baragli, University Of Pisa
Adam R. Reddon

Spatial reasoning is among the most fundamental of cognitive processes and is essential for survival. Domestic horses (*Equus caballus*) demonstrated the ability to solve spatial reasoning problems by successfully navigating detour mazes with both symmetrical and asymmetrical obstacles. Thirty-six female Italian saddle horses took part in two detour tasks. Some horses showed consistently lateralized behaviour when detouring around the obstacles while, other horses switched from lateralized mode of response in the symmetrical task to non-lateralized behaviour as the asymmetry of the obstacle increased. This may reflect a weaker underlying lateralization of neural function in these animals. Non-lateralized horses may be more capable of modifying their detour strategy as the difficulty of the task increases. Moreover, the non-lateralized horses detoured the barrier via the short route more often than chance,

suggesting a greater capacity for spatial reasoning in these animals. The horse's ability to form spatial concepts could have implications for their welfare. In modern husbandry system, horses are often kept in small stalls for several hours per day. It is possible that horses perceive the stall as an impassible obstacle separating them from their social fellows, which may induce anxiety of frustration, therefore compromise the animal's welfare.

S4.4 Dominance and Body Condition in Horses: Can behavioural ecology improve our understanding of equine obesity?

Sarah Giles, University Of Bristol
Christine Nicol, Pat Harris, Sean Rands

Obesity now affects between 20 to 45% of the domestic leisure horse population. It can lead to metabolic abnormalities and severe health and welfare problems. The risk factors for obesity in domestic equines are not well-defined. Our previous studies suggest that measured diet intake and exercise level are not solely responsible for the variation in body condition observed in outdoor, herd-living animals. This may be due to individual differences in grazing and energetic intake. Predictions from behavioural ecology relating to herd dynamics and associated behavioural traits, such as social status, suggest that behavioural interactions may influence energetic intake in outdoor living horses. Subsequently, when applied to a clinical setting, social status may be a predictor of obesity risk. This study explored the association between the individual behavioural trait 'dominance rank' (established through a feeding trial) and body condition, in outdoor, herd-living horses. We found a strong positive association ($p=0.001$) between social status and body condition. Using these data and supplementary longitudinal case studies we consider the likely mechanisms behind, and direction of, this association.

We will discuss these results with reference to their potential to enhance our understanding of factors influencing obesity susceptibility in these populations.

S4.5 Favoring horses' positive perceptions of the domestic environment: how do horses' perception of humans and welfare interact?

Martine Hausberger, University Of Rennes 1
Clemence Lesimple, Carole Fureix

Cognition is a concept that deals with how individuals perceive and process the environmental information in order to produce appropriate responses. Humans can be considered as a major element in horses' immediate environment, especially through the direct work-related relationship these animals share with humans.

However, a large part of the working horses might suffer from negative appraisal of the human-horse interactions, as revealed by the high rates of accidents involving horses reported in professionals.

Here we will present a set of results highlighting how suffering from poor welfare (inferred from the presence of severe vertebral problems) could affect horses' relational behaviour and might even "contaminate" the way horses react to humans in subsequent interactions. This, in turn, might also trigger poor welfare states. Indeed, work stressors have been shown to impact on the daily life of horses outside the work sessions, and repeated interspecific conflicts might, as in humans, lead to psychological stress and poor welfare. Keeping that in mind, we will present training/working practices which trigger good human-horse relationship and welfare states, therefore favoring horses' positive perceptions of the domestic environment.

Symposium 5 Avian cognition

S5.1 The Cognitive Chick: Objects and Space in an Avian Brain

Giorgio Vallortigara, University Of Trento

I discuss evidence revealing abilities in new-born domestic chicks to identify objects that move out of view, to grasp intuitive physical concepts underlying basic object mechanics, and to represent the geometrical relationships among extended surfaces in the surrounding layout. Some of the abilities associated with these core knowledge systems are observed in chicks in the absence (or with very reduced) experience, supporting a nativistic foundation of cognitive mechanisms.

S5.2 What is the relationship between innovation and intelligence? Is cognition still the key?

Ludwig Huber, Messerli Research Institute, Vetmeduni Vienna
Anna Kis, Julia Mueller-Paul, Anna Wilkinson

Many non-human animals are extractive foragers, some having even advanced manipulatory skills, but only very few use tools in the wild. This is a big puzzle in cognitive biology. What is the relationship between tool use and intelligence? If intelligence or general cognition is defined as the ability to change behaviour in novel situations and to generate (invent) new behaviours, one should find innovative species being the most potent problem solvers.

One line of research to answer this question would be to test individuals of such innovative species in a broad range of technical or physical tasks. We have done so

with species from two avian taxa that are regarded as particularly suited in this respect: parrots and corvids. In this talk I shall focus on some key examples of problem solving in a few species of these taxa, including instances of innovative tool use, performance in means-end tasks, and comparative investigations of analogical and causal reasoning.

S5.3 Can birds learn abstract rules?

Carel ten Cate, Institute Of Biology, Leiden University
Caroline van Heijningen, Michelle Spierings, Jiani Chen

A key property distinguishing language and the vocal communication in other animals is our ability to apply abstract rules (syntax) to create an infinite set of linguistic utterances. There is a debate on whether this ability is uniquely human, and evolved in consort with language, or whether it originates from more general cognitive abilities that might also be present in other animal species, either by common descent or by independent evolution. A powerful tool to explore the presence of such abilities in animals is by using the Artificial Grammar Learning (AGL) paradigm. In this paradigm, developed to examine the rule detection skills of young infants and human adults, strings of meaningless vocal elements, ordered according to specific algorithms that are assumed to be relevant in linguistic contexts, are presented to the subjects. Hereafter it is tested whether the underlying rules have been detected. Like humans, many songbirds produce structured vocalizations, acquired by learning. Hence they make an interesting group to examine rule learning.

We will present several AGL experiments in which explore the rule learning abilities of zebra finches. We compare our results with those obtained in other species and in humans.

S5.4 Cache Protection in Clark's Nutcrackers: Complex Cognition or Trial Order Effects?

Elske Van Der Vaart, University Of Groningen & University Of Reading
Rineke Verbrugge, Charlotte Hemelrijk

Corvids, the extended family of crows, are known for their complex social cognition, especially in the context of caching. When hiding food underground, both ravens and Western scrub jays seem to keep track of who is watching, and then take appropriate countermeasures to prevent future theft. In a recent study, another corvid, the Clark's nutcracker, was shown to demonstrate similar behavior. This is surprising, as Clark's nutcrackers are mostly solitary, and thus do not seem to require sophisticated anti-pilfering strategies.

In the present study, our objective was to discover whether a cognitively simpler explanation might account for the reported results. We used a computational model of a kind of 'virtual bird', developed in previous work. Its behavior depends on a set of basic assumptions about corvid cognition, and a well-established model of human memory. We implement two different versions of this model, one which assumes that the birds remember whether they were watched, and one which does not, and show that both account for the empirical data equally well. In particular, we show that the complicated trial order used in the original experiment may have unexpected consequences.

We conclude with testable predictions that could differentiate the two hypotheses in future.

S5.5 Clark's nutcrackers (*Nucifraga columbiana*) rely heavily on geometric information for spatial orientation

Debbie Kelly, University Of Manitoba
James Reichert

All mobile species must orient, yet we know surprisingly little about how this process is achieved. Orientation is the fundamental step required for navigation, as it allows the traveler to determine in which direction to begin heading. Only once one has successfully oriented can navigation begin. Classic studies have shown that the two types of cues used by animals to orient are features and geometry. Features are objects within an environment (e.g., trees or buildings), whereas geometry is the metric relationship between objects or surfaces (e.g., distances or directions). However, the mechanisms by which these spatial cues are integrated are not known.

In the current study, we investigated the effect of experience on the weighting of featural and geometric cues during a spatial search task by a food-storing bird, the Clark's nutcracker. Four groups of birds were trained to locate food hidden at one corner of a fully-enclosed rectangular arena. Two groups were initially trained with features whereas two other groups were initially trained with geometry. Of the featurally trained groups, one was retrained with geometry. Likewise, of the geometrically trained groups, one was retrained with features.

We found that unlike other avian species examined using similar procedures, nutcrackers showed a primary weighting of geometric information.

S5.6 Using nest building in birds to examine the basis of physical cognition

Susan Healy, University Of St Andrews
Kate Morgan, Simone Meddle, Ida Bailey

Over the past 20 years, tool manufacture and use by birds has fundamentally changed the way we regard avian cognitive abilities. However, this change in view has largely confined to the corvids, which are now not uncommonly referred to as ‘feathered primates’. It is our contention, however, that nest building by birds shares two key features of tool manufacture, appropriate material choice and appropriate material manipulation. Further, the coupling of these features with the diversity in complexity of nest structure across bird species, allows for a comparative approach to determining the cognitive abilities that may underpin ‘physical cognition’ in birds.

We will present experimental data from manipulations of material for use in nest building by zebra finches in support of our contention.

Symposium 6 Adaptive Behavioural Variation

S6.1 Alternative Reproductive Tactics: A Case Study from Horseshoe Crabs

H. Jane Brockmann, University Of Florida

In many species individuals have more than one way of reproducing. When these alternatives are discontinuous or discreet, then they are referred to as alternative reproductive tactics (ARTs). Some ARTs are fixed during development, but most are flexible phenotypes whose expression depends on environment (e.g. population density) and/or individual status (e.g. age or condition). ARTs evolve when there is intense competition, multiple ways of gaining fitness, crossing fitness curves and when there is selection against intermediate phenotypes (i.e. disruptive selection). If, in addition, the success of a tactic is affected by its frequency in a population then the phenotypes can be maintained at stable frequencies. Horseshoe crabs (*Limulus polyphemus*) have male and female ARTs; males either pair at sea and spawn with females at the nesting beach or seek spawning pairs on shore and fertilize eggs through sperm competition; females either spawn with one or multiple males. We have shown that these tactics are conditional; that their success depends on the operational sex ratio, tactic frequency and their mates’ behavior; and that tactics differ in their costs, benefits and tradeoffs.

Taken together, the study of ARTs provides insight into the evolution and maintenance of behavioral variation in populations.

S6.2 Sexual selection and individual differentiation

Sasha Dall, University Of Exeter

Interest is burgeoning in the evolution and maintenance of individual differences within

populations across the animal kingdom, from a variety of perspectives. Recently, ecologists have started to develop functional explanations for such variation, particularly if it is behavioural in origin. Despite this effort, the role of sexual selection is only rarely considered explicitly. From this perspective, I discuss the maintenance of both key aspects of individual behavioural differentiation: intra-individual consistency and inter-individual variation. In the process, I hope to stimulate broader appreciation of how sexual selection can promote individual differentiation of any sort within populations across a wide range of social and mating systems.

S6.3 Adaptive behavioural variation in social environments

Niels Dingemans, University Of Munich / Max Planck Institute For Ornithology
Yimen Araya-Ajoy

Over the last few decades, it has become evident that between-individual differences in suites of correlated behaviours (“animal personalities” or “behavioural syndromes”) characterize a broad range of animal taxa. Various adaptive hypotheses have been suggested, and empirically tested, for why natural selection might favour variation at this level of behavioural organisation. One key hypothesis predicts that personalities are favoured because social interactions lead to a diverse array of social niches. We use aggressiveness data of 12 nest box populations of wild great tits, to test whether patterns of between- and within-individual variation are indeed a function of the social environment. We further document the consequences of personality variation by asking both whether the social environment affects behavioural phenotypes and how social environment affect fitness, and thereby reveal how the presence of personality structure affects evolutionary processes.

S6.4 Integrating proximate and ultimate causes of social plasticity

Rui Oliveira, ISPA

Animals must adjust the expression of their social behaviour to the nuances of daily social life and to transitions between life-history stages, and the ability to do so impacts on their Darwinian fitness. According to an integrative framework for understanding the proximate mechanisms and ultimate consequences of social plasticity it is achieved by rewiring or by biochemically switching nodes of the neural network underlying social behaviour in response to perceived social information. Therefore, at the molecular level, it depends on the social regulation of gene expression, so that different neurogenomic states correspond to

different behavioural responses and the switches between states are orchestrated by signalling pathways that interface the social environment and the genotype. At the evolutionary scale social plasticity can be seen as an adaptive trait that can be under positive selection when changes in the environment outpace the rate of genetic evolutionary change. In cases when social plasticity is too costly or incomplete, behavioural consistency can emerge by directional selection that recruits gene modules corresponding to favored behavioural states in that environment.

As a result of this integrative approach I expect to show how knowledge of the proximate mechanisms underlying social plasticity is crucial to understanding its costs, limits and evolutionary consequences, therefore highlighting the fact that proximate mechanisms contribute to the dynamics of selection.

S6.5 Determining the mechanistic origins and functional consequences of behavioral tactics in foraging societies

Jonathan Pruitt, University Of Pittsburgh

The evolution of sociality often fundamentally alters the fitness landscape where ancillary traits evolve. One perennial prediction from sociobiology is that group living will facilitate the proliferation of behavioral tactics, thereby fostering behavioral diversity within populations. Here I document an iterative bifurcation in behavioral types associated with the evolution of sociality in spider societies, and then assess the mechanistic causes and functional consequences of this behavioral variation. I do so using four exemplar species that each hails from an independent origin of sociality. I approach my questions by generating artificially-reconstituted colonies of known group size and phenotypic composition and then tracking their performance. Finally, I present preliminary data on how (I) group-living per se and (II) group composition stability unite to influence the development of behavioral variation and individual consistency.

S6.6 Pulsed resources and the pace-of-life syndrome in eastern chipmunks

Denis Reale, UQAM

Pierre-Olivier Montiglio, Patrick Bergeron, Murray Humphries, Fanie Pelletier, Dany Garant

The Pace-of-life syndrome hypothesis states that the maintenance of individual personality differences, along with hormonal, metabolic and immunological differences, is explained by their implication into broader life-history trade-offs. These trade-off can also be affected by spatial-temporal heterogeneity, and lead to the coexistence of distinct pace-of-life

genotypes in a population or to possible plastic pace-of-life strategies that can track the change in resources. Beech seed production shows strong inter-annual variation and has a dramatic effect on Eastern chipmunks reproduction and activity. In this presentation we analyse how pulsed resources can affect a whole suite of personality, life-history and reproductive traits in this population. We also assess the phenotypic plasticity and the genetic basis of chipmunk personality and life history.

S6.7 Explaining variation in the existence of animal personalities, and in relationships between individual state, early experiences and personality

Andrew Sih, University Of California At Davis
Barney Luttbeg

Recent models have sought to explain why animals exhibit behavioural consistency across time and/or across contexts (i.e., why animals have a personality). We seek to explain not only why animals have a personality, but more broadly, to explain variation in the phenomenon. When do we expect animals to exhibit long-term, consistent differences in behavioural type versus a lack of consistent differences? To address this variation, we present a general framework based on the relative importance of positive versus negative feedbacks between state variables (e.g., assets, condition, information state, morphology, physiology) and behaviour. Positive feedbacks tend to cause divergence into different behavioural types while negative feedbacks tend to erode consistent differences in behaviour. We illustrate the interplay of positive versus negative feedbacks with specific models. We then discuss predictions on major issues about personalities including: 1) when do we expect early experiences to have major effects (or not) on an individual's later behavioural type? 2) When do we expect animals with higher assets to be cautious and unaggressive versus bolder and more aggressive? And 3) when do we expect populations to exhibit a bimodal distribution of behavioural types as opposed to a continuous range of variation in behavioural types?

S6.8 Predicting individual differences in developmental trajectories for 'boldness', based on information from ancestors and information from personal experience

Judy Stamps, University Of California Davis
V. Krishnan

Although it is widely acknowledged that development is affected by information from ancestors (e.g. via genes and maternal effects) and by personal experience, it is not clear how information from these

different sources should be combined with one another. We have adopted a Bayesian perspective to ask how variation among individuals in their prior distributions (reflecting differences in information from their ancestors) would affect the developmental trajectories of those individuals if they were all exposed to the same set of experiences during ontogeny. Here we show how this approach can be used to predict individual differences in developmental trajectories for 'boldness' when subjects develop under conditions consistently indicative of 'safety' (i.e. no exposure to cues from predators, from aggressive conspecifics, etc.). In this situation, our models predict that average boldness should increase with age, that the behavior of initially shy individuals should change more across ontogeny than that of initially bold individuals, and that differential consistency in boldness should be lower for very young juveniles than for pre-pubertal juveniles. Empirical support for these predictions is available for squids, pigtailed macaques and killifish, suggesting that animals might rely on Bayesian-like processes to combine information from different sources during development.

S6.9 Adaptive behavioural variation: Introduction to the symposium

Michael Taborsky, University Of Bern

To understand consistent individual variation within populations we need to (1) scrutinize underlying selection mechanisms, and (2) clarify how different phenotypes can coexist. Selection mechanisms responsible for persistent phenotype variation include negative frequency dependence, positive feedback potentially extending across different contexts, state dependence, social responsiveness, density dependence, and disruptive selection. The latter mechanism in particular has been held responsible for the distinction between alternative tactics with bimodal or multimodal trait distributions, and individual specializations characterized by overall unimodal distributions of traits within populations. However, disruptive selection might act much more generally than commonly believed.

To understand the evolutionary mechanisms underlying consistent behavioural variation within populations we need to abandon the somewhat artificial distinction between phenotype distributions with one or several modes. An integrative approach is required to identify the commonalities and important differences between alternative tactics and individual specializations within a behavioural syndrome. This will be illustrated with examples from different taxa.

S6.10 Adaptive behavioural mechanisms and individual variation - two sides of the same coin?

Franz J. Weissing, University Of Groningen

Most theoretical models for the evolution of behaviour focus on traits like aggressiveness, choosiness, or parental care. The evolution of the mechanisms underlying such behaviour has received much less theoretical attention.

Here I discuss several models for such mechanisms, including the evolution of (1) neural networks determining the reaction of an organism to external stimuli; (2) a simple inference mechanism drawing conclusions on the basis of noisy information; and (3) a sender-receiver system for animal communication. Intriguingly, in all these models natural selection does not lead to a single evolutionarily stable mechanism. Instead, two or more variants stably coexist. For example, the evolution of statistical inference does not lead to Bayesian updating but to the coexistence of individuals that are either consistently over-optimistic or consistently over-pessimistic. Similarly, the evolution of communication leads to the emergence of coexisting dialects. Such variation in mechanisms evolves in a predictable way, reflecting the degree of environmental uncertainty and the physiological constraints underlying the 'architecture' of behaviour. Obviously, individual variation in behavioural mechanisms leads to consistent individual variation in behaviour. The phenomenon of 'animal personalities' may therefore be a consequence of the fact that the evolution of behavioural mechanisms is often governed by diversifying selection.

S6.11 Adaptive personality as a means of improving reintroduction success

Samantha Bremner-Harrison, Nottingham Trent University

Brian Cypher

Knowledge of personality type can assist in the conservation practices of reintroduction or translocation. However, little study has been done on the variation of personality between individuals in potential source populations subject to differing environmental selection pressures. This study examined personality differences between San Joaquin kit foxes (*Vulpes macrotis mutica*) in urban and natural habitats using three measures of boldness. Overall, urban foxes were found to be bolder than foxes in natural lands, however, whilst differences in boldness were significantly higher between urban vs. rural adults, there was no significant difference between juveniles or pups suggesting environmental selection for optimal boldness relative to habitat pressures. Furthermore, in an environment where high boldness was associated with increased mortality, a trade-off was observed whereby highly bold individuals who survived to breeding age showed an increase in reproductive output than less bold conspecifics.

S7.1 Acrobatic vervets and the choreography of play fighting

Sergio Pellis, University Of Lethbridge
Vivien Pellis

During play fighting, juvenile vervet monkeys make spectacular jumps accompanied by rotations and gyrations. The puzzle is why such complex acrobatic manoeuvres are performed. It could be that, in such play, these movements provide the animals with training in physical skills. But that would imply that these movements are inserted into the sequence of action in a way to provide acrobatic practice, not a combat advantage. If so, analysis of how the movements of the two animals are correlated should reveal out of sequence acrobatic insertions. Detailed inspection of videotaped sequences of play fighting both in captive and free-living vervet monkeys show that the acrobatic manoeuvres are almost all intimately linked to the attack and defense of the shoulder area that is gently bitten during play fighting. That is, the acrobatic movements are produced by the functional needs of attack, defense and counterattack, indicating that in the absence of the appropriate movements by the partner, the acrobatic maneuvers are not performed. The study illustrates that taking into account the dynamic context within which movements occur can be critical in interpreting their value to the performers involved.

S7.2 Size effects on Cooperative Play Fighting in Domestic Dogs

Peter Henzi, Univer
Kerri Norman, Louise Barrett

In order for a play-fighting bout to continue, it must be cooperative and reciprocal in the sense that neither partner should gain consistent advantage over the other, so that the bout does not become one-sided and animals lose motivation to continue.

In this study, we paired a target dog with partners of differing size to assess the dynamics of play, and test the hypothesis that animals would self-handicap when paired with a partner of differing size. We show that dogs converge on similar patterns of reciprocal play, by altering the dynamics of their engagement to reflect size differences. These results are interpreted in the context of the literature on self-handicapping, but we also bring in elements from Powers' perceptual control theory (PCT) to account for the consistencies and differences across dyads.

S7.3 Of Roaches and Robots: A Neuromorphic Approach to Ethology

Heather Bell, University Of Lethbridge

Combat between male Madagascar hissing cockroaches (*Gromphadorhina portentosa*) is relatively complex, and is characterized by several distinct behaviour patterns.

We hypothesized that what appear to be discrete behaviours emerge from the interaction between two factors: 1) the two animals trying to simultaneously achieve the same goal, that of flipping the opponent over on to its back, and 2) the constraints imposed on their movements by their body morphology. Two approaches were used to test this hypothesis. First, by analysing video of male cockroaches engaging in combat using motion tracking software, and second, by constructing robots with quasi-realistic neural architecture. Data from both the real and robotic roaches were consistent with the hypothesis - manoeuvring to target the opponent's flank, and so flip the opponent, creates a context within which stable inter-animal configurations arise. These stable configurations are in the form that have been labelled distinct 'behaviour patterns' in the literature, yet arise from the correlated movements of the two animals. The findings from the present study suggest that readily observed behaviour patterns may emerge from the rules of interaction rather than being encoded solely in the nervous system.

S7.4 Is behaviour the control of perception? A computer model of personal space during a dyadic interaction

Warren Mansell, University Of Manchester

An animal's control of its distance from conspecifics is often studied within ethology, yet it is also a key feature of several theories within social psychology. Indeed, it has often been assumed, but not tested, that personal space is controlled during human conversations. Perceptual Control Theory (Powers et al., 1960; Powers, 1973) is a theoretical and modelling framework that has been applied across the life and social sciences to understand control. In essence, it proposes that 'behaviour is the control of perception' - behaviour varies dynamically with changes in the environment in order to keep a range of hierarchically organised perceptual variables controlled by the organism. We tested whether personal space is a controlled perception using a computer model to predict the distances between people in a dyadic conversation.

First, nine groups of five students talked in two different pairings and their distances from one another were measured. Second, a computer model of two

negative feedback loops based on perceptual control theory was used to infer the preferred personal distance and effort in maintaining this distance (gain) for each individual. Third, the model was used to predict the actual distance between novel pairings of the same individuals. The computer model correlated moderately with the behavioural data, confirming its validity. We also report on current extensions of this methodology designed to enhance its ecological validity, theoretical integrity and predictive capacity.

S7.5 The Dynamic Nature of Emotional Expressions

Alexandra Muehlhauser, Dep. Of Anthropology, University Of Vienna
Sergio M. Pellis, Peter Henzi, Heather Bell, Warren Mansell, Louise Barrett

Most of previous research on facial expressions is based on static images. In social interactions, facial expressions are characterised by an onset, apex and offset, thus making the dynamics an integral part of expressive behaviour. It lies at hand to assume that evolutionary selection pressures favoured the integration of the dynamics in the interpretation of emotional expressions. Previous studies indicate that facial dynamics change the perceived meaning of smiles. The aim of this study was to test whether the perception of emotional expressions in general depends on facial dynamics.

We generated expressions of basic emotions (two prototypes each) in one male and one female avatar based on AU activations. We modified the length of onset and apex with a constant offset resulting in 56 stimuli per sex. 113 participants assessed the valence and arousal of these stimuli.

Dynamics affect the attribution of emotions significantly. Emotional expressions with a long onset were rated as happier and less angry than ones with a short onset.

The findings of this study suggest that the dynamics affect the meaning of facial expressions, and it seems that the dynamic pattern of an expression overrides the role of specific AU activations in the generation of meaning.

Symposium 8 Numerical competence: from apes to ants

S8.1 Humans and Nonhuman Primates Show Similar Skill in Estimating Uncertain Outcomes During Quantity Judgments

Michael Beran, Georgia State University
Bonnie Perdue, Audrey Parrish, Theodore Evans

When information is incomplete but a choice must be made, individuals sometimes can rely on past experiences to guide their responding. For example,

one might rely on how many items one has been getting across a series of quantity judgments to determine whether a currently offered quantity is a good bet or not compared to an unknown quantity. Chimpanzees (*Pan troglodytes*), capuchin monkeys (*Cebus apella*) and humans (*Homo sapiens*) were presented with such a test. After making a series of comparisons of two known quantities, they were faced with choices where only one option was known. Performance was highly similar for all species and was guided by past outcomes. All species shifted from selecting the known option to selecting the unknown option as the known option went from being more than the average rate of return to less than the average rate of return. This also was true with a variety of manipulations of the unselected set after a choice was made. This comparability across species suggests that tallying ongoing average rates of return during repeated quantity judgments occurs spontaneously and likely serves an adaptive purpose when having to deal with uncertain quantity choices.

S8.2 Fish as a model to investigate non-symbolic numerical abilities

Christian Agrillo, University Of Padova
Maria Elena Miletto Petrazzini, Angelo Bisazza

During the last decades the debate surrounding non-symbolic numerical abilities has been enlarged to encompass basal vertebrates, such as fish. Data collected by free choice tests and training procedures indeed support the existence of rudimentary quantity abilities in several fish species. In particular, poeciliid fish (guppies and mosquitofish) have been often used as model species. In this talk we will review the current state of knowledge on numerical competence in poeciliid fish, with particular regard to three main issues regarding numerical abilities in nonhuman animals: the relation between numerical and continuous quantity, the supposed existence of a precise subitizing-like process, and the ontogeny of numerical abilities.

The evidence reported in literature is strongly suggestive of similar numerical systems in fish and mammals. We suggest that our nonverbal numerical abilities might have evolved from a common ancestor dating back to before the divergence of bony fish and tetrapod lineages.

S8.3 The use of ideas of information theory for studying animal numerical competence: an insight from ants

Zhanna Reznikova, Institute Of Systematics And Ecology Of Animals
Boris Ryabko

Most of the existing experimental schemes for studying numerical processing in animals are restricted by studying subjects at the individual level, or by the use of artificial communicative systems. In contrast, the information-theoretic approach that we elaborated for studying number-related skills in ants employs their own communicative means and, thus, does not require the subjects to solve any artificial learning problems, such as learning intermediary languages, or even learning to solve multiple choice problems. Using this approach, it was discovered that members of highly social ant species are able to pass information about numbers and to perform simple arithmetic operations with small numbers.

The scheme of the experiments is based on the information-theoretic idea that in a 'reasonable' communication system the frequency of usage of a message and its length must correlate. Facing a task in which a food source appeared on a 'special' 'branch' of a comb-like counting maze much more frequently than on other ones, scouting ants were forced to develop a new code based on arithmetic operations. We suggest that applying ideas of information theory and using the natural communication systems of highly social animals can open new horizons in studying numerical cognition.

S8.4 Quantity Estimation in Black Bears (*Ursus Americanus*) and Gorillas (*Gorilla gorilla gorilla*)

Jennifer Vonk, Oakland University
Michael Beran

Three American black bears and three Western Lowland gorillas were trained to select from arrays of dots the array containing either the smaller or larger quantity of dots.

On some trials greater quantity was congruent with a greater amount of area covered by the dots, whereas, on other trials, quantity was incongruent with area. All subjects learned to discriminate larger from smaller quantities with static dots. Although they used area as a cue, they were also able to use number to guide their choices. At least one bear was able to accurately choose the larger array even when the dots moved around chaotically, and even when he had to attend to a subset of moving dots among a larger array. These findings indicate that the ability to differentiate moving subsets of items is not unique to group-living species and may be shared broadly among mammals. In order to directly compare the ability of bears to non-human apes using identical procedures, we are currently investigating quantity discrimination following the same procedures in a group of adult male gorillas. Our studies are the first to carefully manipulate number, area, and ratio with both static and moving stimuli in these species.

S8.5 Symbolic representation of the numerosities 1-8 by hooded crows (*Corvus cornix L.*)

Anna Smirnova, Moscow State University

A two-alternative simultaneous matching-to-sample task was used. Previously, after extensive training, the two crows acquired the general identity matching-to-sample rule. Experiment 1 and Experiment 2 used numerosities 1-4 and 5-8 correspondingly. Each experiment first included the demonstration trials and then the test trials. In the demonstration trials a sample and the comparison stimuli belonged to the same category: heterogeneous graphic arrays or Arabic numbers. After making a correct choice, the birds found the number of mealworms that was the same as the number of elements in the array, or as the Arabic number. In the test trials a sample and the comparison stimuli were from different categories: if a sample was an Arabic number, the comparison stimuli were arrays, and vice versa. The test trials with non-differential reinforcement were intermixed with identity matching trials from the demonstrative set (one test trial after three identity trials). Each experiment included two tests: Test 1 with the familiar pictured arrays and Test 2 with the new one. In the Experiment 1, in the Test 1 the crows made 33 and 36 correct choices over 48 trials ($p < 0.01$); in the Test 2 the crows made 34 and 37 correct choices over 48 trials ($p < 0.001$). In the Experiment 2, in the Test 1 one of the two crows made 39 correct choices over 48 trials ($p < 0.0001$); and in the Test 2 crow made 41 correct choices over 48 trials ($p < 0.0001$). These results demonstrated that the crows were able to spontaneously associate numerosities with numerical symbols (Arabic numbers 1-8).

S8.6 Small brains, small numbers and big decisions

Ximena Nelson, University Of Canterbury
Robert Jackson

Predation success of communal predators may depend on the actions of its neighbours. We consider the foraging decisions made by juveniles of *Portia africana*, a jumping spider that preys on small oecobiid spiders that live under sheets of silk (nests). *Portia africana* settle near oecobiid nests, ambushing their prey as they leave. One or more *P. africana* may sometimes join another at the same nest and, when the oecobiid is captured, they may share the meal. Using dead spiders positioned in lifelike posture arranged in a series of different 'scenes', we investigated how naïve *P. africana* use number-related cues in conjunction with non-numerical cues when deciding whether to settle at a nest. *P. africana* make predatory decisions based on the presence of a nest, the number and identity of spiders inside and outside a nest and how spiders are positioned relative to each other and the nest. *P. africana* prefer to join conspecifics at a nest

when there is one additional *P. africana*, instead of zero, two or three. We also show that factors related to continuous variables and geometric pattern are unlikely explanations for our findings

S8.7 Proto-counting in the striped field mouse (*Apodemus agrarius*)

Nataliya Vorobyeva, Novosibirsk State University
Sofia Panteleeva, Zhanna Reznikova

We investigated numerical competence in striped field mice, a common-dwelling, agile and exploratory species, whose cognitive abilities have never been studied before.

We used a classic scheme of training animals with food reward to distinguish between quantities of arbitrary visual stimuli. Each animal received three training trials where the right choice was rewarded and the wrong choice was punished (by placing an animal into a dark box), and then it passed through the examination when no food reward was used. In total, 6642 training trials and 2216 examinations were conducted with 24 animals. Training them to distinguish between quantities of geometric figures, we found that mice not only discriminate between clearly distinctive quantities such as 5 versus 10, but also demonstrate high accuracy in distinguishing between small (2 versus 3) and large (5 versus 6, and 8 versus 9) quantities of elements that differ only by one ($P < 0.01$, Fisher's angular transformation). They successfully learned to discriminate numbers precisely, even at a 0.89 ratio (8 v. 9). As far as we know, this is the first evidence of proto-counting in small rodents.

S8.8 The origins of individual differences in Number Sense: evidence from twin studies

Yulia Kovas, Tomsk State University And Goldsmiths College

Maria Tosto, Tatiana Tikhomirova, Yulia Bubnova, Ksenia Sharafieva, Maja Rodic, Anna Budakova, Sergey Malykh

Individual differences in mathematics are largely driven by the same genetic and environmental factors that drive variation in other cognitive abilities. However, behavioural genetic research also suggests some unique genetic and environmental influences on mathematical development. This aetiological specificity may be related to the universal intuition about approximate quantity, or 'number sense'. Recent research has demonstrated that the precision of number sense varies across people and that it may be fundamental to our acquisition of formal mathematics in later life.

We present the first genetically sensitive study that explores the relative contribution of genetic and

environmental factors to several measures of 'number sense'. The tests were administered to a sample of 16-year-old UK twins, as part of the Twins' Early Development Study (837 pairs of monozygotic twins; 1422 pairs of dizygotic twins). The multivariate nature of the study allowed us to examine the genetic and environmental sources of the covariation among the measures of number sense, mathematics, and other cognitive abilities. We also present complementary results from a sample of Russian twins.

The results offer the first insight into the nature of the number sense in humans, and have important implications for conceptualising mathematical ability and disability.

S8.9 Experiment-naive baboons (*Papio anubis*) represent numbers using the analog magnitude system

Kelly Hughes, University Of Rochester
Allison Barnard, Regina Gerhardt, Louis DiVincenti Jr, Jenna Bovee, Jessica Cantlon

Researchers continue to debate the nature of non-human primates' numerical representations, for which two non-exclusive cognitive mechanisms have been proposed: (1) a discrete object-file system limited to quantities < 5 , and (2) an analog system which is limited by the ratio between two quantities. Evidence has accumulated in favor of the analog system, but much existing research is complicated by primates' previous numerical experience. To address this issue, we tested eight experiment-naive olive baboons (*Papio anubis*) in their ability to discriminate between small (< 4), large (> 4), or span (small vs. large) number pairs, presented simultaneously or sequentially. According to the object-file hypothesis, baboons will only accurately choose the larger quantity in small pairs, but not large or span pairs. Conversely, the analog system predicts that baboons will be successful with all numbers, and that success will be related to pair ratio. In this study, all pair types were discriminated at above chance levels, and accuracy was negatively correlated with the ratio between the numbers presented. This behavior was present from the first test sessions, and did not change substantially over continued testing and experience. These data suggest that a single, coherent analog representation system underlies native quantitative abilities in primates.

S8.10 Core knowledge of number: A comparative approach

Rosa Rugani, University Of Padova
Giorgio Vallortigara, Lucia Regolin

Studies on the ontogenetic origins of human knowledge provide evidence for a small set of

separable systems of core knowledge dealing with the representation of inanimate and animate objects, number and geometry. Because core knowledge systems are evolutionarily ancient, they can be investigated from a comparative perspective, making use of various animal models. Here, I discuss evidence showing precocious abilities in non-human species to represent the cardinal and sequential aspects of numerical cognition with large and small numerosness, and rudimentary arithmetic with small numerosness. Studies suggest that the abilities associated with core knowledge systems of number are observed in animals in the absence (or with very reduced) experience, supporting a nativistic foundation of such cognitive mechanisms.

S8.11 Algebraic rule learning in zebra finches and humans

Jiani Chen, Leiden University
Danielle van Rossum, Carel ten Cate

Syntactic rule abstracting is critical to human language learning. Pre-linguistic infants already show the ability to generalize algebraic-like rules. It is hotly debated whether this ability is human- and language-specific or can also be found in other animals. Few studies have directly compared the learning of algebraic-like rules by human and non-human animals.

We presented zebra finches and human adults with comparable training and tests with the same artificial stimuli consisting of XYX and XXY structures, in which X and Y were zebra finch song elements. Human adults were able to categorize novel stimuli consisting of novel element types into different groups according to their structures. In contrast, zebra finches did not show the same pattern as humans but were able to discriminate novel stimuli when these were composed of familiar element types from the training. We suggest that zebra finches have a stimulus bound generalization, but we got no evidence for an ability of algebraic generalization.

To sum up, the results of this experiment may indicate a primitive ability in rule abstraction in zebra finch.

Symposium 9 Post-conflict affiliation: applications for conflict management in humans

S9.1 A broad post-conflict affiliation hypothesis

Corina Logan, University Of California, Santa Barbara

Post-conflict affiliation (PCA) involves positive interactions after conflicts and is found in mammals, birds, and fish. It exists in a few different forms, including former opponent affiliation (reconciliation), bystander affiliation (a former opponent affiliates with

a bystander), quadratic affiliation (bystanders affiliate with each other), and intra-victim affiliation (after an inter-group conflict, members of the losing group affiliate with each other). We lack PCA hypotheses applicable to all taxa and all forms of post-conflict affiliation, however the pieces for such a hypothesis exist. I gather these pieces in one place, apply the broad hypothesis to all forms of PCA, and re-iterate the predictions of this hypothesis, namely that PCA behaviour will vary across taxa according to the interaction and associated costs and benefits of three relationship quality components: value (fitness benefits), compatibility (affiliative levels), and security (consistency of interactions). I discuss applications from this hypothesis for human conflict management by suggesting that PCA can occur at various levels of organisation (between individuals or groups) and that we can increase PCA behaviour by increasing the relationship value among interactors.

S9.2 Intergroup conflict and intragroup affiliation

Andy Radford, University Of Bristol

Theoreticians have long suggested that intergroup conflict could influence the level of intragroup cooperation or affiliation displayed. Despite the prevalence of intergroup conflicts in many social species, however, few empirical studies have investigated this potential link in non-human animals. My work on a group-living bird, the green woodhoopoe (*Phoeniculus purupureus*), has shown that group members increase their affiliative behaviour (specifically the preening of one another) following conflicts with rival groups. Moreover, there is a greater increase in this allopreening following long conflicts that are lost compared to short conflicts that are won, and when conflicts involve unfamiliar groups rather than established neighbours. The increase in postconflict affiliation results from greater preening of subordinate group members by the dominant pair. Intergroup conflicts in woodhoopoes are characterised by the involvement of all group members, but this is a relatively rare situation – in most species, only some group members are involved in any given conflict. I predict that patterns of involvement in intergroup conflict will influence which individuals donate and receive subsequent affiliative behaviour. It is often suggested that human cooperative behaviour arose as a consequence of warfare, but considerations at the individual level could provide new insights into the evolution of sociality.

S9.3 Relationship quality and post-conflict affiliation in macaques

Bonaventura Majolo, University Of Lincoln

Conflicts between group members may generate a number of social interactions within the group, including selective avoidance between opponents, affiliation between them (i.e. reconciliation), and/or triadic and quadratic affiliation with individuals not involved in the former conflict. In this talk I will review the literature on post-conflict affiliation in non-human primates with a special focus on reconciliation and triadic affiliation, and on studies conducted on the genus *Macaca*. I will compare post-conflict affiliation in two macaque species (i.e. *Macaca fuscata* and *M. sylvanus*) differing for their dominance style (i.e. despotic versus tolerant, respectively). I will discuss the importance that factors such as relationship quality, context of the conflict and inter-individual distance play in determining the occurrence of post-conflict affiliation. Finally, I will evaluate how socio-ecological and cognitive differences among species and methodological differences across studies (e.g. in terms of behaviours used to study post-conflict affiliation and to calculate relationship quality) affect our understanding of the evolution of conflict management strategies. Such differences are important when comparing studies on non-human animals (including non-human primates) with research conducted on humans.

S9.4 Parental divorce in humans: implications for children and the role of the social network

Marjolijn Das, Statistics Netherlands

Bonds within the nuclear family are among the strongest social bonds that humans form. The nuclear families are in turn embedded in wider social networks, among which is the extended family. Grandparents in particular play an important role: they offer financial and practical support such as childcare, and they do so especially when their children are in difficulty. Parental divorce is a disruptive event with far-reaching implications both for the parents and for third parties, most notably the children. It has lasting negative effects on indicators of children's social status in adulthood. Social status, in turn, is related to fitness. Also in other socially monogamous species, the offspring's fitness is higher when both parents care for the children compared to only one (reviewed in Reichard, 2003). I hypothesise that children derive fitness benefits when their parents have a good relationship. Building on this, hypotheses can be derived about a) conflict management behaviour and stress of children after parental conflict and divorce and b) the influence of other third parties, in particular the grandparents. The hypotheses can be generalized to conflict management behaviour of third parties in other species and situations.

S9.5 An Investigation of Social Skill, Relationship Value, and the Relational Consequences of Post-conflict Affiliation in Captive Chimpanzees (*Pan troglodytes*)

Peter Verbeek, Miyazaki International College

This paper reports on an investigation of the long-term effects of friendly post-conflict affiliation (PCA) between opponents and between opponents and bystanders in captive chimpanzees. The study tests the general prediction that the extent of any long-term positive relational consequences of PCA depends on the pre-existing quality of the relationship of the individuals involved. It is also predicted that relationship value among the chimpanzees in the study varies as a function of the individual levels of social skills of the partners in the relationship. The study chimpanzees are wild or captive born and housed in various social groups. It is predicted that individual differences in birth origin (wild vs. captive), developmental history, age, and dominance status will be co-factors in the predicted links between social skill, relationship quality, and the presence or absence of long-term positive effects of PCA. The results will be discussed in the context of research on the effects of early experience on social skills and post-conflict reconciliation in young children.

Symposium 10 Conserving the systems we study: the wider relevance of behavioural research

S10.1 Extinction of behaviors: the evolutionary consequences of anthropogenically induced behaviors

Oded Berger-Tal, Ben-Gurion University Of The Negev
David Saltz

Behavior serves as a mediator between genes and the environment by regulating the effects of the environment on the fitness of organisms. Thus, diversity of behaviors is crucial for populations to function in a changing environment. Anthropogenic alterations to the environment may cause behavioral changes in many species (e.g., habituation, avoidance). Since these behaviors usually enable animals to adapt to the disturbance, preventing a demographic decline and in some cases even increasing population size, they had been considered superficially beneficial conservation-wise.

However, such behavioral changes may pose a less obvious yet significant risk – namely, a shift in the selective forces that may lead to the disappearance of certain behaviors. This can hamper the population's ability to withstand unforeseen future environmental changes and may ultimately lead to altering the evolutionary trajectory of the species. In this talk I will discuss the different factors affecting the chances of a behavior to go extinct. These include the type of stressor and the rapidity of its appearance, whether

the behavior is genetically-wired or learned, and whether behavioral diversity in the population is the result of monomorphism of mixed strategies or polymorphism of pure strategies. I will further discuss the management implications of these different factors.

S10.2 Long-term behavioural studies and their contribution to conservation: examples from the Amboseli elephant project

Phyllis Lee, University Of Stirling
Keith Lindsay, Cynthia Moss

Elephant populations are under severe threats from poaching and human land-use changes. The Amboseli Elephant Research Project, a seminal study of African elephants in southern Kenya, is now in its 40th year. From the outset, we have focused on individual animals, their demography, ecology and social relationships. This approach has resulted in ground-breaking discoveries about elephant biology and behaviour, leading to a clearer understanding of biological and psychological needs of elephants and what is required to sustain such wild populations into the future.

Forty years of survivorship and age-specific reproductive data from a protected population enables understanding of key parameters for modelling population declines and potential recoveries. In addition, while Amboseli's elephant population has generally coexisted with local pastoralist communities, recently human-elephant conflict as a result of changing land use patterns has increased. Solutions to conflicts, based on an understanding of both human and elephant needs, are being developed through dialogue with stakeholders, and corridors and dispersal areas essential for elephant and other wildlife movements are being identified. If people are to coexist with intelligent, behaviourally flexible and wide-ranging megafauna, then appreciation of the problems and development of responses from the animals' perspectives, are essential.

S10.3 Evidence for the influence of social learning and life history on crop raiding behavior in African Elephants

Patrick Chiyo, University Of Notre Dame
Cynthia Moss, Susan Alberts

Understanding factors that influence the spread of crop raiding behavior in elephant populations is important for the conservation and management of human-elephant conflict.

We investigated; 1) the influence of age and association on the probability of being a raider among

known free ranging male African elephants, 2) the influence of age on the patterns of raiding using elephant droppings left in raided farmland. We found that; 1) compared to younger males, older males were more likely to be raiders, and older males that raided were more likely to have raided previously, 2) Males were more likely to be raiders when their closest associates were also raiders or when their second closest associates were raiders older than them. These results suggest that learning from associates has a major influence on the acquisition of raiding behavior in younger males whereas life history factors have a major influence on raiding behavior in older males. To manage human-elephant conflict, our results suggest that targeting older individuals may reduce crop raiding in the short term. In the long-term however, reduction in conflict will require measures that minimize access of elephants to crops by employing land use practices compatible with elephant conservation.

S10.4 Adjusting to 'poor habitats': the conservation value of protecting deforested land

Krista Milich, University Of Chicago
Colin Chapman

Behavioral plasticity may be particularly important for wild primate populations who face habitat loss or degradation. Using the endangered red colobus monkey (*Procolobus rufomitratus*) of Kibale National Park, Uganda, we examine behavioral differences between individuals living in protected, old-growth habitats, unprotected forest fragments, degraded riverine forest, and protected, previously logged habitats.

We hypothesized that compared to individuals in old-growth areas, individuals in any of the degraded habitats spend: 1) more time feeding, 2) less time on affiliative behaviors, and 3) less time traveling. We argue that these behavioral adjustments represent a strategy for maintaining successful reproduction in stable, albeit degraded, habitats. However, they do not appear to offset the stress of living in a fragmented environment, especially considering these groups continue to decline in number, have low reproductive hormone concentrations, and some have higher stress hormones.

These results help inform conservation management plans for red colobus, as well as the other 13 species of primates living in or near Kibale. This study aims to provide original data on the impact of habitat quality on behavior in primates and considerations to inform management strategies.

S10.5 Human hunters and their primate prey: Conservation applications of behavioural research in Ecuador

Sarah Papworth, National University Of Singapore
E.J. Milner-Gulland, Katie Slocombe

The investigation of predator-prey interactions has a long history in animal behaviour, but most studies have focused on non-human predators. Population declines of prey species because of human hunting are well documented, and much conservation effort has been dedicated to quantify hunting sustainability, which requires information on both animal and human behaviour.

We present behavioural data on hunters and their primate prey, and demonstrate the practical applications of this information for conservation. Firstly, we present an interdisciplinary study of human hunters, showing how methods developed in diverse disciplines, from anthropology to physics, can be used to inform our understanding of hunter behaviour. In particular, methods from animal behaviour can be used to describe the spatial distribution of hunters, improving our understanding of hunting sustainability. Secondly, we demonstrate how understanding primate behaviour can help conservation practitioners accurately count populations, which has implications not only for quantifying hunting sustainability, but also monitoring conservation success and improving the allocation of scarce time and resources. Finally, we consider the relative importance of this information for conservation, and consider possible roles and responsibilities for behavioural researchers within the conservation agenda.

Symposium 11: Play

S11.1 The origins of play

Gordon Burghardt, University Of Tennessee

Our understanding of the evolution and phylogeny of playfulness in animals is surprisingly minimal, largely because the function of play in both human and nonhuman animals remains controversial.

Consequently, biologists and even many psychologists have largely ignored play as a deeply rooted behavioral phenomenon meriting serious attention, since it seemed restricted to endothermic vertebrates with large brains. Improved criteria are now available for identifying play in species where play is not already acknowledged to exist. After documenting phenomena that meet such criteria in all classes of vertebrates and several groups of invertebrates (e.g., cephalopods, crustaceans, spiders, insects), the factors underlying the apparently independent evolution of such behavior will be explored. These include life history, ecology, sociality, physiology, and development. Together these underlie the Surplus Resource Theory of play. Besides being able to test this theory phylogenetically, modeling these factors with simulations is helping to

test which ones may be most critical in the evolution of play.

S11.2 The evolution of play-fighting behaviour

Tim Fawcett, University Of Bristol
Rufus Johnstone

Play-fighting is common in juvenile mammals, but its existence remains an evolutionary puzzle because it is costly and yields no immediate benefits. According to the dominant hypothesis, play allows young animals to develop their motor skills through training, leading to improved success in adult fights. However, evidence from neurological and developmental studies is inconsistent with this explanation.

Another possibility is that young animals are uncertain of their ability to win fights and use play-fights as a low-cost opportunity to gain information. Here we compare these hypotheses using dynamic game models. In our models, individuals compete for access to fitness-enhancing resources through potentially costly conflicts based on the classic Hawk–Dove game. We assume that play-fights, in which no resources are at stake, either increase strength (motor-skills hypothesis) or reduce uncertainty about strength (information-gain hypothesis). In both scenarios, we find that selection favours a period of juvenile play-fighting before individuals progress to adult conflicts over resources. Investment in play-fighting increases success in adult conflicts, conferring a fitness benefit which can sustain play-fighting even if it is costly in the short term. We use this theoretical framework to generate testable and contrasting predictions about patterns of play-fighting both within and across species.

S11.3 Why do dolphins play?

Stan Kuczaj, USM

Play is an important aspect of dolphin life. It provides contexts in which dolphins create novel experiences for themselves and their playmates. The behavioral variability and individual creativity that characterize dolphin play yield ample opportunities for social learning and sometimes result in innovations that are reproduced by other members of the group. Although adults sometimes produce innovative play, calves are the primary source of such activities. Calves are also more likely to imitate novel play behaviors than are adults, and so calves contribute significantly to both the creation and transmission of novel play behaviors within a group. Not unexpectedly, then, the complexity of dolphin play increases with the involvement of peers. The opportunity to observe and/or interact with other dolphin calves enhances the effects of play on the acquisition and maintenance of flexible problem

solving skills, the emergence and strengthening of social and communicative competencies, and the establishment of social relationships. It seems that play may have evolved to help young dolphins learn to adapt to novel situations in both their physical and social worlds, the beneficial result being a set of abilities that increase the likelihood that an individual survives and reproduces.

S11.4 Why do bonobos play as adults? A serious discussion on animal fun

Isabel Behncke, University Of Oxford

My focus is on the rarest form of play: play in mature individuals. I study play and other social behaviour in a habituated community of wild, habituated bonobos (*Pan paniscus*) at Wamba, DR Congo. Bonobo adults show unusually high levels of play - particularly by adult males. In general, adult play occurs in 'social brain' taxa, ie species with large brains, longevity, complex cognition and intense sociality. Even among these groups, bonobos show exceptionally high levels and complexity of adult play. Why would this be? I explore the variable and protean nature of play in the context of evolution of complex sociality. I propose that under conditions of *uncertainty, variability in behaviour is adaptive*, and play rewards and enhances such variability. Also, play could increase social tolerance and flexibility, thereby enhancing the benefits of social life.

S11.5 Play behaviour as a welfare indicator

Suzanne Held, University Of Bristol
Marek Spinka

Play has long been identified as a potential welfare indicator: it disappears when animals are under fitness challenge and is thought to be accompanied by a pleasurable emotional experience. But animal play is a tricky behavioural phenomenon, characteristically flexible and variable within and between species, with its proximate mechanisms and ultimate functions still not fully understood. Its relationship to animal welfare is therefore complex and merits a focused theoretical investigation. The talk will review evidence on one aspect of the play-welfare relationship: its utility as a welfare indicator. It considers whether play always indicates the absence of fitness threats, and whether and how it indicates the presence of pleasurable emotional experiences. The evidence suggests that play does indeed hold promise as a welfare indicator. However, it also points to difficulties in its study and interpretation, and raises some unresolved questions.

S11.6 Play, Playfulness, Creativity and Innovation

Patrick Bateson, University Of Cambridge

In the past the study of play has been treated as a non-subject. Since often it isn't serious (in the short-term), it was mistakenly regarded as not being a serious topic for research. In recent years, however, the growth of interest in this form of behaviour has exploded. Play can occupy a substantial part of the waking-life of a young mammal or bird. Problems of definition have been greatly eased, partly because the many punning uses of 'play' have been identified and excluded from the definition. Play may nevertheless be a heterogeneous category. On the other hand, playfulness may be a unitary motivational state. Playful play as opposed to activities that merge into aggression is characterised by positive mood, intrinsic motivation, occurring in a protected context and easily disrupted by stress. As in scientific research, such play may lead nowhere. Nevertheless, I shall argue that playful play, in particular, sometimes provides the experience that can generate novel solutions to challenges set by the social and physical environment. I distinguish between such creativity and its implementation in innovative acts. The distinction between creativity and innovation is not often made with animals but is especially clear in humans. Creative people are often not especially innovative and innovative people are often not especially creative, relying on the ideas of others.

Symposium 12: The coevolution of behaviour and emotional states

S12.1 The adaptive value of emotion and of reasoning

Edmund Rolls, Oxford Centre For Computational Neuroscience

In Rolls' theory of emotion (2005) it is argued that emotions are states elicited by reinforcers which are the goals for action, the rewards and punishers. It is argued that emotions solve a fundamental problem in Darwinian evolution, for it is much more efficient for genes to specify goals for actions, rewards and punishers, rather than actions or responses. It is shown that the orbitofrontal cortex is important in emotion for it represents primary, unlearned, gene-specified, reinforcers including the taste and texture of food and face expression; performs rapid learning, and reversal, of stimulus-reward associations; and with the pregenual cingulate cortex has activations that are directly correlated with pleasure, the conscious reports of the subjective state associated with rewards. These reward systems in our brains provide inputs to our value based decision-making mechanisms in the ventromedial prefrontal cortex which can correct decisions based on confidence estimates before the outcome is known.

It is shown using integrate-and-fire neuronal networks that decision-making is inherently probabilistic because of noise caused by the random firing times of neurons in the brain (for a given mean rate). It is argued that this mechanism for decision-making applies to decisions involving a choice between the emotional, implicit, evolutionarily old, brain systems, and the rational (reasoning) explicit conscious system that enables gene-specified goals to be deferred, in a decision between the phenotype (the individual) and the selfish genotype ('phenes' vs genes) (Rolls 2012). This has implications for free will, and determinism.

Rolls, E.T. (2005) *Emotion Explained*. Oxford University Press: Oxford.

Rolls, E.T. (2012) *Frontiers in Integrative Neuroscience* 6: 68.

S12.2 Emotions, moods and decision-making

Mike Mendl, Bristol University

Liz Paul

Research on animal emotions has generally focused on investigating how animals respond to situations assumed to induce discrete emotional states (e.g. fear). This 'discrete emotion' approach has advanced our understanding of neurobehavioural systems underlying specific emotions. However, it lacks an overarching framework that can incorporate and integrate a wide range of possible emotional states. 'Dimensional approaches' that conceptualise emotions in terms of universal core affective characteristics (e.g. valence (positivity vs negativity) and arousal) offer such a framework.

Here we present a dimensional framework that provides a structure for integrating discrete emotions, suggests how short-term discrete emotions map on to longer-term 'mood' states, and indicates how mood states may function to guide decision-making, especially under ambiguity where decisions can be critical to survival (e.g. deciding whether a rustle in the bushes is predator or prey). We give examples from several species which support the hypothesis that decision-making under ambiguity may be adaptively influenced by current emotional state, and hence that one important functional role of emotions may be to guide decision-making in this context.

S12.3 The evolution and optimality of emotions

Pete Trimmer, University Of Bristol

Mike Mendl, Elizabeth Paul, John McNamara, Alasdair Houston

We consider a well-known representation of emotions, which we term core affect space. In core affect space, an emotion corresponds to a position on a two-

dimensional graph of arousal against valence. We identify why the representation makes sense from an evolutionary perspective under particular conditions. To do so, we show how it can be related to another well-known model in neuroscience and behavioural ecology, the drift-diffusion model. We also suggest how further such work may deepen our understanding of how emotions and decisions are intertwined.

S12.4 An evolutionary approach to mood

Melissa Bateson, Newcastle University

Daniel Nettle

Moods differ from acute emotional states in that they are longer lasting, and are detached from immediate triggering stimuli. Mood appears to be an integrative function of the organism's acute emotional experiences over time. For example, in the case of anxiety, an individual who experiences repeated punishment sets a lower threshold for the detection of potential threats in the next period of time. In our talk, we will address the question of why it is adaptive to have moods over and above acute emotions.

We argue that having a mood system, which adjusts thresholds for responding to cues of punishment (or reward) in the light of each emotional experience, rather than an architecture where those thresholds are fixed, is advantageous where there is auto-correlated variation in the prevalence of events in the environment, and/or autocorrelation in the individual's physical condition. The higher these auto-correlations, the more detection thresholds should show temporal persistence. However, the adaptive benefit of the capacity for dynamically changing but persistent mood will be highest where the degrees of auto-correlation are intermediate. We will illustrate our arguments with data from European starlings showing that manipulating either the birds' perceived probability of predation or their physical condition produces the predicted changes in anxiety-related behaviour.

S12.5 Human approach avoidance anxiety: a novel cross-species paradigm

Dominik Bach, University Of Zurich

Marc Guitart-Masip, Raymond Dolan

Anxiety behaviour in animal approach-avoidance tasks, such as the open field, elevated plus maze, and various conflict tests, is thought to stem from hippocampal theta oscillations. Knowledge about similar mechanisms in humans is ambiguous, mainly because no comparable test bed exists. Human experiments commonly employ social anxiety paradigms or investigate patients with generalised anxiety disorder. Here, I present a virtual computer game for humans, drawing on ideas from approach-avoidance conflict in

a foraging environment that approximates an open field task. By manipulating threat probability, we vary avoidance motivation and thus conflict, and show that humans show behavioural and brain responses similarly to animals in classical approach–avoidance tasks. Behaviour in this task is modulated by benzodiazepines and by hippocampus lesions. Hence, we provide a novel paradigm that furnishes an ecologically valid measure of anxiety behaviour in humans.

S12.6 Cross inhibition of drives improves activity selection

James Marshall, University Of Sheffield
Angelique Favreau-Peigne, Lutz Fromhage, John McNamara, Alasdair Houston

Efficient action selection is a crucial aspect of animal behaviour. Different competing physiological and behavioural requirements must be satisfied in the most effective manner possible, and these will have different and changing importances to the animal over time. In managing the competition between different behaviours, pathological outcomes such as deadlock, or dithering, between behaviours must be avoided. Here we present a simple dynamical model, based on aspects of the Lorenzian theory of drives, that manages competition between two activities, such as feeding and drinking, when there is a cost for switching between behaviours. Drawing inspiration from neuroscientific data and models of perception, we examine the effect of cross-inhibition of drives, and show that this novel mechanism robustly improves activity selection, by reducing the frequency of costly switches between behaviours.

These results highlight the importance of integrating function with mechanism in the study of animal behaviour, and the potential value of revisiting aspects of Lorenz's theory of behavioural drives.

Symposium 13 A Barrel of Monkeys (and Apes):
New Directions in Nonhuman Primate Personality
Research

S13.1 Reactivity and Self-Regulation in Human Children and Chimpanzees

Esther Herrmann, Max Planck Institute For Evolutionary Anthropology
Antonia Misch, Victoria Hernandez-Lloreda, Michael Tomasello

The two main components of temperament, reactivity and self-regulation, are crucial how individuals react daily to events in the environment and to their emotional, cognitive and social development (Posner & Rothbart, 2000). It has been hypothesized that human temperament differs from that of other great apes in

ways which may facilitate the expression of more complex forms of human cooperation and cognition (Hare & Tomasello, 2005).

We compared children at 3 and 6 years of age with one of humans' two nearest relatives, chimpanzees, on a battery of temperament tasks. Chimpanzees were less shy/ fearful to approach novelty than six-year old children. Furthermore, six-year-old children had better inhibitory and attentional control skills than chimpanzees. They were able to inhibit a pre-potent response in order to gain greater rewards or finding a new solution to a problem much better than were the chimpanzees. Six-year-old children were also more focused on a task during a distracting noise and more persistent than chimpanzees. Three-year-old children, however, did not show better inhibitory and attentional control skills than chimpanzees on any of these tasks.

These results suggest that the origins of human self-regulation lie within our general primate heritage, but that species-unique skills of self-regulation emerge roughly at school age.

S13.2 Comparative macaque personality structure

Mark Adams, University Of Sheffield
Bonaventura Majolo, Julia Ostner, Oliver Schülke, Alexander Weiss

Personality assessments of nonhuman primates using observer ratings have identified individual differences that are seemingly homologous to those found in humans. The personality structures of more closely related species, such as chimpanzees and orang-utans, also appear to resemble human personality to a greater degree compared to more distantly related species, such as rhesus macaques. This suggests that dimensions of individual difference in behavior have a phylogenetic signal.

To test this, we assessed personality in three other species of macaques (Assamese, Barbary, and Japanese) and quantified the equivalence of personality dimensions across species using an analysis based on fuzzy set theory that was sensitive to slight variations in the meaning and item content of each dimension. All macaque species were consistent in having a single Friendliness domain that captured sociability and affiliativeness, which are separate dimensions in great apes. Macaque species varied in dimensions related to social competence and aggressiveness: species with highly hierarchical societies had a single dimension while egalitarian social structure was associated with two independent dimensions. Personality structure in primates may therefore be an adaptation to socially-driven opportunities for alternative behavioral strategies.

S13.3 Cue reliability predicts the use of personality in decision making in a wild primate

Alecia Carter, University Of Cambridge

Harry Marshall, Robert Heinsohn, Guy Cowlshaw

Phenotypic plasticity should be selected for in stochastically changing environments with reliable cues. Conversely, where information is unreliable, other mechanisms may be used to make decisions. Foraging decisions have recently been shown to depend on personality, but only during experiments in which the information available to individuals is unreliable.

We investigated the effect of cue reliability and personality (boldness) on foraging decisions in socially foraging, wild chacma baboons *Papio ursinus* during natural foraging and in experimental food patches. We found no effect of personality on foraging decisions during natural foraging. Foraging decisions appeared to be made flexibly in response to reliable environmental cues such as habitat type and patch size. However, when we manipulated cue reliability to become unreliable during foraging experiments, individuals used personality to make foraging decisions. We suggest that where reliable environmental cues are available to foragers, plastic behaviour in response to the cues may be favoured, whereas unreliable cues could result in the use of animal personality to make decisions. If our interpretation is correct, a failure to provide the same quality of social and environmental cues in an experimental setting may lead to an over-inflation of the perceived importance of animal personality in the literature.

S13.4 Personality in chimpanzees at Gombe National Park

Alexander Weiss, The University Of Edinburgh

Personality ratings of captive chimpanzees reveal six domains. The first is typically labeled "Dominance" and associated with competitive prowess. The remaining domains --- Extraversion, Conscientiousness, Agreeableness, Neuroticism, and Openness --- are similar to human personality domains. These domains were found to be consistent across raters and time, related to behavior, influenced by genes, and not anthropomorphic projections. Still, these ratings were obtained from mostly captive samples and may therefore reflect behavioral syndromes associated with captivity. I examined whether similar domains exist in wild chimpanzees. Subjects were 142 wild chimpanzees comprising nearly the entire population of the two major communities in Gombe National Park. Raters were working and retired field assistants. The questionnaire was a brief version of a questionnaire used to assess captive chimpanzees. Preliminary

analyses suggest that interrater reliabilities are good and that the domains, while not identical, are comparable to those of captive samples. Moreover, in a subsample rated 32 years earlier, there was strong evidence for personality consistency.

These findings indicate that, while there is some possible evidence for behavioral syndromes related to captivity, these effects were modest to moderate in size. These findings also highlight the potential in studying the behavioral ecology wild chimpanzee personality.

S13.5 Development of affiliative networks in former laboratory chimpanzees (*Pan troglodytes*) following resocialisation

Elfriede Kalcher-Sommersguter, Karl-Franzens-University Graz

Signe Preuschoft, Karl Crailsheim, Cornelia Franz-Schaider

In all social mammals and especially in higher primates early deprivation within a sensitive period during ontogeny may lead to social deficiencies later in life.

We investigated the affiliative networks including social play and allo-grooming of three social groups consisting of adult former laboratory chimpanzees who had spent decades in solitary confinements. For this we conducted 237 hours of scan sampling distributed over three sample periods following resocialisation. We expected individuals with the experience of an early deprivation (EDs, i.e. onset of deprivation at a mean age of 1.2 years) to differ significantly in their ability to form affiliative networks from later deprived individuals (LDs, i.e. onset of deprivation at a mean age of 3.6 years). Accordingly, social network analysis, based on the distribution of weighted measures, revealed significantly less tight or even fragmented and instable affiliative networks within the two groups consisting of a majority of ED individuals compared to the tightly knit networks of the LD-majority group over a two-year period following resocialisation. Thus, even though all three social groups developed affiliative networks subsequent to resocialisation, only the LD-majority group succeeded in the maintenance of consistent networks over the two years of group life.

S13.6 Do individual differences in metabolism predict personality differences in grey mouse lemurs?

Melanie Dammhahn, Departement Des Sciences Biologiques, University Du Quebec, Montreal
Pauline Vuarin, Pierre-Yves Henr

Recently it has been suggested that consistent individual differences in behaviour, i.e. personality traits, are part of the pace-of-life syndrome because

they evolved in response to the same ecological conditions that shaped physiology, life-history and ecology. However, empirical evidence for this behaviour integrating pace-of-life syndrome is scarce. Using a laboratory experiment, we aimed to test whether (1) individual variation in resting metabolic rate (RMR) are consistent and related to variation in personality traits in a facultative heterothermic small primate, the grey mouse lemur (*Microcebus murinus*), (2) this relationship is stable under different environmental conditions, and (3) individual variation in energy saving strategies is related to RMR and behavioural phenotypes. We quantified exploration and boldness using repeated open-field, novel object and maze tests for 24 adult males. We measured RMR twice via respirometry and torpor-based energy saving over 15-days. We found individual consistency in boldness, exploration and RMR. Further, individuals with high RMR were more explorative and expressed less energy-saving torpor. These results lend moderate support to the hypothesis that higher metabolic rates are associated with higher use of behaviours that facilitate energy acquisition and a reduced need to offset maintenance costs via energy saving and, thus, to the pace-of-life syndrome.

Symposium 14: Cognitive control in spatial navigation: systems and cellular mechanisms and clinical implications

S14.1 The role of the retrosplenial cortex in navigation in dynamic environments

Malgorzata Wesierska, Nencki Institute Of Experimental Biology

The retrosplenial cortex (RSC) is involved in networks underlying navigation and spatial memory formation. Its role in memory function is studied via a set of place avoidance maze-like tests, in which processing of spatial representation involves visual cues. In the place avoidance test the rat has to remember and avoid entering into a shock zone on the arena. The location of the shock zone could be described by distal, mainly visual stimuli and/or relevant proximal stimuli and information from self-motion. Different task variants allow for the study of various modes of navigation (such as allothetic or idiothetic) and cognitive control, which is based on stimuli segregation. We use all variants of the place avoidance test to study the role of RSC in cognitive control of spatial information. To assess the involvement of the retrosplenial areas in spatial memory we mapped expression of *c-Fos* in dysgranular (RSD) and granular (RSG) areas. We found that damage of the RSC impaired performance in place avoidance that required segregation of relevant and irrelevant stimuli and that the RSG and RSD areas differed in their temporal contribution to spatial learning during the active place avoidance task.

These results suggest involvement of the retrosplenial cortex in the segregation of spatial information.

S14.2 Organizing distinct streams of information in activity of hippocampal cell assemblies

Eduard Kelemen, University Of Tuebingen

The hippocampus is crucial for organizing different streams of information in the brain – a process known as cognitive control. The mechanisms underlying cognitive control at the neural network level are largely unexplored. To address this, we recorded hippocampal ensemble activity in rats when two streams of information (representing two dissociated spatial reference frames) were concurrently relevant. We found that cell activity was organized by dynamic grouping – neurons active at the same time (within hundreds of milliseconds) had a tendency to process the same type of information, and the two streams of information were intermittently represented in ensemble discharge at different times. The information represented at a particular time was determined by the behaviorally relevant parameters of the current environment.

Next we asked whether dynamic grouping is also used to coordinate memories experienced during distinct behavioral episodes. In rats performing two different tasks in sequence we observed hippocampal activity corresponding to the first task intermittently present while the animal was performing the second task. The representations were organized by a similar dynamic grouping mechanism, but with distinct temporal parameters. Dynamic grouping thus appears as a general mechanism organizing information processing in hippocampal ensembles on multiple behaviorally relevant levels.

S14.3 Using immediate-early genes to map changes in neural activity in spatial learning and in models of brain disorders

Stepan Kubik, Institute Of Physiology Academy Of Sciences Of The Czech Republic

Neural activity accompanying behavior engages expression of immediate-early genes in activated neurons. This expression is a part of a molecular cascade leading from neural activity to synaptic plasticity. Interfering with IEG expression disrupts synaptic plasticity maintenance and impairs long-term memory consolidation in a number of tasks. In hippocampal area CA3, expression of the IEG *Arc* is triggered in complete ensembles by as little as a single passage through a place providing a mechanism for encoding one-trial experience. In contrast, recruitment of CA1 neurons into *Arc*-expressing ensembles is more

incremental and occurs over multiple repetitions. Inactivation of medial septum ameliorates hippocampal theta rhythm and hippocampus-dependent learning, leaving location-specific discharge of hippocampal neurons relatively spared. This activity, however, does not induce *Arc* expression in hippocampal neurons, emphasizing its link to plasticity and learning rather than mere activity. Complete absence of behaviorally-induced *Arc* expression in the retrosplenial cortex after inactivation of the hippocampus suggests that learning-related plasticity in this region critically depends on hippocampal output. Systemic MK-801, which is used to model schizophrenia in rats and humans, impairs hippocampus-dependent cognitive coordination on rotating arena and alters IEG expression in the hippocampus.

S14.4 Spatial memory and cognitive control deficits in animal models of brain disorders

Ales Stuchlik, Institute Of Physiology, Academy Of Sciences Of The Czech Republic

Spatial navigation is perhaps the most popular behavioral model in study of relation of brain to behavior. It requires multiple processes such as recognition of places and positions, cognitive control and continuous updating of changing information. Dysfunctions of these processes are found in many animal models of brain disorders such as schizophrenia or neurodegenerative conditions. The talk will present a deficit in navigation, visuospatial working memory and cognitive control in an animal model of schizophrenia, effect of antipsychotics and specific receptor ligands. Deficits in cognitive control seen in neurodegenerative and excitotoxic models including beneficial effects of novel neuroprotective substances will be presented.

Aim of the lecture will be to stress the immense importance of studying behavior in animal models of brain diseases for understanding disorder-related deficits in cognitive control and to show how important these approaches are for preclinical searching of efficacious and safe pharmacotherapy aimed at cognitive deficits. Supported by AS CR M200111204, IGA MZ NT13386 and GACR P304/12/G069.

S14.5 Dissociated reference frames on a rotating platform in human

Kamil Vlcek, Inst Physiol Acad Sci

Navigation in an environment with two dissociated reference frames (RF) has been suggested as a model of cognitive control in space. Reaching a goal defined in one of the RF requires that one selects the relevant

frame of reference and reorient relative to this RF to estimate his/her own position. We used a virtual environment with a rotating platform dissociating the RFs of the room and the platform to study spatial cognitive control in human. The subjects should point at and then reach hidden goals upon showing their name on a screen. The time to point to a hidden goal seems to be strongly influenced by the RF of previous goal: changing the goal RF was associated with a longer pointing time. The switch costs can be the result of the process of reorientation in the relevant RF and/or the activation of the associated spatial representation. In the presentation we will explore the hypothesis that internal representations of two dissociated RF are not accessible simultaneously, suggesting that mental maps of the two dissociated RFs are stored in memory as two independent representations in human.

S14.6 Male sexual signals that underlie female spatial learning and hippocampal neurogenesis in mice

Emma Hoffman, University Of Liverpool
Sarah Roberts, Lynn McLean, Rob Beynon, Swamy Thippeswamy, Lucy Pickavance, Jane Hurst

For most mammals, including mice, scent is important for communication with competitors and potential mates; unlike auditory or visual signals, scent marks provide long lasting signals of identity, location and competitive ability even when the scent owner is elsewhere. Acquiring memories of individual scent mark locations is likely to be important in allowing females to be selective and locate a preferred male when ready to mate. Males invest in competitive marking around their territories, exposing females to numerous scent marks from competing males. In mice, male scent can condition a preference for its remembered location, stimulated by a specific sex pheromone in male urine. Male scent from dominant territory owners also stimulates neurogenesis in the hippocampus of female mice, an area of the mammalian brain associated with spatial memory. To assess how differences in male expression of specific scent components influence female spatial preferences, we used conditioned place preference tests comprising multiple scents and locations. We also quantified hippocampal neurons in female mice exposed to different male scents or specific scent components to determine whether the same sexual signals that stimulate spatial learning also stimulate hippocampal neurogenesis.

Symposium 15: Relationship Quality and Social Bonds

S15.1 Components of relationship quality: a review

Elisabeth Sterck, Utrecht University

New techniques are becoming available to measure associations between individuals in species where thus far following individuals was elusive. This will yield association patterns. A next step in the analyses will be to determine whether these are only emerging patterns from individual movements patterns, or that encounters with particular individuals have an additional meaning. In primates, a whole body of theory addresses the meaning of encounters and individuals maintain differentiated social relationships with their group mates.

A review of the available primate and bird literature reveals that social relationships have multiple components, and that two independent components are found in all studies: dyadic variation in the rate of aggression and in affiliation (also labeled friendship). However, these two components of relationship quality may not be universal. Whereas dyadic variation in the rate of aggression may be widespread, dyadic variation in affiliation may only be found in taxa where familiarity enhances benefits of sociality.

S15.2 How does social bonding between unrelated females increase reproductive success?

Elissa Cameron, University Of Tasmania

In many social species, females form close bonds with other members of their group. These social bonds have only rarely been investigated except in primates. Primate studies show that reproductive success is increased for females with stronger bonds, usually between kin. In equids, females form long-term social groups consisting of unrelated members. We previously demonstrated that social integration between these unrelated females increased birth rates and foal survival, and reduced harassment by males. We concluded that social integration has strong direct fitness benefits such that social bonds could evolve based on direct benefits alone, without depending on kin selection. Here we test whether strong relationships between individual females or more general social integration have a greater impact on reproductive success, and whether relationship longevity influences the benefits received. Furthermore, we show that foals of more integrated mares themselves develop stronger social bonds with peers and, at dispersal, become integrated into new groups more quickly. Thereafter, these young females maintain better condition, breed at a younger age, and have more success raising foals.

Finally, we show how behaviour of a mare changes following the loss of her closest associate. Our study shows that social integration has long-term, cross-generational reproductive benefits.

S15.3 Structure and reproductive correlates of female social relations in plural-breeding rodents

Tina Wey, University Of California At Davis
Joseph R Burger, Luis A Ebensperger, Loren D Hayes

Examining the structure and reproductive correlates of social relations in diverse taxa is important for broad understanding the adaptive value of sociality. Reproductive benefits of female social bonds have been documented, usually in highly complex societies, but other species have opportunities for reproductive consequences of female relations.

We explored the patterning of female associations and the relationship between association networks and pup production in degus (*Octodon degus*), a plural-breeding and communal nesting rodent. Despite high turnover in group membership, females had significantly preferred social partners, and some preferences persisted across seasons, suggesting lasting social relations. Per capita direct female fitness was not related to group cohesiveness but was negatively related to heterogeneity of association strengths, suggesting potential costs of within-group social variation. The specific drivers of these preferred social relations in degus are currently unknown. I compare results in degus with patterns of female affiliation from another plural-breeding rodent species, yellow-bellied marmots (*Marmota flaviventris*), in which female affiliation is negatively correlated to annual reproductive success, and discuss the structure and potential roles of female relations in these plural-breeding rodents without cooperative care.

S15.4 Male-female bonds in a promiscuous primate

Julia Ostner, University Of Göttingen
Linda Vigilant, Jyotsna Bhagavatula, Mathias Franz, Oliver Schalk

Close associations between adult males and females are rare among group-living, non-monogamous mammals. Although heterosexual friendships have been described in baboons, these are short-term affairs serving as protection against infanticide and thus tightly linked to the presence of vulnerable infants. Long-term association may be adaptive in situations of low male monopolization potential where it pays to invest in a particular female partner instead of spreading the effort among many females. Here we use long-term data on male-female and male-infant association in wild Assamese macaques to show that close male-female associations were stable for at least 2 or 3 years. We further show that patterns of male association with infants from birth to two years were predicted by genetic paternity as well as past mating success, thereby creating potential for paternal care. Evidence for increased future mating success for males with their closely associated female partner was

inconclusive. We thus postulate that particular demographic and life history circumstances may favor male-female friendships by creating a positive feedback between male-female-infant associations driven by paternal care and male-female associations promoted by increased mating access to drive the evolution of long-term male-female bonds.

S15.5 The role of social bonds in cooperative decision rules

Jorg Massen, Universität Wien

Cooperation is a widespread phenomenon among social animals. If all participants contribute equally to the cooperative act, the benefits of cooperation for the collaborators are rather straightforward; i.e. to gain access to resources one is not able to get alone. Yet, cooperation is prone to so-called free-riders. Therefore, to maximize their own pay-off and to avoid being exploited, individuals need to keep track of the effort and reward trade-off of both themselves and their collaborators. Recent research on reciprocal altruism suggests that these decision rules mainly rely on emotional depictions of your collaborators and thus do not rely on highly cognitive tit-for-tat reasoning. However, these studies mainly concern species that live in stable social groups in which each individual has at least some sort of emotional bond with each group member. In contrast, fission-fusion species also interact with relative strangers, which may need more cognitive decision rules, since an emotional bond is lacking.

I would like to present some preliminary data on cooperation in a species with much fission-fusion dynamics: the raven. Using different experimental set-ups, I try to unravel the decision rules these ravens use when cooperating with conspecifics of varying relationship quality; i.e. from good friend to complete stranger.

S15.6 Memory for social bonds in ravens

Thomas Bugnyar, University Of Vienna
Kathrin Weigersdorfer, Markus Boeckle

Life in groups structured by social relationships is cognitively challenging. It requires individuals to recognize and remember group members and, within those, to distinguish affiliates from non-affiliates. Dealing with different time periods of separation, as it is the case in systems with high degrees of fission-fusion dynamics, may impose particular challenges on the memory part. Whereas long-term individual recognition has been demonstrated in some non-human animals, memory for social bonds, i.e. different types of relationship quality to former group members

and kin, has received little attention. Using a play-back design, we here tested captive ravens for their ability to discriminate i) former group members from non-group members, ii) former affiliates from non-affiliates, iii) their own offspring from other offspring and iv) their parents from other adults after different times of separation.

Our findings indicate that ravens remember some social bonds even after years of separation. We discuss emotional and cognitive mechanisms as basis for memory.

S15.7 Exploring the relationship between empathic response and social buffering in chickens

Joanne Edgar, University Of Bristol
Elizabeth Paul, Christine Nicol

Emotion transfer within a social animal group will depend on a number of social factors, including an individual's capacity for emotional empathy and the extent to which social buffering occurs. Emotional empathy occurs when an observer detects an emotional response in a demonstrator, triggering a matching emotional state in the observer. Social buffering is the amelioration of demonstrator distress caused by the presence of an observer. Despite the potential for interaction between the two social phenomena, previous research on empathic response has been conducted almost entirely in isolation from work on social buffering. Having previously demonstrated that mother hens show behavioural and physiological arousal in response to chick distress, our current work examines whether, and to what extent, the capacity for empathy in mother hens affects their chicks' recovery from a mild stressor. We describe studies in which we utilise natural variation in mother hens' empathic capacity to study the interaction between empathic response and social buffering. Additionally, by artificially modifying maternal behaviour in the hens, we examine how the hens' maternal behaviour ameliorates the chicks' distress response. Our prediction is that individual variation in empathic capacity will influence the extent to which social buffering occurs.

S15.8 Comparison of the influence of social relationships and hierarchy in crows (*Corvus corone*) and ravens (*Corvus corax*)

Miriam Sima, Max-Planck Institute For Ornithology
Theresa Matzinger, Thomas Bugnyar, Simone Pika

Although some bird families are known for their relatively complex social systems, studies on social relationships in birds are rare. However, it has recently been shown that members of the corvid family, ravens and crows, form long-term partnerships in addition to

group formations with relatively high degrees of fission-fusion dynamics. Since, the majority of studies focused on a single species only, the current study had two aims: First, we wanted to investigate the influence of social relationships and hierarchy in competitive foraging situations. Second, we wanted to compare two closely related species with regards to influence of dominance and affiliative relationships.

Hand-raised ravens and crows were confronted with two feeding situations in which we varied the level of how food could be monopolized (1 Piece or 2 Pieces) during their first year of life.

Our results suggest that developing a linear rank hierarchy decreases the agonistic behaviour in competitive situations. In addition, we found a species difference, with “friendships” (non-kin and non-mates) being more important in ravens than in crows. Implications of these results will be discussed in relation to relatedness, social system and ecological challenges.

S15.9 The role of personality in a social network: tracking the association patterns of wild great tits

Lysanne Snijders, Wageningen University
Erica Van Rooij, John Burt, Kees Van Oers, Marc Naguib

Many animals do not associate at random. Individuals can selectively choose who to avoid or who to approach, but can also have different tendencies to socialize in at all. Personality, the consistent difference in behaviour between individuals, can make this social behaviour of individuals predictable and it can allow others to respond with selective avoidance or association. Until now researchers were unable to simultaneously approximate the personality of individuals and quantify their pair-wise associations in the wild. We overcame this by using the new tracking technology, Encounternet, in a natural population of personality-typed great tits.

In March 2012 and 2013 we equipped a large number of personality-typed wild great tits with Encounternet tags sending signals every 5 seconds. These signals could be received by a large number of wireless stations distributed throughout the field site. By triangulating locations we were able to extract, out of several thousands of simultaneous observations, hundreds of close range encounters.

Here we will present the results which provide interesting insights into the role of personality in a social network.

S15.10 Vocal exchanges as indicators of social bonds in bottlenose dolphins

Vincent Janik, University Of St Andrews

Vocal matching is a well-known phenomenon in animals capable of vocal learning such as song birds and delphinids. The bottlenose dolphin is an interesting species for the study of such vocal exchanges.

Bottlenose dolphins do not produce song, but have close social bonds to selected individuals in a fission-fusion society. In their social behaviour, bottlenose dolphins are similar to many primate species while their vocal learning skills place them close to song birds and parrots. Bottlenose dolphins use learned, individually distinctive signature whistles to broadcast their identity to conspecifics. When meeting at sea, individuals exchange signature whistles before groups join. However, when close associates are separated, they copy each others' signature whistles to maintain contact. Playback studies show that copying an individual's signature whistle elicits a vocal reply by the animal that was copied. Thus, copying of signature whistles is an effective way of addressing conspecifics. Signature whistles of males that form alliances also become more alike over time broadcasting their association to conspecifics. Thus, bottlenose dolphins using signature whistles in exchanges not only address selected individuals but also broadcast the existence and quality of social bonds to eavesdropping animals in the social network.

S15.11 Referential gestural signalling: New insights from ravens (*Corvus corax*)

Simone Pika, Max Planck Institute For Ornithology

Referential acts play a crucial part in our every day communication since human language is, in its essence, a referential system. Reference can be made via icons, indices and signs but also via ostensive/inferential communication, in which the behaviour of the actor directs the attention of the recipient to particular aspects of the environment. The earliest uses of ostensive/inferential communication can be observed in human children around the age of nine to twelve months. However, what about comparable gestures in our closest living relatives, the nonhuman primates or other animal taxa? The present paper aims to provide a brief overview of the state of the art to encourage future research into the evolutionary origins and uses of referential gestural signaling. Social bonds may be a key factor in understanding this form of communication.

Symposium 16: Sensation, Communication, and Foraging in Bees

S16.1 How is division of foraging labour regulated in honey bees?

Ricarda Scheiner, University Of Potsdam

Honey bees display a complex division of labour. In addition to age-dependent division of labour among nurse bees and foragers, division of labour occurs between same-aged bees, for example among foragers. While some worker bees specialize on collecting pollen, others collect nectar. The different types of foragers differ in many behaviours ranging from sensory responsiveness to learning. This talk will focus on mechanisms regulating age-independent division of labour and related behaviours.

S16.2 Bumblebee learning across different sensory modalities

Karen Smith, Royal Holloway
Nigel Raine

Bees make decisions about which flowers to visit using multimodal cues (including colour and odour), however almost all studies examining variation in learning have focussed on assessing performance in one sensory modality. We therefore know little about whether individual bees show similar learning performance in tasks they learn using different sensory modalities, or whether individuals specialise in one modality. In this study we tested the performance of 76 bumblebee (*Bombus terrestris*) workers, from four colonies, in both a visual and an olfactory learning task. In the visual task free-flying bees learnt both to associate yellow as a predictor of floral reward and to ignore blue (unrewarding) flowers. The olfactory learning task used the proboscis extension reflex (PER) paradigm to differentially condition individual bees to associate one of a pair of floral odours as a predictor of reward. PER conditioning is commonly used to assess learning in honeybees, but has rarely been used in bumblebees. Our results show significant variation among workers in each colony in their performance in both the visual and olfactory learning task. However, we found no consistent evidence to suggest either a correlation, or a trade-off, in individual performance in the learning tasks using different sensory modalities.

S16.3 Majoring and minoring in bumblebees revisited

Tamar Keasar, University Of Haifa - Oranim

Foraging bumblebees focus mainly on one flower species (their "major"), and occasionally visit other flowers ("minors") that are less rewarding. Minoring allows tracking of potential alternative food sources that could become more profitable with time. This is expected to be adaptive when resources are poor and fluctuating, but to reduce foraging efficiency when they are abundant and stable.

I tested how reward schedules within and between food sources, and the temporal stability of rewards, affect minoring and foraging success. *Bombus terrestris*

workers collected sucrose solution from artificial flowers in two-phase laboratory experiments. The bees first foraged on three types of rewarding flowers. In the second phase, a fourth, non-rewarding type of flowers was added. Subsequent probings of non-rewarding flowers were regarded as "minoring" visits and were related to the bees' foraging experience. Minoring increased when the three rewarding flower types: (a) provided low mean rewards; (b) had identical profitabilities; (c) fluctuated in profitability over the course of the experiment. Simulation models suggest that recent rewards, obtained during the bees' last 1-2 visits, strongly influenced their foraging choices. Reliance on short-term foraging experience may constrain the bees' ability to identify the most profitable food source, a possible mechanism underlying minoring.

S16.4 The buzz about nocturnal bees

Hema Somanathan, Indian Institute of Science Education and Research

Most bees are diurnal and their foraging activity ceases when the sun sets. However, some bees have made evolutionary transitions to nocturnality. Nocturnality has evolved in at least 4 families of bees. Among them, most are crepuscular or nocturnal only when there is a moon in the sky. Some others, such as *Apis dorsata*, the Giant Asian Honeybee, are mostly diurnal but can turn nocturnal seasonally. The Indian carpenter bee, *Xylocopa tranquebarica*, is obligately nocturnal and is known to fly even on moonless nights in the Western Ghats of India while congeneric sister species *X. tenuis* and *X. leucothorax* are diurnal. By using a comparative approach, I examine visual adaptations that have accompanied the transition to nocturnality in these bees and try to address ecological conditions that maintain nocturnality in this bee.

S16.5 Impacts of iridescence on bee foraging behaviour

Heather Whitney, University Of Bristol

The evolution of many floral features has been driven by coevolution with, and adaptation to, animal pollinators, and many of these features provide examples of interspecific communication. Iridescence is a form of structural colour which changes hue according to the angle from which it is viewed. As well as producing vivid visual signals, in animals iridescence has been found to have a multifunctional range of roles. Iridescence has also been found in plants. As in animals, the structures by which the colour is produced are diverse, as potentially is the range of functions iridescence may have. It has recently been found that

floral iridescence, due to ordered petal cuticular nanostriations that produce a diffraction grating, is widespread and can be used as a cue by pollinating insects. I have been investigating the impact of different types of iridescence on the visual system and foraging behaviour of bumblebees.

S16.6 Active sensing: flight behaviour constrains the learning of coloured patterns in bees

Natalie Hempel De Ibarra, University Of Exeter
Keri Langridge, Claudia Wilke, Olena Riabinina, Misha Vorobyev, Elizabeth Nicholls

A foraging animal has to differentiate when to learn what. This can be influenced by the way it moves through the environment. We present evidence that bees adjust their flight behaviour to aid learning of colours and patterns within the limits set by their goal-oriented flight manoeuvres.

We trained bumblebees to vertical coloured targets and recorded their unconstrained approach flights. Although reward was delivered in the centre of the target bees approached it preferentially from below, both on single-coloured and two-coloured stimuli. If the contrast line in two-coloured stimuli was on-centre, bees developed an asymmetric preference for the colour of the lower half. When trained in a serial discrimination task, bees centred their approach flight and learnt both colours equally. When the contrast line was moved off-centre into the lower or upper half of the pattern, bees showed systematic changes in approach behaviour and subsequent colour preferences. Differences in approach height between pattern treatments correlated with relative colour preferences during subsequent tests. Our study highlights that morphology and action patterns influence how animals solve sensory and cognitive tasks.

S16.7 Bumblebee flight control in naturalistic environments

Emily Baird, Lund University
Marie Dacke

Although the visual flight control strategies of flying insects have evolved to cope with the complexity of the natural world, investigations into flight behaviour have typically been performed indoors using simplified two-dimensional artificial visual stimuli. How well do the results from these studies reflect the natural behaviour of flying insects considering the radical differences in contrast, spatial composition, colour and dimensionality between these visual environments? To answer this question, we investigated the flight control behaviour of bumblebees flying in both naturalistic and artificial two- and three-dimensional visual

environments. We find that bumblebee flight control is not strongly affected by the visual differences between artificial and naturalistic environments. Furthermore, we find that, in three-dimensional environments, both foreground and background visual information play an important role in flight control. Together, these results have implications not only for understanding the mechanisms of visual flight control in bumblebees, but also for the results of past and future investigations into visually guided flight control in other insects.

S16.8 In sickness and in health: examining the effects of disease on bee flight patterns

Juliet Osborne, University Of Exeter
Matthias Becher, Stephan Wolf, Peter Kennedy

It has been shown that pathogens affect honeybee foraging trips, but it is still unclear whether these pathogens have an impact on the quantity of forage returned to the colony, and whether there is consequential effect on colony growth.

We have been studying the impacts of the varroa mite, viral load and *Nosema* spp. on the flight patterns of individual bees and the foraging behaviour of colonies using harmonic radar tracking and longer term colony assessments. We have also developed a model (BEEHAVE) of honeybee colony dynamics and foraging behaviour. This is being used to establish whether relatively subtle effects on individual behaviour caused by pathogens are likely to have an impact on honeybee colony growth and development.

I will present empirical and simulated results to illustrate the interactions between honeybee pathology and foraging in realistic landscapes at the individual and colony level.

S16.9 How is the reward magnitude translated into memory formation?

Dorothea Eisenhardt, Freie Universitat Berlin
Kathrin Marter

The availability of nectar is signalled to honeybees by naturally occurring stimuli. Honeybees learn the association of these stimuli with a food reward and form a memory about this association.

We here ask if and how honeybees learn about the reward magnitude, i.e. the duration of the reward and the reward concentration.

We elucidate this question quantifying behaviour of individual honeybees in a well-known learning paradigm, the classical olfactory conditioning of the proboscis extension response (PER).

Results from this on-going study will be presented, revealing that honeybees are able to learn the reward magnitude and that reward duration and reward concentration affect learning and memory formation

differentially. We will discuss our results within the framework of honeybee foraging behavior.

S16.10 Influence nutritional state and amino acids on learning and memory in adult foraging honeybees

Geraldine Wright, Newcastle University

Essential amino acids are an important part of every animal's diet. Most animals balance their needs for essential amino acids using feedback about their nutritional state that guides foraging decisions. Animals eat foods containing nutrients in deficit and avoid nutrient surplus. Adult forager caste honeybees are unlike other animals, in that they forage mainly for others and only need amino acids for somatic maintenance.

Here, we examined how nutritional state affected the way that amino acids in food rewards influenced honeybee olfactory learning and memory. With the exception of iso-leucine, high concentrations of amino acids were repellent to honeybees when added to sucrose solution. If honeybees had been fed the day prior to training on a solution containing amino acids, they were more likely to learn to associate a solution containing amino acids with reward.

These results are contrary to predictions of nutritional models and suggest that feedback about the nutritional quality of solutions acquired from previous experiences influences the reaction to these nutrients when experienced in subsequent foraging bouts.

S16.11 Neonicotinoid pesticides impair olfactory learning in the honeybee

Sally Williamson, Newcastle University
Annie Gott, Geraldine Wright

Honeybees and other pollinating insects are currently in decline in both Europe and the USA. One of the factors implicated in this loss of pollinators is exposure to agricultural chemicals such as pesticides. The effects of neonicotinoid pesticides in particular has generated a great deal of interest, due to their effects on behaviour even at the sub-lethal doses found in nectar. We have previously reported that imidacloprid impairs olfactory learning and memory in the honeybee (Williamson and Wright 2013), but the effects of other commonly used neonicotinoids have been less well studied.

We have used a differential conditioning assay to assess the effects of several different neonicotinoids on the ability of honeybees to perform olfactory learning tasks. Bees were taught to associate distinct floral odour components with either a positive outcome (a sugar reward) or an aversive stimulus (bitter quinine). The results show that while imidacloprid, and

clothianidin, impaired the ability to learn the positive association, bees treated with these compounds still learned to avoid the aversive stimulus. Thiamethoxam treatment however completely impaired the bees' ability to distinguish between the olfactory cues, causing equal responses to both the positively reinforced and the negatively reinforced odours. These findings could have implications for the ability of bees exposed to neonicotinoid pesticides to perform the olfactory learning tasks necessary for optimal foraging behaviour in field conditions.

Symposium 17: Cognition and sexual selection: how does one influence the other?

S17.1 Beautiful minds, brawny brains, and calculating choosers: Towards a better understanding of the interactions between cognition and sexual selection

Jason Keagy & Neeltje Boogert, Michigan State University

In this introduction to the symposium we will present a novel conceptual framework that incorporates the many ways in which cognition and sexual selection may interact. We will review our own work illustrating the relationship between male cognitive performance and female preference. Then we will describe examples of how cognitive ability can influence mate choice decisions, and review what comparative studies of brain evolution might tell us about the relative importance of sexual selection as an evolutionary force for cognitive evolution.

In addition, we will use our framework to highlight the most important gaps in our understanding of the interactions between cognition and sexual selection, such as the extent to which genes versus environmental conditions affect cognition, sexual displays and mate choice decisions and the actual benefits animals may acquire by mating with individuals with better cognitive ability.

Our review will emphasize the dynamic nature of the relationship between cognitive traits and sexual selection processes. We will suggest that a combination of lab and field studies, as well as standardization of cognitive tests, will be necessary to make substantial progress.

S17.2 Cognition testing in the wild: a cognitive challenge for experimenters too?

Joah Madden, University Of Exeter
Jess Isden

Abstract cognitive testing in the wild is still rare, and presents a cognitive challenge for experimenters as much as for the animals they are trying to test. Many studies on wild individuals focus on testing elements of natural

behaviours. We argue that in order to gain a true representation of overall cognitive abilities we need to develop methodologies for transferring classic, psychologically accepted methods of cognitive testing from the lab to the field. The breeding behaviour of male bowerbirds appears to offer an ideal system for such classic, abstract testing. Individually marked males repeatedly return to their bowers over a period of months and appear to discriminate and classify coloured objects for use as bower decorations. Males habitually and readily interact with novel objects. We explored a range of cognitive processes in a population of wild spotted bowerbirds, including colour association and reversal, spatial memory, problem solving and folk physics, using a suite of tests based on classic psychological paradigms. However, we found that several tests could not be easily transferred to wild conditions.

Here, we outline the constraints and challenges presented when transferring lab based tests to the wild, and discuss whether failure of individuals to complete cognitive tests accurately in the wild reflects limitations in their cognitive ability or in the inability of the researchers who study them.

S17.3 Development of avian mate choice: Culture, condition and cognition

Katharina Riebel, Leiden University

Successful reproduction requires finding a suitable mate and some are more suitable than others. Given the high stakes involved, some of the most complex signalling and information processing in animals occurs in this context, such as mate advertisement singing in birds. Song is learned early in life, and can thus be subject to fast cultural change, raising the question as to how extragenetic, i.e. cultural inheritance, affects perception of songs in female songbirds, the intended receivers of these signals. Reporting from our own work with zebra finches (*Taeniopygia guttata*), I will show how experimental study of the development of song provides us with a powerful approach to test how individual experiences shape signalling behaviour and cognitive performance (both in producing and decoding these learned signals). For our study system, we can demonstrate that how females respond to particular mating signals varies consistently between individuals depending on the type of songs they have heard when young, on their rearing conditions and their own phenotypic quality. Female mating preferences thus show substantial plasticity resulting both from cultural transmission and state-dependency of the cognitive processes underlying mate choice, suggesting a different role for female preferences in signal evolution than sketched by traditional models.

S17.4 Multimodal signalling: A perceptual integration approach

Ryan Taylor, Salisbury University

Female mate choice can exert strong selection driving the elaboration of male traits. In the túngara frog, *Physalaemus pustulosus*, males inflate a large vocal sac while producing courtship calls. The call is both necessary and sufficient for mate attraction and the vocal sac increases attractiveness of the call; females do not respond to an inflating vocal sac absent the call. In this study we presented females with spatially separate components of auditory signals (male vocalizations) coupled with a robotic frog as the visual signal component (inflating vocal sac). Female túngara frogs have previously been shown adept at grouping spatially disparate auditory signals, effectively responding as if the two components are emitted from the same location. This ability to create auditory groups was disrupted when we added the robofrog visual cue to one of the separated acoustic signals. In human psychophysics, it is well known that visual input can alter auditory perception. Like humans, these data suggest female frogs may perceptually integrate multimodal signals in a similar fashion. Thus integration of multiple signal components into salient perceptual units may form an important basis for complex signal evolution.

S17.5 Sexual Selection and Human Sex Differences in Brain and Cognition

David Geary, University Of Missouri

Darwin's principles of sexual selection—intrasexual competition and intersexual choice—have been successfully applied to the study of sex differences in behavior and physical ornaments across hundreds of species. Competition and choice should operate on brain and cognitive systems in the same way they operate on behavior and ornamentation, but have been less systematically studied, with a few exceptions. Psychologists have studied sex differences in human cognition for more than 100 years and in brain organization and functioning for several decades, but very little of this work has been informed by Darwin's insights. The merging of sexual selection with the extensive research base on human sex differences in brain and cognition will provide unique insights into how sexual selection operates to shape brain and cognition and will provide a richer, theoretically informed understanding of human sex differences.

I will provide an overview of sexual selection in humans, describe how components of this competition and choice can be used to make predictions about sex

differences in brain and cognition, and will illustrate several of these differences.

Symposium 18: Human life-history: integrating development, physiology, and ecology

S18.1 The stress response system: A physiological mediator of life history development

Marco Del Giudice, University Of Turin
Bruce J. Ellis, Elizabeth A. Shirtcliff

In this talk I discuss the role of the stress response system as a key mediator of life history development in humans. I will argue that the stress response system works as a mechanism of conditional adaptation, regulating the development of alternative life history strategies. Different patterns of activation and responsivity in early development modulate differential susceptibility to environmental influence and shift susceptible children on alternative pathways, leading to individual differences in life history strategies and in the adaptive calibration of stress responsivity. This life history perspective lies at the core of the Adaptive Calibration Model (ACM), the first comprehensive evolutionary-developmental theory of individual differences in stress responsivity. The ACM builds on life history concepts to advance a taxonomy of four prototypical responsivity patterns. Here I present empirical evidence supporting the ACM taxonomy, as well as new theoretical work on the adaptive matching of stress responsivity to local environmental conditions. I conclude by discussing how the ACM may contribute to boost the role of life history theory in developmental psychology and psychopathology.

S18.2 An evolutionary approach to incremental development with continuously incoming information

Willem Frankenhuis, Radboud University Nijmegen
Karthik Panchanathan

Models of phenotypic plasticity tend to ignore that development is often an incremental process. In previous work, we examined how natural selection might shape ontogenies when gradual phenotypic construction trades off with sampling cues to the environmental state.

In this talk, we present a follow-up model in which sampling and specialization are not mutually exclusive: Individuals sample throughout their lifespan, while simultaneously constructing their phenotypes. Organisms have the option of reversing their development, at some cost, which is a function of the number of increments developed in the suboptimal direction. We use stochastic dynamic programming to compute optimal policies for a range of evolutionary

environments. We explore different prior probability distributions of environmental states, values of information, functions mapping correct specializations to fitness gains, and functions mapping incorrect specializations to fitness losses (costs of reversing). Results show that in some developmental periods, organisms forego phenotypic construction and only sample; organisms may continue along the same developmental trajectory even when new information informs them the associated environmental state is unlikely (implying a sensitive window earlier in development); and individual differences in susceptibility to information may arise from differences in sampling histories, specifically the degree of consistency of the sampled cue set.

S18.3 Psychosocial acceleration: Adaptation to the external environment or internal state?

Ian Rickard, Durham University
Willem Frankenhuis, Daniel Nettle

Early social adversity is associated with accelerated pubertal maturation, early childbearing, and other reproductive traits. This example of phenotypic plasticity is of great interest to psychologists, biologists, epidemiologists and makers of social policy. The most commonly cited explanation for these patterns is that evolutionary pressures have given rise to advantageous strategies whereby individuals change their reproductive biology and behavior so that it is adapted to features of the external environment. We present an alternative hypothesis, which while not mutually exclusive with the aforementioned explanation, is different in several respects: the 'internal prediction' hypothesis. On this view, an unsupportive early childhood induces irreversible costs in development, which reduce an individual's expected lifespan and expected number of healthy (fertile) years. The adaptive response to such a situation is to accelerate sexual maturity and begin reproducing early. We discuss how, while these two models explain the same broad epidemiological phenomenon, they give rise to many alternative predictions, and how the results of tests of these predictions have implications for our fundamental understanding and the eventual design of interventions.

S18.4 Intralocus sexual conflict over human height

Gert Stulp, University Of Groningen
Bram Kuijper, Abraham P. Buunk, Thomas V. Pollet, Simon Verhulst

Intralocus sexual conflict (IASC) occurs when a trait under selection in one sex constrains the other sex from achieving its sex-specific fitness optimum. Because of their different life histories, selection

pressures on body size often differ between the sexes across many species, including humans: among men individuals of average height enjoy the highest reproductive success, while shorter women have the highest reproductive success. Given its high heritability, IASC over human height is likely. Using data from sibling pairs from the Wisconsin Longitudinal Study, we present evidence for IASC over height: in both shorter and taller sibling pairs (relatively) more reproductive success (number of children) was obtained through the sister than through the brother of the sib-pair. In contrast, in average height sib-pairs most reproductive success was obtained through the brother relative to the sister. In conclusion, we show that IASC over a heritable, sexually dimorphic physical trait (human height) affects Darwinian fitness in a contemporary human population.

S18.5 What Can Cross-cultural Correlations Tell Us About Human Nature?

Thomas Pollet, VU University Amsterdam
Joshua Tybur, Willem Frankenhuis, Ian Rickard

Many recent studies in the field of evolution and human behaviour have tested hypotheses by examining correlations between group-level (e.g., country, state, region) variables. Variables collected for each aggregation are often taken to be representative of the individuals present within them, and relationships between such variables are therefore presumed to reflect individual-level processes. There are several reasons to exercise caution when extrapolating from the macro- to the individual-level. We describe four issues that present substantial obstacles to drawing inferences about individual level processes from analyses conducted at the aggregate level. These are (1) the ecological fallacy, whereby relationships apparent at the aggregate level do not accurately represent individual level processes; (2) the use of unequal sample sizes, which gives undue weights to aggregations comprised of smaller number of individuals; (3) non-independence of data points, which violates the assumptions of inferential techniques associated with null hypothesis testing; (4) cross-cultural non-equivalence of measurement (differences in construct validity between groups). We provide examples of how each of these can create problems in the context of testing evolutionary hypotheses about human behaviour, and more broadly animal behaviour.

Sym 19: Measuring and understanding positive emotions and welfare in farm livestock

S19.1 Cognitive processes as the links between emotions and welfare to achieve better animal quality of life

Alain Boissy, INRA UMR1213 Herbivores
Randy Oppermann Moe, Lena Lidfors

Animals are sentient beings capable of experiencing emotions, as acute and transient processes, which are actually an important determinant of welfare, as a prolonged affective state. However scientific investigation of emotions, and particularly positive ones, has long been neglected. We will highlight a pragmatic framework to scientifically explore emotional experiences in animals from recent advances in cognitive psychology and affective neurosciences.

First, we will show in sheep how emotions are triggered by elementary cognitive processes, whereby the challenging situation is evaluated from a limited number of criteria including the novelty of the triggering situation, its predictability and controllability. The nature of the emotions the animals feel can be thus inferred from their evaluative abilities. Then, the interactions between emotions and cognition will be explored to understand the development of prolonged affective states.

Second, we will focus on specific cognitive processes (i.e. positive anticipation, contrast and controllability) for investigating positive emotional experiences, illustrated by recent experiments in poultry and sheep. Useful strategies for enhancing positive experiences will be outlined from this knowledge and practical applications will be suggested to enhance animal quality of life.

Possible links between positive experiences and alleviation of the negative effects of stress or diseases will be explored.

S19.2 Using vocalisations to measure positive and negative emotions in goats

Elodie Briefer, Institute of Agricultural Sciences
Federico Tettamanti, Alan G. McElligott

Public and scientific interest in positive animal welfare has greatly increased. Positive welfare is not only the absence of negative emotions, but also the presence of positive ones. However, techniques for understanding and assessing animal emotions are lacking.

This study was aimed at finding convenient and non-invasive tools to assess positive and negative emotions in goats (*Capra hircus*). We investigated behavioural, physiological and vocal indicators of emotions.

First, we conducted an experiment with goat kids, which consisted of separating them to various degrees from their mothers, and analysing the vocalisations they produced. We found changes in several

parameters between a situation where kids could interact vocally and visually, but not physically with their mothers, and complete isolation.

In a second experiment with adults, we measured behavioural, vocal and physiological responses in three emotional situations. These were: 1) isolation (negative-low arousal), 2) food-related frustration (negative-high arousal), and 3) food reward (positive-high arousal). Comparisons between situations of opposing valence, but similar arousal revealed several indicators of valence. Similarly, comparisons between situations of similar valence, but different arousal revealed numerous indicators of arousal. These non-invasive vocal indicators of emotions could be applied to other livestock in order to assess welfare.

S19.3 Happy as a pig in mud? Assessing the expressive quality of animal behaviour

Françoise Wemelsfelder, Animal and Veterinary Sciences Group

Dynamic models of animal sentience and emotion are gaining momentum, making possible an integrated approach to welfare assessment in which emotion is an expressive aspect of, rather than a separate state from, behaviour. Qualitative Behaviour Assessment (QBA) is a 'whole animal' methodology designed to characterise and quantify the expressive quality of animal demeanour, using descriptors such as relaxed, fearful, agitated or content. Such terms are frequently applied in studies of animal temperament and personality, and QBA extends this to include the assessment of animal experience.

This presentation will review research to date aimed at validating this approach, evaluating stronger and weaker aspects. In this light it will discuss QBA's relevance for assessing positive emotion in farm animals, and indicate future directions of research and practical application.

S19.4 Positive affects in lambs: appeasing effects of stroking

Sophie Hild, Inra
Marjorie Coulon, Delphine Briand, Raymond Nowak,
Xavier Boivin

Previous studies suggest that early gentling of artificially-fed lambs increases the animals' affinity for their caretaker, with an appeasing effect of the familiar human in social isolation. Yet, the animal's response during gentling has not been described, particularly regarding previous experience of it.

Ewe-lambs were submitted either to the presence of a female caretaker (N=16), or to gentle stroking by this caretaker (N=16). Treatments started from birth in sessions of 6 min, 3 times a day and decreasing to 3 times a week over 2 months. Lambs were then submitted for 9 min to 1) stroking by their familiar caretaker, 2) her simple presence, at one-week interval and in randomized order.

We found that all animals, particularly those used to stroking, showed human-oriented behaviours (e.g. contact seeking). Compared to simple human presence, stroking induced an overall decrease in general activity and a decrease in heart rate and sympathetic activity. Vagal activity, reflecting a resting state, decreased with gentling in lambs used to stroking and increased in naive lambs.

We conclude that gentling seems to have appeasing effects on lambs used to human presence, particularly if the experience is new to them.

S19.5 How to assess positive emotions in pigs

Inonge Reimert, Wageningen University
T. Bas Rodenburg, Bas Kemp, J. Elizabeth Bolhuis

Good welfare of farm animals is in the interest of farmers, society and animal welfare scientists. Good welfare means, among other things, the experience of positive emotions. The question is how do we know whether an animal is experiencing positive emotions? Emotions are considered to be composed of behavioural, (neuro)physiological, cognitive and conscious components. The last component has not been proven to exist in animals yet. The other components, however, can and have been used to assess emotions in animals.

We investigated the behavioural component, because this is the most convenient one to use on farms. Experiments with pigs confirmed that play behaviour and bark vocalizations are behavioural indicators of positive emotions, and tail wagging could be a possible new indicator of positive affect in pigs. In addition, we also found that play can lead to play in other pigs, thereby likely spreading the positive emotional state, a process called emotional contagion. This could lead to better welfare for the whole group and not only the individual animal. Moreover, nosing behaviours also seem to play a role in good welfare.

Symposium 20: Animal sentience and welfare:
What can ethology offer?

S20.1 Beastly bias - species choice, legislation and animal welfare.

Robert Hubrecht, UFAW

Legislative controls on animal species used in research usually indicate which species are protected and may give guidance on species choice. However, there is little consistency; US and EU regulations differ greatly on the species protected. Scientific reasons, or availability usually determine species choice, but animal welfare based regulations may also apply, eg, European legislation requires that ‘animals with the lowest capacity to experience pain, suffering, distress or lasting harm that are optimal for extrapolation into target species’ be used. Societal reasons can also prevail. During ethical review some species can be favoured and UK legislation requires special justification for the use of non-human primates equids, dogs and cats. The scientific rationale for these choices is often weak. Criteria used to argue for preference such as encephalisation, complexity and behaviour are not reliable indicators of sentience and there is no evidence that pain perception varies. Legal controls need to take account of public views, but these may not reflect scientific knowledge. Legislators regulators and researchers making species-choice decisions need to be aware of social issues, but also should be as explicit as possible about their reasons for considering that one species would suffer more than another in a particular study.

S20.2 What does it take to be sentient?

Victoria Braithwaite, Penn State University

Determining whether non-human animals are aware and have the capacity for subjective experiences is a difficult task, and some have argued that it is an impossible one. Yet, with a greater understanding of both brain and behaviour in a growing number of animals, we now appear to be approaching a position where we can empirically address animal sentience. To move forward we need to reconcile what we mean by sentience; there are many definitions, but too often these are confused or conflict one another. Thus we need to develop a common vocabulary to ensure that we understand and agree what we are addressing. We should also recognize that the task will span different disciplines and so will need active participation and dialogue among researchers from relevant fields.

In this presentation, I will propose a framework that will describe key neural and behavioural components that are needed for animals to be aware, and I will then suggest a comparative approach that allows us to address this in different animal species.

S20.3 Behavioural integrity - an ethological concept of animal welfare

Hanno Wuerbel, University Of Bern

Although concerns about animal welfare are based on the assumption that (some) animals are sentient and thus capable of suffering, the scientific study of animal sentience and feelings has remained controversial. However, even if we were able to assess animals’ feelings, it is unclear how this would help us in assessing animal welfare. Is good welfare the absence of suffering, a fair balance between states of suffering and pleasure, or constant pleasure? I will argue that even if direct measures of feelings were available, we would need some criterion of “behavioural integrity” to determine animal welfare. Behavioural integrity refers to both the naturalness of the animals’ behavioural repertoire and the normality of its expression. Much of early days applied ethology devoted to developing welfare-friendly housing systems for farm animals was implicitly based on criteria of behavioural integrity. If defined in terms of (i) behaviour that is strongly internally motivated and (ii) behavioural responses for which eliciting stimuli are likely to be present in the animal’s environment, behavioural integrity represents an ethologically justified and ethically valuable concept of animal welfare, and it relieves ethologists of solving the ‘hard problem’ of consciousness.

S20.4 How valid is the ‘naturalness’ of behaviour as a basis for judging animal welfare?

Marian Stamp Dawkins, University Of Oxford

The extent to which an animal performs ‘natural’ behaviour is often seen as a criterion of good welfare (for example, it is one of the ‘Five Freedoms’ that are widely used in drawing up animal welfare legislation). Ethology, with its emphasis on the adaptiveness of behaviour and the study of animals in the wild, has therefore assumed a central role both in the assessment of welfare and in suggesting improvements in the form of ‘enrichments’ to the environments of animals in farms, zoos, laboratories and peoples’ homes. The emphasis on natural behaviour also finds resonance with non-scientists, who often assume that what is ‘natural’ and ‘free’ and outside must be better for welfare than any alternatives. The basis of these claims and the hidden assumptions underlying them will be critically examined with a view to clarifying how animal welfare legislation should be formulated in the future.

S20.5 Animal sentience - a critical examination of the extent and limits of empirical investigations of consciousness

Liz Paul, University Of Bristol

Mike Mendl

How widely is animal sentience – the capacity for conscious feelings and experiences – distributed across the animal kingdom? Although this question is one which has generated interest amongst generations of ethologists, attempts to answer it experimentally have usually been received with deep suspicion. The default position is that consciousness is private, inaccessible to observation and measurement, and therefore scientifically intractable. Our aim is to re-consider this default approach, not by arguing against it, but by suggesting that although the private nature of first-person perspectives on conscious processes means that there is a definitional bar to their direct investigation, this should not completely prevent consideration of consciousness as an evolved, material process (i.e. not ephiphenomenal or metaphysical). Taking the pragmatic correlates-of-consciousness approach now common in perceptual and cognitive neuroscience, it is possible to argue that, despite the private nature of conscious processing, human beings also can be said to be conscious in the sense of being able to report on their phenomenal experiences. Detailed information exists concerning the types of information processing that is “conducted consciously” in humans, and we suggest that it will be informative to investigate whether and in what forms similar types of processing can be observed in animals.

S20.6 Can we infer pain in crustaceans from behaviour experiments?

Robert Elwood, Queen’s University Belfast

Nociception is the ability to detect and respond to noxious stimuli by reflex reaction. No aversive feeling or experience of pain is suggested. For pain to be inferred various criteria should be fulfilled. I report on several experiments on crustaceans involving discrimination avoidance learning, prolonged rubbing and motivational trade-offs. The responses are more complex and prolonged to be explained by nociceptive reflex. When shore crabs are offered a choice of dark shelters in a brightly lit arena they swiftly learn to avoid one that is paired with shock. Prawns show prolonged rubbing of antennae treated with chemicals associated with pain in vertebrates and this is reduced with local anaesthetics. Hermit crabs trade-off their requirement for quality shells and avoidance of shock and those receiving shock show a long-term motivational change with respect to their current shell. They are also more reluctant to leave a shell in which they are shocked if exposed to odours of predators. These findings cannot be explained by reflex responses and instead are consistent with pain. I also note the reluctance to accept evidence on invertebrates that would be accepted as showing pain in vertebrates.

Symposium 21: Comparative cognition: shared and unique solutions for special behaviour

S21.1 From egocentric views to spatial cognition: multiple pathways to behaviours.

Antoine Wystrach, University Of Sussex

The many different approaches to spatial cognition have left theoretical gaps when trying to compare across species. For instance, categorising spatial behaviour as being egocentric (taxon system) or allocentric (locale system) is often used to draw a line between the cognitive abilities of invertebrates and vertebrates. Here I regroup ecological, behavioural and neuroethological knowledge from insects to humans and propose a broader picture of spatial-cognition. Rather than an egocentric vs. allocentric, a more ecologically relevant segregation concerns the recognition and use of scenes vs. individual objects. These two systems seem to have evolved for different reasons. On the one hand, scene recognition enables discrimination of locations and directions by encoding salient and stable visual elements across the visual field, independently of their individual recognition. Scene recognition enables accurate and robust navigation and seems to be shared by most visually guided animals. On the other hand, object recognition evolved in some animals — for reasons other than navigation — specifically for recognising relevant objects that can be found at different locations. Object recognition can nonetheless serve navigation if a known object is in sight. Because of their early separation and divergent function, I argue that those two systems are based on different visual input and leads to different spatial behaviours, shedding light on the similarities and differences across species.

S21.2 Using insects to understand the minimum cognitive requirements for route navigation

Michael Mangan, University Of Edinburgh

Given that many animals face similar challenges in moving through their environment, it is no surprise that we see convergent navigation strategies. One such behaviour pattern, that can be observed in many animals, such as bees, pigeons and daydreaming humans, is the use of habitual idiosyncratic routes when navigating through familiar environments. The world knowledge of experienced ant foragers is manifest in such habitual routes, with ants being existence proof that small brains can produce exquisitely efficient, robust navigation in complex environments. New technologies now allow us to quantify the sensory information available to ants as they navigate, this has been useful in reducing the influence of anthropomorphic assumptions about available cues and likely mechanisms. We now are

building a picture of contextually organised procedural route memories that tell an ant what to do, not where it is. Ants can thus perform complex habitual routes, without the need for waypoint laying or place recognition, using visual information extracted from the coarse layout of the panorama, rather than detailed information about specific landmarks. I will suggest that these mechanisms might represent useful hypotheses for aspects of route navigation in larger brained animals.

S21.3 Egocentered strategies for spatial reorientation by geometry in avian species

Tommaso Pecchia, CIMec Centre for Mind/Brain Studies, University of Toronto

Avian navigation has fascinated researchers for more than a century. Seminal contributions from semi-naturalistic experimental settings have shown that efficient visuo-spatial processing underlies several local navigation abilities in aves. Homing pigeons rely on a flexible representation of the visual landmark topography to navigate over familiar terrains. Food-storing birds extensively rely on visual cues for accurate food-cache recovery. Small-scale laboratory studies have further deepened our understanding of spatial representations in avian species. A still lively debated issue relates these studies to the question of whether and how birds encode geometric cues (metric and sense) to reorient themselves in an environment. A large body of converging evidences based on small-scale spatial tasks suggest that birds are endowed with mechanisms dedicated to the analysis of the environmental geometry for spatial reorientation. Recent laboratory studies in arrays of discrete objects from our laboratory suggest that both a precocial and an altricial bird achieve efficient geometric reorientation by relying on purely egocentered strategies and representations. These studies suggest intriguing commonalities between navigation mechanisms among distantly related animal species.

S21.4 Combining memories in spatial behaviour: commonalities among diverse species

Anthony McGregor, Durham University
Yutaka Kosaki, Joe Austen

Spatial behaviour relies on the association of environmental cues with actions or consequences. When two or more cues signal the same outcome, theories of associative learning most commonly predict that learning based on one of the cues will restrict learning based on the others. Although there are demonstrations of this cue competition in spatial learning, demonstrations of immunity to competition

are relatively common. Some studies have even shown opposite effects, known as potentiation and augmentation, in which the presence of one cue (A) in combination with another (X) enhances learning based on X when it is tested in the absence of A. These effects have been shown in species as diverse as ants, rats, Clark's nutcrackers, and humans. Here we demonstrate potentiation of learning a goal location in rats based on one set of cues, provided by the walls of the arena, by the presence of another, a discrete landmark. We show a similar augmentation effect in humans using similar cues. In both cases we show between-cue associations can account for the findings, but argue that perhaps these associations are unique to spatial behaviours.

S21.5 A comparative analysis of constituent processes in human and rodent spatial navigation

Derek Hamilton, University Of New Mexico

The ability to navigate from one location to another is present in all animals, and diverse behavioral strategies have evolved in the service of this capacity. The most commonly studied form of navigation in mammals is termed place navigation, which refers to the process of navigating to a particular location (e.g., a goal) based on its spatial relationship to a constellation of external stimuli located some distance from the goal location. Laboratory tasks developed to measure place navigation, such as the Morris water task for rodents and the virtual Morris water task for humans, have been central to advancing our understanding of the behavioral processes, neural circuits and neurobiological processes involved in spatial navigation. In these tasks subjects are required to navigate to a hidden escape platform in a circular apparatus (pool or virtual pool) surrounded by a constellation of distal visual cues. Because the apparatus is spatially ambiguous, a commonly held belief is that performance in these tasks is exclusively based on learning where the goal is located in the distal cue frame of reference. This view has had a profound impact on how researchers have conceptualized the meaning of behavioral data, related physiological phenomena (e.g., place cells) and the function of neural circuits involved in navigation. I will present data obtained in rats and humans that strongly question this standard view, by showing that distal visual cues provide orientation information and disambiguate the otherwise ambiguous apparatus reference frame, but are not used to identify precise spatial locations within the distal cue reference frame. Data demonstrating corresponding dissociations in the neural circuits involved in navigation controlled by distal cue and local apparatus reference frames will also be presented. The broad conclusions to be drawn are 1) that the privileged status attributed to distal cues in the control of navigation is not accurate, 2) there is a major, if not primary, function for the

spatially ambiguous local apparatus reference frame in navigation, 3) control by distal cue and local apparatus reference frames can be dissociated behaviorally and neurobiologically, and 4) the overall pattern of behavioral outcomes and the neural dissociations associated with them hold considerable generality.

S21.6 Vibrissal active sensing during locomotion as a window into attentional processing in the rat

Kendra Arkley, University Of Sheffield
Robyn Grant, Ben Mitchinson, Tony Prescott

During exploration, rats make rhythmic back and forth sweeps of the macrovibrissae, or whiskers, to sample the environment around their snout and head. This behaviour, known as 'whisking', is important for object recognition, maze navigation, jumping, and many other activities. Here, we advocate that the whiskers are used by the animal to attend to salient areas in its local environment, and furthermore that the physical loci that the macrovibrissae occupy at each instance signifies where the animal's spatial attention lies. Using high-speed videography, we were able to consecutively examine the whisking and locomotion behaviour of rats trained to run laps of an arena. Rats locomoting on smooth floors 'looked-ahead' into space with their whiskers, such that, faster running speeds were correlated with greater head lift, and whiskers protracted further in front of the snout. This look-ahead strategy reflects a change in attentional state, with the animal opting to focus on the direction of travel, thus aiding collision-avoidance. When locomoting on an uneven 'holey' floor, rats were forced to scan ahead with their whiskers for safe foot placements, suggesting the movement and position of the whiskers may actively guide the placement of the fore-paws.

Symposium 22: The cognitive continuum: filling in some of the gap between humans and other species

S22.1 Conceptual Behavior, Inference, and Optimal Molding in Human and Non-Human Animals: A Comparative Theoretical Investigation

Ronaldo Vigo, Ohio University
Andrew Halsey

With a simple classification experiment, Smith et al. (2004) showed that there are significant differences between the concept learning performance of Rhesus monkeys and humans with respect to a key family of categorical stimuli consisting of four objects defined over three binary dimensions. In what follows, we propose that these differences may be best explained and predicted using categorical invariance theory (CIT;

Vigo, 2009a, 2011a, 2011b, 2012). CIT characterizes an organism's ability to form a concept from any categorical stimulus as a function of the structural complexity of the stimulus and the pattern detection capacity of the organism. Based on this characterization, we introduce two quantitative indices, a pattern detection index and a conceptual-space index, that provide a potential standard for understanding and measuring on a continuum the inductive (i.e., concept formation involving dynamic categorical stimuli) and deductive (i.e., concept formation involving static categorical stimuli) capacities of various species of animals. We measure deductive capacity by focusing on the learnability of the "atoms" of deductive reasoning (i.e., the modal concepts; Vigo, 2009b, 2009c). Finally, to supplement our theoretical framework, we propose and discuss potential standard empirical protocols for testing the conceptual capacity of different species of animals including bottlenose dolphins and dogs.

S22.2 Additional Studies of Exclusion in Grey Parrots

Irene M. Pepperberg, Harvard University

Grey parrot abilities for visual inferential reasoning by exclusion were tested in two experiments. The first replicated a study of Mikolasch et al. (2011), which in turn replicated that of Premack and Premack (1994) with apes, to learn if our subjects could succeed on this task. Here parrots watched an experimenter hide two equally desirable foods under two separate opaque cups, surreptitiously remove and then, in view of the birds, pocket/eat one of the foods, leaving birds to find the still baited cup. The experiment contained controls for various alternative explanations for the birds' behavior, but birds might still have avoided a cup from which something had been removed rather than specifically tracking the eaten food. Thus, in the second experiment, some trials were run with one food slightly more preferred than the other, during which two items of each type were hidden and only one of the items were removed from one cup. Sessions also included Experiment 1-type trials to see if birds tracked when and when not to use exclusion. Thus birds would be rewarded for attending closely to all the experimental aspects needed to infer how to receive their preferred treat. Three of four birds succeeded fully.

S22.3 Rational Rats: Causal Inference and Representation

Aaron Blaisdell, University Of California, Los Angeles

David Hume posed a dilemma: How do we derive cause-effect relationships in the absence of direct causal perception? His answer was that knowledge of the causal texture of the world was merely an

inference (or illusion) derived from observed statistical regularities. Recent challenges from Philosophy, Statistics, and Psychology argue that we can go beyond the information given (i.e., contingency) by dissecting cause-effect relationships using our own actions (i.e., interventions) on the world. I will present evidence that like humans, rats can a) build causal models (i.e., causal maps) of the world using associative processes; b) derive causal inferences from causal maps and their interventions on them; and c) can use imagery to fill-in missing details of the world that are expected but hidden from perception. I also reveal some limitations in inferential capabilities of rats. These experiments raise important questions about the interface between learning and cognition.

S22.4 Calculating priority: what shall I do next?

Robert Biegler, NTNU
Gerit Pfuhl

Franklin and Ferkin (2006) wrote that ‘Every autonomous agent [...] spends its waking life in the moment-to-moment responding to the only question there is: “What shall I do next?” We propose that this decision can be made by calculating the priority of each behavioural option. In very simple organisms, such as some bacteria, the priority of each possible action is simply proportional to the magnitude of the expected outcome. More complex rankings can be achieved by multiplying magnitude first with the motivation related to expected outcomes, then the probability of achieving a desired outcome (feasibility), and finally urgency. This computation may be carried out within a hierarchical system of goals that differ in specificity. We propose that simple cognitive systems and more powerful systems share the most specific and the most general levels of the hierarchy, and that computational power is added by filling in intermediate levels through learning and developmental mechanisms.

S22.5 Perceptual simulations as a fundamental cognitive mechanism

Mathias Osvath, Lund University

The idea of the brain, or the mind, as essentially a prediction-making simulator has been advanced by numerous theorists and researchers. Despite this, studies on planning abilities in corvids and great apes, has been treated with skepticism. Instead of agreeing with that the results can be explained by perceptual simulations of potential events – as the mechanism works in humans – the critics rely on associative learning mechanisms (even if such mechanisms do not fit the data). This approach is taken because learning mechanisms are regarded as “lower on the psychological scale”. However, perceptual simulations

could be a fundamental mechanism ubiquitous among birds and mammals. The simulations are mainly based on the perceptual and hippocampal architecture of the brain, which are well-developed in these animals. Such simulations fit neatly into an evolutionary account where recent parts of the brain play tricks on the older regions: perceptual simulations are treated as “the real thing” by the motivational system, which in effect becomes directed towards the future. This mechanism pervades human behaviour and is the seat of many skills, both in the social and the physical domain. I will present results that support that this probably is the case for other species as well.

S22.6 Mirror self-recognition in the cleaner wrasse

Masanori Kohda, Osaka City University
Takashi Hotta, Hirokazu Tanaka, Tomohiro Takeyama,
Lyndon Jordan

Mirror self-recognition (MSR) is documented in some higher vertebrates such as apes, elephant, dolphin and magpie, that have large cerebrum and high social intelligence. These animals of MSR typically progress following three phases of behavior when facing a mirror: (i) social responses, (ii) repetitive exploration behavior for mirror reflection, and (iii) recognition of mirror reflection as self where we can examine whether they can do MSR by mark test. Recent studies reveal that at least some social fish, e.g. the cleaner fish *Labroides dimidiatus*, show enhanced cognitive abilities such as self-control and transitive inference, which might be associated with self recognition, but researchers still images that understanding of self or MSR is beyond the fish ability. Here we show a successful MSR study with mark test using the cleaner wrasse, with striking similarity in the progression of the three phases. During mark test, fish took position in front of mirror to see the mark (visible only in mirror image) more frequently than sham-mark test. Furthermore, 3 of 4 individuals scraped its marked throat correctively on the bottom as if to remove ‘ectoparasites’, exclusively after observing the mark in mirror reflection. These results provide the first evidence of MSR in fish.

Symposium 23: Comparative studies of social learning, cognition and culture

S23.1 A phylogenetic perspective on social learning: Humans, apes, and monkeys compared

Lydia Hopper, Lincoln Park Zoo

Only by replicating the same methodological design with multiple species can we gain a phylogenetic perspective on primate social cognition. To test both ape and monkey species, and to enable comparisons with humans, I have studied human and nonhuman

primates following the same protocol. To study nonhuman primate social learning specifically, through a combination of group 'open-diffusion' tests and controlled 'ghost' conditions, I have sought to gain a perspective on whether certain species are capable of social learning and, if so, what mechanisms typify this learning. Following this rationale, studies with a bidirectional task revealed that both ape (*Pan troglodytes*) and monkey (*Saimiri boliviensis*) species were only able to operate the task themselves after observing a trained model, but not when presented with it without instruction. Not only did these primates learn a solution but, in a group setting, they also matched the specific method used by their conspecific model. Comparisons between these species, along with human children and *Cebus apella* also tested with comparable methods, allows us to gain a greater understanding of how social learning mechanisms are employed differentially in response to task complexity and how these mechanisms relate to cognitive abilities more generally.

S23.2 Social Diffusion of Tool Use In Chimpanzees and Children

Andrew Whiten, University Of St Andrews
Christele Borgeaud, Andrew Whiten

Behavioural tradition has been an active topic in animal behavior since the renowned Japanese macaque studies of half a century ago, yet controlled field experiments to clearly identify social learning began only recently. We provisioned wild vervet monkeys with two bowls of maize corn died different colours, with one initially made strongly distasteful using bitter mountain aloe. Over four sessions, 109 monkeys in four groups learned to take one colour and avoid the other. Four months later we offered both coloured foods untreated, just when a new cohort of infants was ready to take their first corn. Vertical social learning was demonstrated strikingly, with 27/27 infants taking only the coloured alternative eaten by their mothers. Just one infant ate the formerly distasteful coloured food, after its low ranking mother did. Ten males migrated from groups where one colour was favoured to a group where the opposite colour was eaten, and all but one conformed directly to the new group colour preference despite their countervailing prior personal experience. The one exception was a male who rapidly achieved high rank on immigration to his new group. These results demonstrate that potent social learning and conformity can shape behaviour in the wild.

S23.3 Model-based transmission biases in chimpanzees and children; implications for understanding the evolution of human culture

Rachel Kendal, Durham University

Lara Wood, Emma Flynn

Social learning alone cannot explain the stability and diversity of human and non-human culture; the involvement of cognitive and ecological factors must be considered. Cognitive transmission biases, guide what, when, and from whom individuals acquire valuable social information and allow them to avoid the costs associated with asocial learning and unbiased social learning. We review several of our recent empirical studies, regarding model-based transmission biases (influencing who is copied), with young children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). The studies trace the individual, and social, learning of differing methods enabling the extraction of rewards (food for chimpanzees and stickers for children) from novel extractive foraging tasks. We use a variety of techniques including controlled dyads of trained-model and naïve-observer as well as naturalistic group-level contexts (open diffusion) with or without trained-models of specified characteristics. Such comparative work may explain similarities in cultural patterns between species, while potentially illuminating ancestral features of humanity's adaptations for culture and the selection pressures that shaped them. In turn, this should highlight whether certain transmission biases are unique to humans and whether these may explain humanity's uniquely strong reliance on culture.

S23.4 Observational learning of tool manufacture in children and chimpanzees

Elizabeth Price, Centre For Behaviour and Evolution, IoN, Newcastle University
Andrew Whiten

Although many species use tools, there is little evidence of the cumulatively complex and constructive technologies so common to human tool use. Despite numerous studies addressing social learning differences across species, relatively few have directly compared how humans and other animals learn to construct tools. In comparison to a study completed with chimpanzees, we investigated whether 2.5 – 4.5 year-old-children could learn to build and modify tools from video footage of an adult model, and further, how much information they required to do so. We found that like chimpanzees, children were able to observationally learn to combine two tool components together. Moreover, they persisted in using the socially learned method two-weeks later even when it was no longer necessary, underlining the potency of socially learned information. Unlike chimpanzees, children were also able to socially learn a more complex method of tool modification, despite an inability to learn the technique independently. We propose that it is their propensity to anticipate and seek functional information in a potential demonstration that allows

children to learn the complex technologies common in human cultures.

S23.5 Automatic Imitation In Capuchin Monkeys

Eoin O'Sullivan, University Of Stirling
Christine Caldwell

In comparative psychological research, imitation is widely regarded as interesting specifically because it is considered to require complex cognitive processes restricted to a few primate species. Simpler forms of imitation (i.e. automatic imitation, social facilitation, and contagion) receive considerably less attention in the literature, presumably deemed of secondary empirical importance. However, these seemingly simple behaviours have been found to facilitate the transmission of behaviours in a wide range of species. Also, recent studies report that automatic imitation plays an important social role; humans and capuchin monkeys (*Sapajus apella*) prefer individuals that have previously imitated their actions. Many studies of imitation assume an evolved, innate cognitive system facilitates imitative processes; however, support is growing for an alternative view that suggests sensorimotor experience (performing and observing the same action) may be essential for the development of imitative ability. In this talk, these automatic, simple forms of imitation will be discussed in the light of this developmental hypothesis. An on-going project with capuchin monkeys aims to specifically test predictions of this approach and data from these studies will also be presented.

S23.6 Causes and consequences of innovation and social learning in wild vertebrates

Alex Thornton, University Of Exeter

Despite major ecological and evolutionary implications, the emergence and spread of novel behavioural patterns through animal group remains poorly understood. The majority of empirical work to date has focused on captive animals, and thus tells us little about the adaptive value of innovation and social learning in the wild, while the learning mechanisms revealed in laboratory experiments may not reflect those operating in nature. Our studies of meerkats and corvids suggest that in vertebrate societies different categories individuals may be responsible for the emergence and subsequent propagation of novel skills. In meerkat groups, the inability of subordinate males to compete with dominants, coupled with their need to exploit new opportunities during dispersal attempts, may drive them to seek out solutions to novel problems. Conversely the tendency of young individuals to learn from others rather than solving novel problems

themselves leads to profound developmental consequences. Contrary to common suggestions, our research indicates that innovation and social learning are not intrinsically cognitively demanding and instead depend primarily on persistence, attention and behavioural inhibition.

S23.7 Cultural transmission of lobtail feeding in humpback whales

Luke Rendell, University Of St Andrews
Jennifer Allen, Mason Weinrich, William Hoppitt

The nature and extent of cultural transmission in wild animal populations is important to understand – because a comparative analysis based only on species amenable to experimental manipulation will be flawed – but is inherently difficult to pin down. Claims that culture plays a large role in the behavioural development of many cetaceans are important to investigate but hard to substantiate because of the difficulties of experimental manipulation. A way forward is offered by the development of network-based diffusion analysis (NBDA), which quantifies how well social network structure explains the observed spread of a given behaviour within a population. We applied NBDA to a 27 year dataset on the spread of lobtail feeding, a behavioural innovation first recorded in 1980, through the population of humpback whales (*Megaptera novaeangliae*) that summer around Stellwagen Bank, USA. Support for models with a social transmission component was between 6 and 23 orders of magnitude greater than for models without social transmission, depending on the form of NBDA model used. Humpbacks are already known to have culturally transmitted song patterns, so our results show that this species relies on cultural transmission for behavioural development in multiple domains, and can maintain multiple independently evolving traditions in its populations.

S23.8 Social networks and information transmission in two corvids

Christine Schwab, University Of Vienna, Austria
Ipek Kulahci, Daniel Rubenstein, Thomas Bugnyar

Ravens (*Corvus corax*) and crows (*Corvus corone*) exhibit a complex and multilayered social system. The reproductive and socially most closely bonded unit is represented by the territorial and monogamous long-term pair. Apart from this unit raven and crow sociality consists of non-breeder flocks that are open groups and characterized by high degrees of fission-fusion dynamics through which individuals may repeatedly interact with numerous conspecifics whereas they may only rarely encounter others. This allows individuals to establish social relationships that may range from

highly valuable ones to neutral to being particularly agonistic, leading to a distinctive social structure of the flock. We make use of these social prerequisites to investigate social learning strategies in these two corvid species. Through observing interactions between individuals we can create social networks of the group in different social contexts which represent the tool to experimentally ask which of these contexts, and hence, which of these structures mainly promote the transmission of a socially learned feature through the animals' group. We discuss results with regard to how they may help to determine to what extent social learning strategies may be context- or species-specific adaptations.

S23.9 Social learning in reptiles

Anna Wilkinson, Messerli Research Institute, Vetmeduni Vienna
Anna Kis, Julia Mueller-Paul, Ludwig Huber

The ability to learn from the actions of another is adaptive as it is a shortcut for acquiring new information. However, the evolutionary origins of this trait are still unclear. Here we present a series of experiments which investigate social-learning abilities of reptiles. We demonstrate that the red-footed tortoise (*Chelonoidis carbonaria*) can learn to solve a previously insolvable task by observing the actions of a conspecific. Further, we will present evidence of imitation in the bearded dragon (*Pogona vitticeps*). Thus our findings reveal that at least some reptile species are capable of social learning that is as complex as that observed in mammals and suggests that the mechanisms underlying social learning are likely to be of ancient origin.

S23.10 Pavlov's bees: why is social learning so widespread?

Ellouise Leadbeater, Institute Of Zoology
Aurore Avargues-Weber, Lars Chittka, Erika Dawson

Recent debate has questioned whether social learning truly deserves the label "social". Solitary animals can learn from others, and comparative studies have revealed that good social learners are usually also typically good at learning individually. Although social species may be adapted to respond to social cues, it has been proposed that the underlying learning processes themselves may be simply associative processes rather than specializations for social life. Yet, the nature of such associations is rarely identified. Here, I will present empirical work that specifically deconstructs learning by observation into first- and higher-order associations, in a bumblebee model system. Bumblebees are highly social, but these findings demonstrate why learning by observing others

explore, rather than by attaining reward or punishment, is open to any animal that can integrate two learnt associations. We place a complex social learning phenomenon within a simple Pavlovian framework that is common to social and solitary species alike.

S23.11 Social Learning, Scrounging, and the Spread of New Foraging Behaviour

Alice Cowie, University Of St Andrews
Kevin Laland, Will Hoppitt

Foraging in groups can provide scope for social learning of new skills. At the same time, it can create opportunities for naive animals to scrounge food produced by competent ones, potentially reducing their tendency to express and/or learn new skills. Using five groups of eight captive budgerigars, *Melopsittacus undulatus*, we examined the effect of these opposing strategies in influencing the spread of novel task-solving behaviour. We varied social learning opportunities by inserting task-competent 'demonstrator' birds into some groups at the start of trials, and manipulated scrounging opportunities by loading some tasks with large quantities of food and others with small quantities.

We found that when birds reaped large rewards from scrounging, they were less likely to express new solving skills. Any positive influence demonstrators exerted on the spread of solving behaviour was seemingly mitigated by the fact that their 'demonstrations' (task solves) not only provided increased scope for social learning, but also for scrounging.

However, upon removal of the demonstrators (typically a group's most proficient and prolific task solver), we found that scroungers were able to switch to become producers. It would seem that heavy scrounging may in fact promote the underlying learning of new skills in budgerigars.

Symposium 24: Developmental programming: integrating brain, physiology and behaviour

S24.1 Parental Effects and the Developmental Origins of Phenotypic Variation

Sinead English, University Of Oxford
Tobias Uller

The potential for variation in parental morphology, physiology, and behaviour to have long-term effects on their offspring has attracted substantial interest among behavioural biologists. Yet, the adaptive significance of these parental effects remain poorly understood – very few models exist and empirical data are often inconclusive. In this talk I outline a general framework for modelling the adaptive evolution of parental effects. I show the importance of environmental

fluctuation and the mechanisms by which organisms access, accumulate, and incorporate information about their environment into development. Using meta-analysis, I show that 'adaptive developmental programming' via parental effects is less common than typically assumed, in contrast to the strong, direct effect of offspring environment. I end by outlining conceptual and methodological shortcomings that may explain these patterns and point towards potential solutions.

S24.2 Understanding the long-term effects of developmental stress in the brain: a functional genomic approach

Valeria Marasco, University Of Glasgow
Pawel Herzyk, Jane Robinson, Karen Spencer

Developmental stress can induce long-term changes into adulthood. The sensitivity of developing individuals to stressful conditions can vary across differing developmental stages, producing a variety of phenotypes in later life. Although the mechanisms remain unclear, accumulating evidence suggests that such effects are mediated via programmed gene expression changes in specific brain regions primarily affected by the actions of glucocorticoid hormones. We examined the long-term global effects of pre- and/or post-natal exposure to glucocorticoids on both hippocampal and hypothalamic transcriptomes into adulthood using the Japanese quail. We experimentally elevated glucocorticoid concentrations *in ovo* and/or in the endogenous circulation of hatchlings. Our results showed that the effects of developmental glucocorticoids were tissue-specific, i.e. stronger in the hippocampus than in the hypothalamus. In the hippocampus these effects appeared to be developmental stage-dependent, with pre-natally stressed birds showing the highest gene expression changes in comparison with the controls. However, expression responses in some of these "pre-natal stress sensitive" genes were attenuated or reversed in birds that experienced the combined pre- and post-natal stress treatments. These data suggest that interactions between the stimuli experienced during the pre- and post-natal development can significantly contribute to determining the programming effects of glucocorticoids in the adult phenotypes.

S24.3 Singing and the stressed brain: early developmental stress and the zebra finch (*Taeniopygia guttata*) song control system

Laura Carruth, Georgia State University
Mahin Shahbazi

Australian zebra finch (*Taeniopygia guttata*) song control nuclei form by 10 days post-hatch and their

development is influenced by various factors including early life stress exposure. Developmental stress alters song nuclei size and song quality in many songbird species, suggesting a direct link between brain and behavior. Although the mechanisms behind these effects are unknown, elevated levels of corticosterone (Cort), acting via glucocorticoid receptors (GR) within song nuclei, may play a role. We have investigated the effects of early Cort-treatment on song nuclei development and singing behavior in adulthood. The distribution, quantity, and subcellular-localization of GR-immunoreactive (GR-ir) neurons were determined in the brains of juvenile and adult males. Distribution was broad and included two song nuclei. There were, however, significant differences in the overall number of GR-ir neurons and their subcellular localization between the two ages. Next we examined if early Cort treatment reduces song quality and song nuclei size in adult males. The treatment decreased song similarity and accuracy and resulted in poorer copies of tutor song, but did not alter mean amplitude or song duration. This suggests a potential role for Cort in mediating adverse effects of early stress and highlights the developmental plasticity of the zebra finch brain.

S24.4 Early-life environment, serotonin transporter genotype, and behavioural profiles in mice

Vanessa Kloke, Department Of Behavioural Biology
Norbert Sachser

Stressful early-life experiences can profoundly affect the behavioural profile. In mice we demonstrated that offspring of mothers living in a threatening environment during pregnancy and lactation, show elevated anxiety-like behaviour later in life. The effects were hypothesized to be primarily mediated by maternal behaviour and were modulated by genetic variation of the serotonin transporter (5-HTT) gene. In a follow-up study we compared the role of a threatening to an enriched early environment for the modulation of the anxiety profile in mice varying in 5-HTT genotype. Early-life adversity was simulated by exposing lactating dams to soiled bedding of unfamiliar males (UMB), signalling the danger of infanticide. An enriched early environment was established by communal nesting (CN). The main findings were: Maternal care was reduced in UMB compared to CN dams. UMB offspring showed significantly lower levels of trait anxiety compared to CN offspring, whereas state anxiety levels did not differ. There was a significant main effect of genotype, with highest levels of state and trait anxiety in 5-HTT $-/-$ mice. The findings corroborate that anxiety profiles in mice can be affected by early environmental conditions and 5-HTT genotype. Notably, state and trait anxiety can be affected independently by the early environment.

S24.5 Stress exposure during early life: are there long-term costs?

Britt Heidinger, University Of Glasgow
Katherine Herborne, Francis Daunt, Pat Monaghan

In response to environmental stressors, young vertebrates generally show an increase in glucocorticoid stress hormones (CORT), which alters behavior and physiology to prioritise short-term survival over other traits, including growth. A high level of exposure to CORT in early life can 'program' the development of a phenotype that is generally more stress-responsive, the potential advantages of which come at the expense of longevity. One mechanism that might produce such trade-offs operating across life history stages is the effect of stress exposure on telomere dynamics, which are linked to age related deterioration and lifespan. We experimentally manipulated stress exposure during the early post-natal period (between days 10-22 post-hatching) in a long-lived seabird, the European shag (*Phalacrocorax aristotelis*) and examined the effect on growth rate, stress-responsiveness at fledging, oxidative stress and telomere dynamics. We found clear evidence that early stress exposure results in shorter telomere length at fledging.

Symposium 25: Celebrating 150 years of mimicry research

S25.1 The evolution of imperfect mimicry

Christopher Hassall, University Of Leeds
Heather Penney, Brent King, Kevin Abbott, Jeff Skevington, Tom Sherratt

Nature contains a number of notable examples of exquisite mimicry. Given the observation that natural selection can produce high-fidelity mimics, it is something of a puzzle as to why other species do not evolve such a degree of similarity to their models. There have been a range of hypotheses put forward to explain the evolution of "imperfect mimicry", and here we provide the first phylogenetically-controlled, systematic test of those hypotheses within a single group: the hoverflies (Diptera: Syrphidae). Based on an analysis of 38 species of hoverflies and 10 stinging Hymenoptera that those hoverflies are thought to mimic, we find no support for hypotheses based on (i) differences between the human and avian visual system, (ii) simultaneous mimicry of multiple models, or (iii) kin selection. However, we find a strong relationship between body size and mimetic fidelity that conforms to the predictions of the relaxed selection hypothesis. This suggests that smaller, less profitable prey species are under reduced selection pressure to evolve high mimetic fidelity due to lower rates of predation. We further explore the phenomenon of behavioural mimicry in this group,

finding it to be restricted to only two genera of relatively high-fidelity mimics.

S25.2 Increasing Batesian mimic abundance is not always costly to the model

Candy Rowe, Newcastle University
Melissa Bateson, Craig Barnett

Batesian mimics are parasitic on their models, benefitting from predator avoidance whilst diluting the defence of their models. The cost to the model is thought to increase with increasing numbers of mimics with naive predators learning to associate the warning coloration with growing palatability. However, a state-dependent approach suggests that models may benefit from increasing numbers of mimics because they provide an additional food source for predators, relaxing predation on the model-mimic complex. We tested this prediction using an established protocol using European starlings (*Sturnus vulgaris*) foraging on mealworm prey (*Tenebrio molitor*). We found that increasing the number of palatable Batesian mimics reduced the probability that a model or mimic was attacked, and that the models did not pay a mortality cost of increasing mimic abundance. Consistent with the idea that predatory decisions were mediated by food availability and the energetic state of the predator, we also found that birds ate more prey and took longer to initiate an attack on prey in the model-mimic complex when Batesian mimics were at high density. Our study provides the first direct support for state-dependent models of mimicry, and demonstrates how the mechanisms underlying decision-making can alter selection pressures on models and mimics.

S25.3 Aggressive mimicry in coral reef fish: the fangblenny-cleaner wrasse system

Karen Cheney, University Of Queensland

Aggressive mimicry is defined as the resemblance of a predatory or parasitic species to another species, in order to approach and attack prey or to gain other benefits such as pollination or transportation. One of the most intriguing examples of aggressive mimicry is found on coral reefs where fangblennies closely resemble cleaner fish in terms of colouration and body pattern. Instead of removing ectoparasites from passing reef fish, fangblennies attack fish to remove dermal tissue, scales and small pieces of fins. Here, I will discuss various aspects of this mimicry system, including: 1) the ability of mimics to switch between mimic and non-mimic colours at will, and how fangblennies adopt their mimic disguise depending on the availability of cleaner fish; 2) how changes in the nature of the relationship between participants, due to shifting environmental conditions or population

dynamics, can affect the success of mimics and 3) how avoidance learning by potential victims can destabilize aggressive mimicry systems.

S25.4 Defensive animal mimicry by plants: facts, hypotheses, experiments and questions

Simcha Lev-Yadun, University Of Haifa - Oranim

While defensive plant mimicry by animals is well known, defensive animal mimicry by plants is not. Suggested defensive animal mimicry by plants has two types: direct animal mimicry, and mimicry of cues for animal action. Proposed direct animal mimicry includes: (1) leaves mimicking caterpillars (Miriam Rothschild), (2) insect egg mimicry (Benson, Brown, Gilbert 1975), (3) caterpillar, ant and aphid mimicry (Lev-Yadun, Inbar 2002), (4) bee and wasp mimicry in orchids (Lev-Yadun, Ne'eman 2012). Proposals for cues of animal action mimicry include: (1) leaf variegation mimicking tunnelling (Smith 1986), (2) animal chewing damage (Niemelä, Tuomi 1987), (3) carrion and dung odour (Lev-Yadun et al. 2009). Observations (Campitelli et al. 2008) and experiments (Soltau et al. 2009) have shown that variegation mimicking tunnelling operate indeed. There is a difficulty in distinguishing between mimicry and exploitation of animal perceptual biases (Schaefer, Ruxton 2009) and between defense and simultaneous physiological and reproductive functions. The common notion "no attack equals no risk" is a critical theoretical mistake. Since defended organisms are attacked less than undefended ones, conventional statistics is not appropriate for the interpretation of experiments. Relevant, realistic experimentation and field studies are needed for this overlooked assembly of potential defensive phenomena.

S25.5 Mobbing, mimicry, and alternative guises

Rose Thorogood, University Of Cambridge
Nicholas Davies

Although mimicry is rare in birds, it is a common tactic used by parasitic cuckoos to defeat their hosts' defences and ensure their own reproductive success. Adult common cuckoos are Batesian-like mimics of dangerous hawks; this deters host attacks and facilitates access to their nests. When there, cuckoos lay exquisitely well-matched eggs to defeat the host's ability to detect and reject the imposter. In other cuckoo species, this arms race has extended to the chick, with impressive visual and/or vocal mimicry fooling parents to care for the unrelated cuckoo. But what happens when the host defeats the cuckoo's mimetic tricks? Here we present results from field experiments with reed warbler hosts and the common cuckoo to show that these hosts use social information to learn when it is safe to attack a hawk-like cuckoo.

While mobbing attacks may combat the cuckoo's mimicry, social learning has, in turn, selected for an alternate plumage polymorphism in the cuckoo. Could social learning also select for polymorphisms in other Batesian mimics?

S25.6 Do we understand the evolutionary consequences of mimicry?

Mike Speed, University Of Liverpool

Theories of Batesian and Mullerian mimics focus on change in colour pattern in prey species. In this talk I will argue that the evolutionary drivers and consequences of mimicry cannot be understood unless the evolution of other key traits is also measured. Most obviously we may see change in niche that results from mimetic evolution. Less obvious, but perhaps as important is that mimicry may evolve to help prey shed costs of investment in secondary defences such as toxins. The focus of mimetic coevolution may then not be between colour patterns in mimetic species, but rather coevolution may be focused on variation toxin investment between mimetic species. I will argue that a more comprehensive framework that includes effects of mimicry on niche and toxin investment may reveal important consequences of mimicry for life history traits.

S25.7 The function of vocal mimicry in spotted bowerbirds

Laura Kelley, Anglia Ruskin University
Susan Healy

Vocal mimicry is characterised by individuals learning and reproducing the vocalisations of another species or an environmental sound. Although estimated to occur in approximately 15% of songbirds, the function and acquisition of vocal mimicry is generally poorly understood. We assessed the evidence for several competing hypotheses concerning mimicry in the spotted bowerbird *Ptilonorhynchus maculatus* by determining (1) what sounds bowerbirds mimicked and (2) the contexts in which mimicry was produced. Bowerbirds mimicked more predatory and aggressive species than predicted and the rate of mimicry increased when birds were subjected to human disturbance. We discuss these findings in relation to the proposed function of mimicry in this species and suggest how such mimicry may be acquired.

S25.8 A kind of magic: Divergent ecological selection on a mating trait

Richard Merrill, University Of Cambridge
Chris Jiggins

Traits under disruptive ecological selection that also influence non-random mating facilitate speciation with gene flow. However, the existence of such 'magic traits' in nature has been considered unlikely. Mimicry in tropical butterflies has long been championed as an example of adaptation driving speciation. In *Heliconius*, unpalatable species converge on the same bright warning-patterns to advertise their distastefulness to predators. Closely related taxa often belong to different mimicry rings, and males use colour pattern during mate recognition. Hybrids display intermediate warning patterns that are unlikely to be recognized as distasteful. *Heliconius melpomene* and *H. cydno* are sympatric across Central and northern South America. Using model butterflies we reveal selection against non-mimetic hybrid colour patterns between these species. To our knowledge, these data provide the first explicit experimental evidence of disruptive ecological selection acting on a trait that is also used during mate recognition. In addition, by testing mate preferences in hybrid males we demonstrate a genetic association between mate preference and wing colour pattern. In particular, male preference for red patterns is associated with the locus responsible for the red forewing band. Thus we demonstrate disruptive selection acting on a mating trait that is genetically associated with the corresponding mate preference.

S25.9 Why does life imitate life imperfectly?

David Kikuchi, University Of North Carolina

Batesian mimicry is widely used to illustrate natural selection's power in generating adaptation, yet mimics are often poor replicas of their model. Such imprecise mimicry poses a challenge for evolutionary theory. We sought to empirically evaluate multiple hypotheses for imperfect mimicry. We specifically asked why different species and populations of nonvenomous colubrid snakes vary in the degree to which they resemble highly venomous coral snakes. We found support for four hypotheses: (1) the relaxed selection hypothesis, which holds that there is little selective benefit to refine mimetic resemblance beyond a certain point if the model is common; (2) the sensory limitation hypothesis, which asserts that selection for improved mimicry might not exist if imperfect mimics exploit limitations in predator cognition; (3) the breakdown hypothesis, which posits that imperfect mimicry reflects an adaptive breakdown of mimicry, as when the mimic occurs outside the geographical range of its model and (4) the selective trade-off hypothesis, which maintains that imperfect mimics represent a trade-off between predator-mediated selection favoring mimetic convergence and other agents of selection (e.g., competition) favoring divergence. Clarifying why selection sometimes does not produce remarkable mimicry can provide novel insights into the evolutionary process.

S25.10 Mimicry supergenes: when and why they should exist

Brian Charlesworth, University Of Edinburgh

It was proposed long ago by Sheppard and Clarke that the colour and pattern polymorphisms in the Batesian mimics of species of *Papilio* butterflies represent supergenes, so that the apparent single-locus inheritance observed in these species is in reality due to several very closely linked genes that rarely recombine with each other. Once a mutation establishing a degree of mimetic resemblance has been established in a population, the selective disadvantage of recombinants among variants contributing to mimetic polymorphisms means that only mutations that are closely linked to this primary mutation can spread; in addition, reduced recombination is favoured by selection. There are therefore good theoretical reasons for expecting supergenes with Batesian mimicry, where polymorphisms can be maintained by negative frequency-dependent selection. Surprisingly, the best molecular genetic evidence for a supergene has come from *Heliconius numata*, a putative Mullerian mimic, where selection is not expected to maintain polymorphisms within local populations. Possible resolutions of this paradox will be discussed, and progress towards characterising other mimicry genes reviewed.

S25.11 Dressing local: multi-model Batesian mimicry suggests multiple selective pressures on geographic coloration divergence in *Allobates femoralis*

Adolfo Amezcua, Universidad De Los Andes
Oscar Ramos, Camilo Rodriguez, Iliana Medina, Pedro Yvo Simoes, Mabel Gonzalez, Albertina Pimentel Lima

Predation risk is reduced in Batesian mimickers because their body coloration resembles aposematic animals. To isolate the role of predation from other selective pressures, Batesian coloration should be studied in geographically variable species that co-occur with different toxic models.

We tested whether geographic divergence in body coloration of the diurnal frog *Allobates femoralis* (Af) was correlated with the coloration of sympatric and toxic frog species. We tested for toxicity of each involved species and analysed frogs' coloration assuming the visual systems of potential predators and closely related frogs. Af coloration was closer in a multivariate space to the coloration of local toxic models than to the coloration of other Af populations. Yet the degree of resemblance varied among the elements of the coloration pattern, in decreasing order: yellow-to-red inguinal patches, whitish

dorsolateral lines, and dark dorsal background. Our results suggest the evolution of Batesian mimicry, but also multiple roles for coloration components, perhaps memorable, disruptive and concealing. Interestingly, the mimetic-model resemblance render them indiscernible for avian and lizard predators, but discernible for simulated conspecific receivers.

Altogether, our data are compatible with an scenario of multiple selective pressures on the coloration pattern of a single species.

Symposium 26: Applying the source-filter theory to an integrated understanding of mammalian vocal signalling

S26.1 Do red deer stags use roar pitch to assess rivals?

Maxime Garcia, University Of Vienna, Cognitive Biology Department

Benjamin D. Charlton, Megan Wyman, W. Tecumseh Fitch, David Reby

The voices of human males are disproportionately lower pitched than those of women. Recent studies suggest that this dimorphism in fundamental frequency (F_0) within humans results from both intrasexual (male competition) and intersexual (female mate choice) selection for lower pitched voices in men. However, comparative investigations indicate that sexual dimorphism in F_0 is not universal in terrestrial mammals. In the highly polygynous and sexually dimorphic Scottish red deer *Cervus elaphus*, more successful males give sexual calls (roars) with higher minimum F_0 s, suggesting that high, rather than low F_0 s advertise quality in this subspecies. While playback experiments demonstrated that oestrous females prefer higher pitched roars, the potential role of roar F_0 in male competition remains untested.

Here we examined the response of rutting red deer stags to playbacks of re-synthesized male roars with different median F_0 s, and found that the strength of stags' agonistic responses was not affected by the F_0 of the roar. This suggests that intrasexual selection is unlikely to influence the evolution of roar pitch, at least in this subspecies.

These results indicate that the F_0 of terrestrial mammal sexual calls may be subject to different selection pressures across species. Further investigations on species characterized by different F_0 profiles are needed to provide a comparative background for evolutionary interpretations of sex differences in the human voice.

S26.2 Communicating quality: advertisement and male assessment in an extremely vocal deer

Benjamin Pitcher, Queen Mary, University Of London

Elodie Briefer, Elisabetta Vannoni, Alan McElligott

The source-filter theory allows researchers to make specific hypotheses regarding the anatomy and physiology of a caller and the acoustic parameters of the resulting vocalisations. These vocalisations are likely to reveal information about the age, body-size, physical condition and arousal of the caller. However it is crucial to investigate the perception of this information by receivers in order to determine how selection has shaped the vocal system in question. Fallow deer males (*Dama dama*) vocalise up to 3000 times per hour during the rut. Groans are individually distinctive and also encode the quality of the caller, with lower formant and fundamental frequencies reflecting higher dominance. Males invest a large amount of time and energy in calling and lose up to 25% of their body weight during the rut. Groans reveal this caller fatigue; becoming shorter and higher pitched through the rut.

Using playback experiments we investigated the perception of putative indicators of dominance and fatigue by bucks. Interpretation of the results of this study in the context of the source-filter theory leads the understanding of how intrasexual selection has contributed to shaping vocal communication systems.

S26.3 A newborn's cry is similar across diverse mammalian species

Susan Lingle, University Of Winnipeg

Tobias Riede

Important characteristics of newborn cries, including the structure, behavioural context, and caregiver response, are similar across mammals including humans, suggesting the hypothesis that mechanisms underlying the production and perception of cries have been conserved throughout mammalian evolution. We provide direct support for this hypothesis by showing that mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) mothers respond similarly to newborn cries of diverse mammalian species as to cries of their own species. They approach a speaker playing isolation or distress calls of newborn marmots (*Marmota flaviventris*), seals (*Neophoca cinerea*, *Arctocephalus tropicalis*), bats (*Lasionycteris noctivagans*), other ungulates and humans (*Homo sapiens*), as long as the fundamental frequency (F_0) falls or is manipulated to fall within a species-specific range. They do not approach to control sounds having the same F_0 or to predator sounds.

These results reveal that acoustic characteristics of newborn cries essential for a response by caregivers are shared across diverse mammalian species and suggest that mammalian caregivers share a neural substrate sensitive to these common acoustic features.

Bioacoustic work may move forward by manipulating selected acoustic traits such as F0 to unveil similarities in mechanisms underlying the production and perception of sound across diverse taxonomic groups.

S26.4 Do fundamental and formant frequencies indicate body size among humans?

Katarzyna Pisanski, McMaster University
Paul J. Fraccaro, Cara C. Tigue, Jillian J.M. O'Connor, Susanne Roeder, Lisa M. DeBruine, Benedict C. Jones, Bernhard Fink, Paul W. Andrews, David R. Feinberg

Two questions critical to our understanding of mammalian sexual selection and communication involve (i) which features of the voice indicate physical or perceived body size, and, (ii) to what degree listeners are able to accurately assess size from vocalizations.

Among humans, evidence suggests that intrasexual variation in size is more reliably predicted by formant frequencies (resonances of the supralaryngeal vocal tract) than by fundamental frequency (produced by vibration of the vocal folds). Voice pitch (perception of fundamental and/or harmonics) is thought to confound within-sex size assessment. We conducted a meta-analysis of 46 adult samples, obtained from 17 published studies and 5 unpublished datasets, confirming that formants correlate with height within sexes (men: $r^- = -0.31$; women: $r^- = -0.25$) better than does fundamental frequency (men: $r^- = -0.13$; women: $r^- = -0.07$). Nevertheless, a series of experiments we conducted reveal that listeners are *more* accurate in assessments of men's relative size when pitch cues are present (voiced speech) versus absent (whispered and sine-wave speech). The facilitating role of voice pitch in size assessment appears to be related, in part, to a denser harmonic spectrum from which to resolve formants. Thus, although voice pitch does not strongly predict body size within-sexes among humans, pitch may nonetheless indirectly aid size assessment.

S26.5 Male hyraxes increase song duration and syntax complexity in the presence of an audience

Vlad Demartsev, TAU
Arik Kershenbaum, Amiyaal Ilany, Adi Barocas, Einat Bar Ziv, Lee Koren, Eli Geffen

A major concern in vocal communication is the efficient delivery of signals to the target audience. This is especially challenging in cases of long and complex vocalisations, which may incur significant costs to the performer. Rock hyraxes (*Procavia capensis*) are social mammals that rely on acoustic signalling as the main mode of communication. Adult male hyraxes produce elaborate and complex vocalisations (i.e., songs) that serve as honest advertisements of their quality. In

various species it has been noted that signalling behaviour changes in the presence of an audience. However, this 'audience effect' has been scarcely documented in wild mammals. By classifying the social context related to natural hyrax songs that we recorded in the wild over the past 11 years, we found a significant audience effect. Songs that were socially induced have an increased structural and syntactic complexity in comparison to spontaneous singing. As far as we know, this is the first evidence of audience effect on the syntactic structure of complex vocal signalling in mammals.

Symposium 27 (CW Version 3): Misconceptions about human social evolution

S27.1 Common misconceptions about the evolution of cooperation in humans

Claire El Mouden, Nuffield College, Oxford University

The social sciences are more likely than ever before to present the results of their research on human behaviour within an evolutionary framework. Human behaviour studies span an array of disciplines, such as economics, sociology, psychology, and of course, evolutionary biology, each of which have their own traditions, conceptual frameworks, and terminology. Consequently there is much disagreement about how to interpret these results within an evolutionary framework, and how to link evolutionary biology and social science. For example, in the social sciences, it is widely accepted that standard evolutionary theory, such as inclusive fitness theory, cannot explain human social behaviours and that novel evolutionary forces, such as group selection and cultural evolution, are required. Furthermore the novel behavioural mechanisms proposed, such as strong reciprocity, are often rejected as implausible by evolutionary biologists, because they either violate standard theoretical assumptions, or confuse proximate and ultimate explanations. I suggest that inclusive fitness theory can explain human sociality, that explaining human behaviour does not require novel evolutionary forces, and that a key reason for these theoretical disagreements stems from misconceptions about the explanatory role of evolutionary theory in experimental studies.

S27.2 Pro-social preferences do not explain human cooperation in public-goods games

Maxwell Burton-Chellew, Oxford University
Stuart West, Claire El-Mouden

Economic experiments are being increasingly used to study human social behaviours. It is a fact that people's behaviour in such economic experiments routinely fails to maximize their personal financial gain, and because

such behaviour typically benefits others, it has been assumed that people are (1) knowingly sacrificing personal gain; (2) intentionally benefitting others; and (3) that such behaviour shows evidence of evolutionary altruism towards group-members that requires new evolutionary theory.

However, this interpretation implicitly assumes that individuals are rational and fully aware of the consequences of their decisions, both for themselves and for others. Furthermore, these behavioural experiments have typically lacked the appropriate control treatments for the purported question(s) they address, and the pro-social intentions have mostly been inferred from post-hoc interpretations of the results of biased experiments.

We use the public-goods game to show that: (1) participants are not rational; and (2) that when the relevant controls are introduced, pro-social theories are neither necessary nor sufficient explanations for the observed behaviours. More generally, we discuss why it is inappropriate to propose evolutionary explanations for the quantitative patterns in such games, and why one cannot simply infer the intentions of participants from the consequences of their decisions.

S27.3 On the use and misuse of the proximate-ultimate distinction

Tom Dickins, Middlesex University

The proximate-ultimate distinction has served evolutionary biology and behavioural ecology well for over half a century. However, in recent years proponents of an Extended Evolutionary Synthesis (EES) have questioned its value. Specifically, the processes of transgenerational epigenetic inheritance have been invoked as novel sources of variation that allow for selection and evolutionary change independent of gene-level changes. I will argue that these processes are the product of proximate adaptations with specific reaction norms and any change invoked at the population level is not equivalent to evolution by natural selection. More recently the concept of *reciprocal causation* has been mooted in order to move away from the proximate-ultimate distinction and to license claims from the EES. Reciprocal causation encompasses processes such as niche construction in which the proximate activities of organisms affect selection pressures, leading to evolutionary change. I will demonstrate that this concept is superfluous to understanding the key phenomena of evolutionary biology and behavioural ecology and that the Modern Synthesis has sufficient conceptual resources to hand. More critically, I will argue that the EES produces no new predictions and prevents the development of key hypotheses in behavioural ecology.

S27.4 Culture and neo-Darwinism

Thom Scott-Phillips, Durham University

More and more psychologists, anthropologists, linguists and other students of human behaviour use evolutionary thinking and theory to inform their research. This development is unequivocally welcome. However human culture, which itself has something of an evolutionary character, introduces a number of complications to this project, to the extent that several (evolutionarily-minded) researchers have argued that it provides a good illustration of why the Darwinian theoretical edifice is incomplete and in need of modification. In this talk I will explain how, on the contrary, human culture can be understood and studied with standard neo-Darwinian theory, and indeed how doing so brings with it new insights and predictions. At the same time, this project will only be fruitful if is applied as a matter of integration rather than reduction. That is, evolutionary approaches do not obviate the existing explanatory constructs of the social sciences; instead, they provide a foundation upon which those same constructs can sit.

S27.5 Human punishment is motivated by inequity aversion not loss aversion

Nichola Raihani, UCL
Katherine McAuliffe

Humans involved in cooperative interactions willingly pay a cost to punish cheats. However, the proximate motives underpinning punitive behaviour are currently debated. Individuals who interact with cheats experience losses, but they also experience lower payoffs than the cheating partner. Thus, the negative emotions that trigger punishment may stem from a desire to reciprocate losses or from inequity aversion. Previous studies have not disentangled these possibilities. Here, we use an experimental approach to ask whether punishment is motivated by inequity aversion or by a desire for reciprocity. We show that humans punish cheats only when cheating produces disadvantageous inequity, while there is no evidence for reciprocity. This finding challenges the notion that punishment is motivated by a simple desire to reciprocally harm cheats and shows that victims compare their own payoffs with those of partners when making punishment decisions.

S27.6 Reputation based partner choice

Gilbert Roberts, Newcastle University

Being seen to be cooperative could pay if the costs of investing in reputation-building displays are outweighed by the benefits of attracting a cooperative

partner. But when can investment in cooperative reputations pay and what is the mechanism underlying honest signalling? By simulating evolutionary dynamics, I investigated the fate of strategies of investing in a cooperative reputation by giving unconditionally to an individual who could never reciprocate versus withholding help; of selecting a partner with a good reputation or taking an arbitrary partner; and of cooperating versus defecting in subsequent iterated dyadic interactions. I found that reputation-building, using reputations in partner choice, and subsequently cooperating could all be favoured. Reputation-based partner choice can be stable when the long term benefits of maintaining honesty outweigh the short term advantages of cheating. I discuss how this differs from costly signalling theory. I also present supporting evidence from economic games in humans which demonstrates how investment in cooperative reputations can reap long term rewards through access to more profitable partnerships. I conclude that reputation-based partner choice provides an important alternative to indirect reciprocity as an explanation for being seen to be cooperative.

Symposium 28: Learning and Speciation

S28.1 Sexual imprinting and learning during courtship determines mate preference within and between stickleback species

Genevieve Kozak, University Of Illinois
Jenny Boughman, Megan Head, Alycia Lackey

Sexual imprinting on parents early in life determines mate preference in a variety of species. Learning may also alter mate preference later in life, particularly during courtship interactions. I compare how learning early and late in life influences mate preference within species (sexual selection) and mate preference between species (species recognition) in benthic and limnetic threespine sticklebacks (*Gasterosteus aculeatus* species complex). I show early learning determines species recognition: females learn to prefer mates of the same species as their father. Females can also learn to avoid heterospecifics during courtship interactions, fine-tuning species recognition. Learning during courtship affects sexual selection within species across sequential mating interactions. During courtship, learning within and between species are distinct processes. By comparing the consequences of learning throughout life, this work gives insight into how learned mate preference may create reproductive isolation between species.

S28.2 The evolutionary effects of learning to avoid heterospecifics

Machteld Verzijden, Lund University

Reproductive character displacement involves differential sexual selection among allopatric and sympatric populations and mate preferences are thought to evolve through indirect selection from reduced hybrid fitness. However, when mate preferences are learned, indirect selection cannot drive mate preference evolution in a similar manner. In fact, I explore the possibility that direct selection on the propensity to learn mate preferences can explain character displacement. In *Calopteryx* damselflies, melanized wing spots are mating cues, the size of which differs between males of two sympatric species, and shows within species variation consistent with character displacement. Female mate discrimination between the males of the two species is learned through experience with males of both species, does this also affect mate preferences for within-species variation in the wing spots? I quantified female preferences for within species wing spot size variation in naïve females, mature females, and in females that had equal amount of experience with males of both species. Between-species experience indeed affected within-species mate preferences for wing spot size, but more so in sympatric than allopatric populations. I hypothesize that the evolutionary impact of learned mate preferences could cause character displacement, and I discuss if indirect or direct fitness benefits can explain this.

S28.3 The evolution of sexual imprinting on compatible genes

Tucker Gilman, University Of Manchester
Genevieve Kozak

Mate preferences learned through sexual imprinting can affect speciation processes. Imprinting strategies determine which traits and individuals are used as models for imprinting and how strong imprinted preferences become. Because different imprinting strategies have different effects on speciation, it is important to understand which strategies are favored to evolve in nature. Existing theory on the evolution of imprinting strategies focuses on “good genes” models, in which imprinting allows individuals to select fitter genes for their offspring and the same genes are fit in every individual. During speciation however, different genes may benefit different individuals. In such cases, imprinting may allow individuals to select mates with genes that are compatible with their own rather than genes that are simply good in all contexts. We used genetically explicit individual-based simulations to explore how imprinting for compatible genes is likely to evolve. We predict the conditions under which evolved strategies are likely to favor speciation.

S28.4 Song discrimination before song learning: Assessing the learning predispositions of young birds in the wild

Daizaburo Shizuka, University Of Nebraska-Lincoln

Sexual imprinting and song learning are important factors affecting assortative mating in many birds. In sympatry with closely related species, song learning could potentially break down assortative mating unless there are mechanisms that ensure heterospecific cues are not learned. Captive studies have shown that species-specific song elements guide song learning in white-crowned sparrows (*Zonotrichia leucophrys*). I studied their sister species, golden-crowned sparrows (*Z. atricapilla*) in the field to determine whether these birds can also discriminate songs prior to learning. Using a set of field playback experiments to nestlings, I show that (a) golden-crowned sparrows respond to territorial songs while still in the nest, starting around 7-8 days old, and (b) nestling golden-crowned sparrows can discriminate between songs of their own species and those of sympatric white-crowned sparrows. The ability to assay early song discrimination in nestling songbirds will open the door to further exploration of how learning predispositions evolve, and how mechanisms of learning predispositions may influence rates of hybridization in the wild.

S28.5 Learned mate preferences in a mixed population of wolf spiders with polymorphic males

Eileen Hebets, University Of Nebraska
Kasey Fowler-Finn

Schizocosa wolf spiders were among the first animals used to document mate choice learning in an invertebrate. Specifically, a subadult female's experience with courtship advances from a mature male was shown to influence both mating behavior and sexual cannibalism. Male phenotypes used in this prior research were artificially manipulated to represent extremes of the continuous natural variation found in males of the focal species.

This study builds upon this prior work by focusing upon a recently discovered population in which males of two distinct forms are found syntopically (brush-legged/non-ornamented males). Microsatellite data indicate that these two phenotypes are not genetically distinct (*i.e.* represent a male polymorphism), whereas similar male phenotypes are genetically distinct in allopatric northern populations. A sister-species relationship is suggested in the northern populations and these phenotypically-pure populations are hypothesized to be derived from an ancestral polymorphic state.

Preliminary mate choice trials indicate that maturation time, subadult female experience (*i.e.* mate choice learning), and courtship timing all influence a female's choice of brush-legged/non-ornamented males. These

factors then potentially influence the proportion of brush-legged/non-ornamented male phenotypes in a population and may ultimately be involved in the evolutionary maintenance and/or divergence of these distinct phenotypes.

S28.6 Niche specialisation driven by both behavioural and physiological trade-offs

Colin Tosh, University Of Newcastle

Niche specialisation and speciation in sympatry are often considered to be processes in which the evolution of behavioural preference is driven by resource-related physiological trade-offs. In truth, both behaviour and physiology are likely to affect the fitness of an organism and here I present a new modelling framework in which both behavioural trade-offs and physiological trade-offs drive the niche specialisation process. Behavioural trade-offs alone can drive the evolution of specialisation but the strength of the trade-offs required to do this is not biologically realistic. The combination of modest behavioural trade-off and extremely modest physiological trade-offs (that would probably be interpreted as 'trade off absent' by traditional means of measurement) can drive the evolution of specialisation. In summary, the combination of these two trade-off types allows the evolution of niche specialisation under relaxed conditions.

Symposium 29: Old dog scientists learn new tricks

S29.1 Ontogeny and Phylogeny in the Sensitivity of Dogs to Humans

Clive Wynne, University Of Florida
Monique Udell

Even the least attentive observer of dogs (*Canis lupus familiaris*) notices that they have a sensitivity to human actions that seems quite exceptional among animals. This widespread observation prompts lay people to refer to their dogs as "reading their minds", and has indicated to some researchers that dogs have an innate sensitivity to human communicative gestures – even though humans do not have an inborn sensitivity to their own conspecific referential actions. We present data from adult and juvenile dogs and grey wolves (*C. lupus lupus*) identifying that dogs' sensitivity to humans is not innate. Rather it is dependent on two forms of learning – both of which are present in the dog's wild progenitor, the grey wolf.

To be sensitive to human communicative gestures dogs must first be exposed to humans during the critical period for social imprinting. Secondly they must have repeated exposure to human actions that predict the delivery of biologically important consequences so that

human actions can become conditioned stimuli. The implication of this account is that there will be dogs that do not follow human gestures, and wolves that do – and we present data supporting these predictions.

S29.2 Prenatal Experience Influences Postnatal Behaviour in the Domestic Dog

Peter Hepper, Queens University
Deborah Wells

Prenatal chemosensory learning may play a role in shaping development and behaviour. The domestic dog, *Canis familiaris*, is a species well renowned for its olfactory acuity. Prenatal chemosensory learning in this species, however, has been largely overlooked. This study examined how prenatal exposure to a chemosensory stimulus (aniseed) via the mother's diet, affected chemosensory preferences of neonatal pups and longer-term food and social preferences. Pups were tested in a two choice test between aniseed and water, and vanilla (a novel odour) and water. Twenty-four hour old pups exposed to aniseed during gestation exhibited a significantly ($P < 0.05$) greater preference for this odour compared to pups not exposed to aniseed, but no preference for vanilla over water. Pups tested 15 minutes after birth showed similar preferences ruling out the possibility of postnatal exposure influencing the preference. At 12 months, dogs showed a significant preference for food impregnated with aniseed over control or vanilla-impregnated food. Moreover this preference generalised to social preferences, dogs preferred conspecifics scented with the prenatally exposed odour over unscented dogs or dogs scented with an unfamiliar odour. Prenatal chemosensory learning is present in dogs and may serve an important role in shaping postnatal behaviour including social and food preferences.

S29.3 Too dog-tired to behave: Self-control in humans and dogs is sensitive to fatigue

Holly Miller, KU Leuven
Kristina Pattison, Camille Bourriseau, Justine Blamplain, Jen Laude

Self-control in humans and dogs appears to rely on a limited energy resource that can be depleted with prior exertion. There is evidence that glucose may be involved, as the consumption of glucose replenishes the depletion incurred by self-control. An alternative explanation is that the detection of glucose by carbohydrate taste receptors, and nutrient sensing neurons, activates the vagus nerve that in turn enhances the neurotransmission of norepinephrine and behavioural control. This hypothesis was investigated in two studies where dogs and humans

were given glucose, fructose or a placebo. Fructose was used because it does not affect blood glucose levels, has non-rewarding post ingestive consequences, but activates the vagus nerve. Dogs were required to exert self-control (or not) and were subsequently given a glucose, fructose, or calorie-free drink before their persistence on an unsolvable puzzle task was measured. Dogs persisted for the same duration after glucose and fructose, and less after placebo consumption. Humans similarly solved more word anagrams following the consumption of glucose and fructose than after the placebo. These observations suggest that vagal activation may be responsible for improving self-control and problem solving in dogs and humans.

S29.4 Why do adult dogs play?

John Bradshaw, University Of Bristol
Anne Pullen, Nicola Rooney

Among the Carnivora, play behaviour is usually made up of motor patterns characteristic of predatory, agonistic and courtship behaviour. Domestic dogs are unusual in that play is routinely performed by adults; socially, with both conspecifics and humans, and also asocially with objects. Solitary play with objects appears to be derived from predatory behaviour: preferred toys are those that can be dismembered, and a complex habituation-like feedback system inhibits play with objects that are resistant to alteration. Intraspecific social play is structurally different from interspecific play and may therefore serve different goals; for example, dogs compete over objects when playing with other dogs, but are interactive when the play partner is human. Dogs are capable of extracting social information not only from games in which they participate, but also from games that they observe between third parties. The majority of dogs do not seem to regard competitive games played with a human partner as “dominance” contests: rather, winning possession of objects during games appears to be simply rewarding. However, a minority of dogs that initiate play with their owners may do so in a context of unresolved conflict within that relationship.

S29.5 Factors influencing problem-solving performance in domestic dogs

Corsin Mueller, University of Veterinary Medicine, Vienna
Stefanie Riemer, Zsafia Virinyi, Friederike Range, Ludwig Huber

Many recent studies on the cognitive abilities of animals have revealed considerable inter-individual differences, the reasons for which are largely unknown. Here I will present a comprehensive analysis of factors

influencing individual problem-solving performance in the domestic dog (*Canis familiaris*). For that purpose, we exposed a group of dog puppies to a set of “intelligence toys” over a period of 15 months. These toys were designed to offer the dogs opportunities to manipulate objects as well as to learn about physical rules such as gravity and connectivity. Between the age of 18 and 24 months, these dogs, as well as a control group without the above-mentioned opportunities, were tested in a series of physical cognition tasks, including the support problem, the trap-tube task, the blocked-tube task as well as a size-constancy task. Additionally, all dogs were subjected to three tasks assessing their level of inhibitory control, an extensive personality test consisting of 15 subtests, and a test assessing dog-owner attachment based on the Ainsworth Strange Situation Test. Taken as a whole, this study provides important information in rare detail on factors influencing individual performance in physical cognition tasks.

S29.6 Dogs’ cortisol and behavioural response to a crying human infant

Min Hooi Yong, University Of Otago
Ted Ruffman

The present study examined whether dogs show an increased stress response when listening to a human infant crying.

When a human hears an infant crying, s/he often responds with an increase in cortisol levels and heightened attention; a response typically described as empathy. We compared dogs' and humans' responses to three auditory stimuli: crying, babbling, and computer-generated white noise. Two sounds were human-produced (crying and babbling), and crying and white noise could be considered aversive. However, only infant crying should evoke an empathic response. Seventy five dogs and 74 young adult humans were assigned to one of the three auditory stimuli. Saliva samples were taken from each participant to determine the cortisol levels prior to and 18 minutes after the onset of the auditory stimuli.

Both dogs' and humans' cortisol levels increased significantly after listening to crying. No significant changes in cortisol levels were reported for babbling or white noise in either species. In humans, crying elicits attention and dogs showed a similar pattern in that they were most alert when listening to crying. The findings for cortisol and behavior converge to suggest that dogs experience a form of empathy - emotional contagion - in response to human infant crying.

Symposium 30: Collective Animal Behaviour

S30.1 Social Networks and Animal Collective Motion

Daniel Franks, The University Of York
Nikolai Bode, Jamie Wood

Computer models have been central to developing an understanding of animal collective motion, and for deriving simple and local individual-based rules. In current models, however, agents are assumed to be interacting in an egalitarian manner: with no social preferences for certain individuals. However, studies of sociality in a wide range of animals have demonstrated that social interactions are structured, with biased preferences between certain individuals. Collective motion and animal social networks have, each individually, received much attention. However, they have not previously been brought together in a combined framework. I will discuss how social networks can impact animal collective motion in terms of group structure, group navigation, and conflicts of interest.

S30.2 Is it Harder to Lead or to Follow? An Experimental Test in Pairs of Foraging Fish

Andrea Manica, University Of Cambridge
Shinnosuke Nakayama, Martin Stumpe, Rufus Johnstone

In many animal groups, coordinated activity is facilitated by the emergence of leaders and followers. Although the identity of leaders is to some extent predictable, most groups experience frequent changes of leadership. How do group members cope with such changes in their social role?

In the present study, we forced role reversal in pairs of stickleback fish by rewarding the shyer follower for leading, and the bolder leader for following. We found that even though bolder fish typically do not act as followers, they were no less successful than shyer individuals when forced into this role. By contrast, shyer fish, which typically do not lead, were unable to capitalise on this role in the way that bolder fish in control pairs did. Markov chain models showed that the reason why bolder fish coped better with role reversal was not that they are more flexible in their behaviour. Rather, for fish of all temperaments, the tendency to follow is malleable, while the tendency to initiate group movement is much more resistant to change. In other words, fish can easily learn to follow, but they cannot easily learn to lead. As a consequence of this inflexibility, temperamental differences within a pair led to improved performance when pair members were allowed to assume their usual roles, but to impaired performance when they were forced to switch roles.

S30.3 Decision making and competitive foraging in slime molds

Audrey Dussutour, CNRS, Universite De Toulouse

Stamatios Nicolis, David Sumpter

Plasmodia of *P. polycephalum* are single, multinucleate cells, often viewed as distributed information processors. Although lacking a central nervous system or processing centre, the slime mould can find the shortest path through a maze, reconstruct complex man-made transport networks with efficiency comparable to their human designers, anticipate the timing of periodic events and perform complex nutrient-intake and risk-management trade-offs to make optimal foraging decisions. However, contrary to multiple studies conducted on distributed systems such as colonies of social insects, no studies on slime molds has considered and examined interactions between slime molds. In this study, we demonstrated that slime molds are able to follow cues left by other slime molds and that they can interact with each other to find a food source.

S30.4 Collective behaviour and cannibalism in migratory insects

Sepideh Bazazi, SBazazi

Iain Couzin, Stephen Simpson, Jerome Buhl, Pawel Romanczuk, Joe Hale, Gregory Sword

I will present work investigating how the behaviour of individuals in response to their nutritional needs can give rise to collective behaviour in migratory insects: desert locusts (*Schistocerca gregaria*), and Mormon crickets (*Anabrus simplex*). The desert locust can form aggregations that extend over several hundred kilometers and can have a devastating impact on vegetation. An investigation into the role of cannibalistic interactions on the migratory group motion of juvenile locusts revealed that collective motion may be driven by cannibalism creating a forced march; individuals in a group move to reduce their risk of cannibalistic attacks from behind and attempt to bite others ahead. Furthermore, examination of locust's nutritional state with respect to protein revealed that diet minimally influences the inherent motion of solitary individuals, but strongly influences social interactions, thus affecting group behaviour. In addition, using a field investigation on adult Mormon crickets, we examined how individuals make attack decisions and how their social context affects their cannibalistic interactions. Strong social effects were found on the encounter duration and on individuals' cannibalistic tendencies, which can affect aggregation behaviour.

S30.5 A crowd is wise for hard tasks but not for easy ones

Takao Sasaki, Arizona State University
Boris Granovskiy, Richard Mann, David Sumpter, Stephen Pratt

“Collective intelligence” and “wisdom of crowds” refer to situations where groups achieve more accurate perception and better decisions than solitary agents. Whether groups outperform individuals should depend on the kind of task and its difficulty, but the nature of this relationship remains unknown. Here we show that colonies of *Temnothorax* ants outperform individuals for a difficult perception task, but that individuals do better than groups when the task is easy. Subjects were required to choose the better of two nest sites as the quality difference was varied. For small differences, colonies were more likely than isolated ants to choose the better site, but this relationship was reversed for large differences.

We explain these results using a mathematical model, which shows that positive feedback between group members effectively integrates information and sharpens the discrimination of fine differences. When the task is easier the same positive feedback can lock the colony into a suboptimal choice. These results suggest the conditions under which crowds do or do not become wise.

S30.6 Collective cognition in human crowds. Decision making under uncertainty

Ralf Kurvers, Institute For Freshwater Ecology And Inland Fisheries

Max Wolf, Ashley Ward, Stefan Krause, Jens Krause

Decision accuracy is a key factor shaping the evolution of behaviour. Decision accuracy in many contexts depends on two dimensions: a high rate of stimulus-specific responses in the presence of a particular stimulus (true positives) and a low rate of such responses in its absence (false positives). For instance, animals under predation danger need to escape when a predator is approaching, but do not need to escape when a non-dangerous animal is approaching. Increasing sensitivity to stimuli (e.g., a smell or sound) increases true positives but comes at the cost of increased false positives, posing a fundamental limitation to decision accuracy. Here we investigate individual and collective decision making in human crowds under uncertainty to study if groups can outperform individuals in the framework of true and false positives

S30.7 Sheep, sheepdogs and the shepherding problem

Daniel Strobom, Uppsala University
Richard P. Mann, Alan M. Wilson, Stephen Hailes, A. Jennifer Morton, David J.T. Sumpter, Andrew J. King

The herding of sheep by dogs is a powerful example of how one individual can cause many unwilling individuals to move in the same direction. Tasks similar

to that of sheep herding are seen in systems as diverse as crowd control, cleaning the environment, and collecting other animals or robot drones. Although single dogs are seen to solve this "shepherding problem" every day around the world, it remains unknown which algorithm they employ or whether a general algorithm exists for shepherding. Here we describe such an algorithm, based on adaptive switching between collecting the sheep when they are too dispersed and driving them once they are aggregated. We show, in a self-propelled particle model, that our shepherding algorithm can effectively herd large numbers of autonomous, locally interacting agents. A side-to-side motion of the shepherd behind the group emerges from interactions between the dog and the sheep. We show that this and other aspects of the herding interactions in our model are consistent with empirical data of real sheep herds. It appears that the shepherding algorithm applied by dogs is simpler and more effective than those previously proposed by engineers, suggesting new methods for the development of mobile robots designed to influence movements of living and artificial agents.

S30.8 Using real predators and simulated prey to explore the adaptive value of collective behaviour

Christos Ioannou, University Of Bristol
Vishwesh Guttal, Iain Couzin

The collective behaviour that occurs in animal groups has been repeatedly shown to have an adaptive advantage, for example in making group decisions. Although collective motion is thought to facilitate avoiding attack from predators, this has not been shown directly due to difficulties in measuring and manipulating dynamic prey behaviour. We present a novel approach to this problem that exposes a projected simulation of moving prey to a live predatory fish, and show that coordinated collective motion reduces the risk of attack. We will then present a new experimental system under development that replaces the projected virtual prey with physical artificial prey that can be consumed by the predator. Real-time tracking of the predator will also allow its position and velocity to be fed back to the prey. The new system will allow examination of collective detection and information transfer in prey, and the predator's attack success and subsequent learning over consecutive trials, none of which was possible in the original study.

S30.9 Shoaling behaviour and leadership in fish selected for large and small brain

Andrea Perna, Uppsala University
Robert Hinz, David Sumpter, Alexander Kotrschal,
Niclas Kolm

One important problem in the study of collective animal behaviour is understanding how phenotypic differences affect the behaviour of individuals within a group, and ultimately the behaviour of the group itself. One element of phenotypic variability with relevance for behaviour are differences in brain size. A larger brain could be associated with longer reaction times and higher energy consumption, it might offer the potential for improved social recognition and have an impact on different sensory or motor skills. We characterised the rules of interaction in populations of guppies (*Poecilia reticulata*) artificially selected for large or small brain size. Large brain fish appear to interact more loosely with their neighbours and form shoals with larger inter-individual distances. According to a "leadership by social indifference" hypothesis, we might expect large brain fish to be more likely to lead the collective movement and influence more strongly the collective decisions of the group. We tested this hypothesis directly by analysing the individual trajectories of small and large brain fish shoaling and interacting together in mixed groups. By implementing the rules of interaction determined empirically into a self-propelled particle simulation with heterogeneous particles we provide a theoretical interpretation of our results.

S30.10 Individual traits structuring leader-follower relations in homing pigeon flocks

Dora Biro, University Of Oxford

The interaction rules that govern collective motion in animal groups represent a burgeoning area of research. Ongoing advances in tracking technology are enabling increasingly accurate reconstructions of individuals' movement paths, allowing researchers to elucidate in unprecedented detail the mechanisms responsible for coordinated group movement. In addition, more and more studies explore the role of individual differences – whether inherent or acquired – in shaping group members' interactions with each other, and the consequences that such inter-individual variation has on group-level properties. In particular, the existence and robustness of persistent leader-follower relations among individuals raises interesting questions about the nature of the attributes that allow certain group members to assume leadership roles. Previous work has shown that in homing pigeon flocks decision-making is hierarchically organized, with certain birds consistently contributing with more weight to the group's movement decisions than others. In this talk I describe a series of recent studies designed to identify what aspect of an individual bird's physical, behavioural, and cognitive attributes may promote leadership, focusing on experiments that examine (and, wherever possible, manipulate) spatial knowledge, navigational experience, age, morphological traits, and

social dominance rank, and discuss the implications of the results for group performance.

S30.11 Collective decisions emerging from entangled individual information processing

David Lusseau, Aberdeen University

Individual behavioural decisions emerge from multiple interactions between the needs of individuals and the opportunities their socioecological landscape offers them. It is advantageous for individuals from group-living species to synchronise their activities in order to maintain group-living benefits. Such individuals can gather both social and private information from multiple socioecological sources in order to make a decision. Collective decisions emerge from the interactions between these individual's trade-offs. Collective decisions can be advantageous when individuals are uncertain about the timing of activities that will best meet their needs. Here I develop a mechanistic model to simulate entanglement in information gathering error between individuals depending on their association rate in social networks. For example, such entanglement could be caused by similarities in perception biases developed through common experiences. I show that entanglement in information sampling error, which could empirically be perceived as social information, influences the benefits of iterated collective decisions. I review these findings within the context of current quantum decision theory.

S30.12 What social information cues drive decision making in animal groups? A model comparison approach

James Herbert-Read, Uppsala University
Richard Mann, Qi Ma, Alex Jordan, David Sumpter,
Ashley Ward

Animals make use of different forms of social information to inform their decisions, but deciphering when and what cues are used in group decision making processes remains unclear. For example, when moving between areas, animals may use dynamic information that is only available over short periods of time (such as the recent movements of neighbours), or more stable information (such as the distribution of neighbours between areas), or both, to inform their decisions to move. Here we investigate what information is used by fish when crossing between two coral patches in an experimental arena. Using a Bayesian model comparison approach, we find that fish only respond to the dynamic information encoded in a previous individual's decision to move. They do not, on the other hand, respond to global information determined by the number of individuals between each patch. We discuss our findings in light of recent

developments in information use in collective movement. Further, we postulate that selectively choosing these different forms of information may be advantageous in different decision making contexts.

Symposium 31: How can we tell if an animal's death is a good one?

S31.1 Dying mice tell their tales: recent research on laboratory animal euthanasia

Joanna Makowska, University Of British Columbia
Daniel Weary

Euthanasia is one of the most common laboratory procedures. Motivation testing has been used to assess responses of animals to euthanasia agents. Approach-avoidance studies have provided rodents the choice between remaining in a chamber with a food reward, but filling with euthanasia agent, versus escaping the chamber and abandoning the reward; this work has shown that CO₂ and argon are highly aversive but isoflurane is less so. Avoidance-avoidance studies have provided rats the choice between remaining in a preferred dark chamber, but filling with a euthanasia agent, versus escaping to a brightly lit chamber; rats always choose exposure to bright light over exposure to CO₂ but often choose exposure to isoflurane over exposure to light. Conditioned place aversion studies have shown that zebrafish choose to avoid a tank where they had experienced exposure to TMS more than one where they experienced clove oil or metomidate. Rats, mice and zebrafish are all motivated to avoid exposure to agents commonly used to kill them; these research methods can identify agents that are less aversive, providing a scientific basis for changes in recommended euthanasia methods.

S31.2 Conditioned Aversion to Rodent "Euthanasia" Agents

Huw Golledge, Newcastle University

Conditioned place aversion (CPA) studies can identify aversive agents by demonstrating the formation of an association between a place (the conditioned stimulus, CS) and an agent (the unconditioned stimulus, UCS), leading to conditioned avoidance of the CS. Because CPA is tested in the absence of the UCS it measures memory of the affective response to the UCS, making CPA a powerful tool for examining whether euthanasia agents cause negative affective states in the period leading up to loss of consciousness.

I used CPA to compare aversion to inhaled euthanasia agents (Carbon Dioxide, Isoflurane and Argon). All three agents caused place aversion in rats. Aversion to argon was stronger than to the other agents. How should these data affect decisions about the way we kill animals?

In an extension of the CPA paradigm I directly compared pairs of euthanasia agents against one another, rather than the conventional comparison of agent against sham. Is a demonstration that one agent causes stronger aversion than another sufficient to conclude that that agent should be rejected in favour of the less aversive agent?

Most CPA experiments use multiple CS-UCS pairings, do multiple exposures confound these experiments since during euthanasia animals are exposed only once?

S31.3 Changes in conscious awareness during manipulations that involve death

Craig Johnson, Massey University

This talk will explore concepts of awareness and consciousness in the context of the various circumstances in which animals are deliberately killed. It will focus on what we can infer about consciousness from what we know about the neurophysiology of perception and also on what probable correlations exist between an animals' perceptive awareness, and the ways in which we attempt to measure this phenomenon.

S31.4 Is euthanasia in cold-blooded vertebrates humane: how do we know they are dead?

Lynne Sneddon, University Of Liverpool
Craig Stevens

Euthanasia is the humane killing of individuals where the onset of death is rapid and minimises any fear, discomfort or suffering. However, studies are needed to identify which approaches are the most humane. Consideration must be given to handling, location of euthanasia to protect other animals, reduction of pain and anxiety, mode and efficacy of euthanasia and monitoring of the animal to ensure they have succumbed. A variety of methods are employed for cold-blooded vertebrates including lethal injection, overdose of immersion anaesthesia in aquatic animals, and inhalant chemicals for species that cannot hold their breath. However, the euthanasia of cold blooded vertebrates can be particularly problematic as the nervous system is especially resistant to hypoxia. Inter-specific differences in physiology necessarily inform the selection of the mode of euthanasia and studies investigating the humaneness of a particular technique are growing.

Euthanasia in reptiles, amphibians and fish shall be reviewed with the aim of discussing major challenges, recent research developments on the behavioural and physiological reactions during euthanasia and potential indicators of death. This presentation shall discuss how we can minimise suffering and improve the welfare of

animals to ensure the most refined protocols are adopted.

S31.5 Can we tell what types of death animals prefer?

Georgia Mason, University Of Guelph

How bad does dying feel? Preference tests, both unconditioned (based on unlearned reactions to stimuli) and conditioned (e.g. based on operants associated with stimuli), are powerful welfare research tools. However, they require animals to be physically capable of expressing approach/avoidance behaviour. The welfare effects of dying typically occur between the first onset of symptoms and unconsciousness; animals exposed to this full experience therefore cannot behaviourally express any aversions they may feel. Conditioned place preference paradigms could help solve this problem. Animals would be exposed to predictive sensory/spatial cues while undergoing a near-death experience (falling into unconsciousness but not dying). Re-exposed to such cues when recovered, do they avoid them? Potential problems include that fully lethal doses may have different affective consequences from sub-lethal, and that these experiences could interfere with memory, lead to false negatives (although not false positives). Subjecting animals to the repeated trials typically needed for this type of conditioning may be ethically undesirable, too. Maximising cue salience could help, along with (in some instances) harnessing Garcia effects, whereby novel flavours associated with malaise can induce conditioned avoidance in one trial. Findings from rodent control will help illustrate the potential of such an approach.

Symposium 32: Primate Cognition - Nuts and bolts in the evolution of primate intelligence

S32.1 Communication in a complex social world

Julia Fischer, German Primate Center

One implicit assumption of the social complexity hypothesis is that navigation in a complex social setting affords exquisite communicative skills. Using baboons as a model, I will explore the variation in social systems and contrast it with the variation in communicative complexity. While the so-called savannah baboons (chacma, olive, and yellow baboons) live in stable female-bonded groups, Hamadryas baboons live in multi-level societies whose core are one-male units. Our studies of the West African Guinea baboons revealed that these live in a fluid multi-level society. I will show that the morphology of the vocal repertoires of these different baboon species is highly fixed, while some variation can be observed in terms of the usage of calls. On the other hand, the responses to calls appear to be molded by the competitive regime and

the social organization of the species under investigation. Thus, neither the variation in social complexity nor the advanced socio-cognitive abilities of the species under study appear to map onto the differentiation of their vocal signals. I will discuss the implication of these findings for the evolvability of different aspects of social behavior, with a specific aspect on the role of evolutionary constraints in the evolution of communication.

S32.2 Is cognition divorced from communication?

Klaus Zuberbuehler University Of Neuchatel

A basic Darwinian principle is continuity, with closely related species generally being more similar than distantly related ones. But how does this principle explain the diversity in primate communication? Some monkey species produce vocal behaviour that is, in many ways, more complex than what has been reported from great apes, despite a long history of research efforts. This is particularly puzzling because a defining human feature is highly complex vocal communication. I will discuss recent empirical evidence to address the apparent chasm between monkey and ape communication and also address the belief that ape vocal behaviour is cognitively uninteresting.

S32.3 From social complexity to cognition: the importance of social knowledge

Thore Bergman, University Of Michigan

Despite considerable evidence of evolutionary links between social complexity and cognition, we are lacking comparative data on how animals use social information in natural settings. Such data are particularly important because similar social interactions can be managed in various ways, each with unique cognitive demands. As an example of this variation, I will compare social knowledge in geladas (*Theropithecus gelada*) and baboons (*Papio ursinus*). Geladas and baboons are closely related primates that differ dramatically in the size and fluidity of their social groups. Baboons live in stable and relatively small groups while geladas form large, multi-level, fluid groups. The social complexity of geladas appears more cognitively challenging than the single-level baboon group. However, I have found that geladas are less reliant on social information than baboons and geladas fail to recognize animals that they regularly associate with. Instead, geladas appear to rely on signals of quality to guide interactions with others. I will discuss how the different ways that baboons and geladas solve social problems impacts our broader understanding of the relationship between sociality and cognition.

S32.4 The cognitive component of conflict management & comparing monkeys and apes

Roman Wittig, Max Planck Institute For Evolutionary Anthropology
Catherine Crockford

Group living creates a dilemma: it incurs both, benefits and costs. Social animals benefit from better defense of resources, less predation pressure and pooling of information. However, they also have to cope with competition by group members amongst other costs. Such tradeoffs favored the evolution of behavioral strategies that maximize benefits and minimize costs. In order to function effectively, conflict management strategies such as reconciliation, consolation or coalitional support seem to require animals to have specific cognitive abilities, for example certain memory capacities or knowledge about the quality of others' relationships. With rising social complexity in the groups or delay of the behaviors' onsets these capacities appear to become even more important. I will present and discuss recent empirical data on wild monkeys and apes including behavioral observations and field experiments. The comparison will contribute to a better understanding of social cognition and will help to derive new hypotheses on possible cognitive differences between monkeys and apes.

S32.5 The limits of prosociality in chimpanzees

Keith Jensen, University Of Manchester

The evolution of human cooperation is one of the major transitions in evolution. How humans came to be "ultrasocial" is a matter of great interest. A productive approach to the question is to test our closest living relatives in tests of cooperation to better understand the psychological substrates that might underpin large-scale cooperation, and that might limit nonhuman primates from achieving this transition. Of particular interest are studies on short-term altruism in which the actor pays a cost to the benefit of another individual. Some studies suggest that chimpanzees "help" in instrumental tasks, demonstrating an understanding of the goals of others, as well as a motivation to see these goals achieved. Other studies find that chimpanzees fail to "share" in resource distribution tasks, suggesting that they are not concerned about the welfare of others. However, chimpanzees in captivity are inquisitive, and it may be that helping and sharing might be by products of personal interest in the test scenario unrelated to the outcomes. In a pair of studies, chimpanzees were given with an apparatus in which doing something led to an altruistic outcome, or another apparatus that produced a spiteful outcome. The absence of difference between apparatuses, and the lack of engagement unless there was a personal benefit, challenges suggestions that

chimpanzees are motivated to help others. It may be that other-regarding concerns are unique to humans and central to our large-scale sociality.

S32.6 Empirical Approaches to studying Causal Cognition

Amanda Seed, University Of St Andrews

One possible route to intelligent problem-solving is representing the objects in the environment in terms of the abstract properties that constrain their interactions, allowing knowledge gleaned in one problem to be transferred flexibly and yet selectively to new challenges. Some researchers claim that our tendency to parse the world in terms of higher-order concepts, and to reason about causal connections between events, is unique to humans (Povinelli 2004; Penn, Holyoak & Povinelli 2008). Contrary to this view I present evidence from different empirical approaches that some non-human primates form abstract, multi-modal representations encompassing physical properties such as solidity and continuity, including possible differences between monkeys and apes. Importantly, there may be critical differences in other psychological processes such as inhibition, motivation and attention that constrain the range of situations in which our closest living relatives can obtain and apply their knowledge; one important limitation may be in the use of tools. Empirical approaches that can pinpoint the cause of failure, as well as success, are important for identifying similarities and differences between causal cognition in human and non-human primate.

S32.7 Do long-tailed macaques reason about their physical world?

Christian Schloegl, German Primate Center & University Of Gottingen

Michael Waldmann, Julia Fischer

Monkeys master a variety of physico-cognitive tasks and in several experiments performed similar to the Great Apes. This led to increasing interest in monkeys' causal understanding and their ability to reason about causal relationships. However, despite an increasing number of studies, the extent and quality of monkeys' reasoning abilities remain unclear, because alternative accounts may explain some performances. Of particular interest is diagnostic reasoning, which is the ability to infer the cause of an observed effect. We present here a series of studies in which we investigated long-tailed macaques' causal understanding for and diagnostic reasoning about the effects objects have on other objects. Rewards were hidden under a variety of items and we tested if the monkeys can use information about the physical

properties and the spatial orientation of these objects to infer whether food has or has not been hidden underneath. Our findings suggest that monkeys may possess some "folk-physical" understanding of causal relationships, but their reasoning skills seem to be restricted to contexts of limited complexity. We discuss our findings in the light of recent claims for causal reasoning in non-human animals.

S32.8 A comparative perspective on causal reasoning, tool use and planning

Jackie Chappell, University Of Birmingham

Ian Apperly, Sarah Beck, Nicola Cutting, Emma Tecwyn, Susannah Thorpe

The evolution of advanced cognition in primates continues to excite debate. The field is divided between those who consider, like Darwin, that the difference in the minds of humans and other animals is "...one of degree and not of kind" (Darwin, 1871; p. 126;), and those who argue that there are fundamental differences in the ways in which human and non-human primates understand the physical world (e.g. Penn et al., 2008). However, in many cases, assumptions have been made about the level of human performance without testing humans under the same conditions as those used for non-human primates. In this talk, I will report experiments testing both human and non-human primates on aspects of technical intelligence such as causal reasoning, innovative tool use and planning. I will show that while there are certainly interesting differences between human and non-human primates in the ways that they solve these tasks, humans also show errors in performance, suggesting that subjects do not have as complete an understanding of the physical realm as previously assumed.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Penn, D. C. et al. (2008). *Behav Brain Sci* **31**, 109-30.

S32.9 Cumulative Technology in Humans

Christine Caldwell, University Of Stirling

Human culture has been described as cumulative and ratchet-like, due to the fact that ideas, behaviours, and inventions, accumulate (typically beneficial) modifications over time. However this property of human culture appears to be absent in even our closest primate relatives. This contrast has drawn the attention of researchers from a range of disciplines, eager to identify underlying cognitive differences between the species which might account for these differences.

In this talk we will report studies that we have completed with human participants, investigating cumulative culture on a small scale in the laboratory using experimenter-set construction tasks. In one of these studies we have found, contrary to some theoretical predictions, that imitation (i.e. copying actions, not just end products) is not necessary for cumulative improvement. In other studies, we have found evidence of strategic shifts in the balance between copying and innovation using these same tasks, which may provide insights into the stability or otherwise of cultural differences between real human populations.

S32.10 Cumulative technology in great apes & Symposium summary

Claudio Tennie, University Of Birmingham

Besides providing a summary of this double symposium on primate cognition, I will talk about cumulative technology in great apes. The view I will present will be a critical one. Based on several lines of evidence, I will argue, technology in great apes is mostly – if not exclusively – of a non-cumulative kind. The underlying reason are that A) great apes usually lack the high fidelity learning mechanisms that help or enable culture to accumulate; B) great ape technology consist of “latent solutions”, i.e. they represent expressions of physical cognition which are fuelled mostly by individual learning (with social learning only playing a minor role, namely of explaining the distribution of behaviours – but not the behavioural forms themselves); C) great apes sometimes “get stuck” with solutions to tasks which could potentially be improved. At the very least, this approach explains the general lack of good examples of cumulative technology in great apes. Future work will show whether this approach holds true even for the few currently suspected cases of cumulative culture in great apes (notably in chimpanzees).

S32.11 Great apes follow trails to locate hidden food

Christoph Voelter, Max Planck Institute For Evolutionary Anthropology
Josep Call

Whether nonhuman primates understand causal relations beyond mere associations is still a matter of debate. In the present study, we presented all four species of nonhuman great apes (N=36) with a choice between two opaque cups. Crucially, we had previously hidden a yoghurt bowl under one of the cups out of apes’ sight while leaving a yoghurt trail to the baited cup. Great apes spontaneously used yoghurt trails to locate the hidden yoghurt bowl. Follow-up experiments ruled out that the apes were simply learning to use the

trails as cue marking the baited cup. First of all, chimpanzees distinguished trails based on the temporal order of cause and effect by screening off trails that were already present before the reward was hidden. Secondly, we produced a trail that was first leading to the false cup and then from that cup to the baited cup. To solve this task the apes had to avoid the cup surrounded by most yoghurt and go for the endpoint of the trail. Chimpanzees also solved this follow-up right away. Therefore, we conclude that apes follow trails that exhibit a causal relation to the reward and are sensitive to the temporal order of cause and effect in this context.

S32.12 Planning to remember: Prospective memory in language-trained chimpanzees (*Pan troglodytes*)

Theodore Evans, Georgia State University, Language Research Center
Bonnie Perdue, Jessica Bramlett, Charles Menzel, Michael Beran

Prospective memory is remembering to execute an intended action at an appropriate future time. We assessed this capacity in language-trained chimpanzees in three experiments in which they had to remember to request a hidden food item at a later time by naming it with a lexigram symbol. In all three experiments, after seeing the food being hidden, the chimpanzees had to retain this memory for 3-30 minutes while participating in a concurrent task of varying complexity, ranging from foraging for preferred food items to matching lexigram tokens to photos of representative food items. Opportunities to name or request the hidden food came at different times during these tasks, and sometimes the chimpanzees had to choose the most opportune moment to make these requests. In most trials of these experiments, chimpanzees remembered to identify the hidden item, and they did so at the most appropriate time, whether that moment occurred during or after the concurrent task, and whether that moment was determined by the experimenter or was left to the chimpanzee to decide. These results indicate that chimpanzees have the capacity for prospective memory and can demonstrate such ability in tasks similar in design and complexity to those used with humans.

Symposium 33: Perception of appearance and its function in sexual selection and mimicry

S33.1 Cuttlefish, camouflage and chromatophores: exploring cephalopod visual perception through rapid adaptive colouration

Sarah Zylinski, University Of Leeds

Coleoid cephalopods (cuttlefish, octopuses and squids) are able to rapidly alter their appearance with a speed

and complexity unrivalled in the animal kingdom. This is primarily achieved via dense intradermal chromatophores, which are under direct neural control and largely visually driven. Cephalopods use adaptive colouration in both communication and camouflage. In the case of camouflage, the cuttlefish *Sepia officinalis* has provided us with a unique insight into non-human visual perception because, in very simple terms, the animal tells us what it can see by the body pattern it uses when on a given background. By testing the body pattern responses of *S. officinalis* to very specific visual stimuli we have begun to understand the mechanisms by which it determines what pattern components to use. Here I discuss some of our findings about how information in the background pertaining to attributes such as edges and texture are extracted and integrated by the cuttlefish.

S33.2 Predictors of detectability of camouflaged targets in natural complex scenes

Feng Xiao, University Of Bristol
Innes Cuthill

Camouflage is a classic example of the power of natural selection. While the general benefits of camouflage are seemingly obvious, understanding the precise means by which the viewer is fooled represents a challenge to the biologist, because camouflage is an adaptation to the eyes and mind of another animal. Various factors have been proposed to affect the detectability of prey: the local contrast in colour and pattern between prey and background (the degree of background matching), the coherence of shape and outline (as opposed by disruptive coloration), and, as a factor extrinsic to the prey, the complexity of the background. The latter has been investigated in lab experiments using artificially patterned prey and backgrounds, but not in the field with natural substrates. In this study, we tested the interaction of all three factors (background matching, disruption and background complexity) using artificial moths on oak trees in natural woodland. Using statistical measures of background complexity and species-specific estimates of local colour contrast, we investigated the best predictors of detection rates by wild bird predators and experimental human subjects searching for the same targets under the same conditions. For both birds and humans, two factors explained most of the variation in detectability: 1) local colour/ brightness match of the target to the tree, and 2) textural complexity of the tree bark.

S33.3 Mimicry is in the eye of the beholder

Baharan Kazemi, Stockholm University
Olof Leimar, Gabriella Gamberale-Stille, Birgitta Tullberg

During mimicry evolution the perceived mimic-model similarity increases and the evolutionary direction could be strongly influenced by predators judgement of similarity. Mimicry evolution is thus more likely to commence in traits that predators use prior to others to categorise prey. If they use such feature-based categorisation, a similarity with the model in such a feature should lead to increased survival. I tested the idea by studying if birds attend to specific features of prey appearance when they learn to discriminate and generalise between them. I used wild Blue Tits as predators and tested the colour, pattern and shape dimension of artificial prey. The birds first learned to avoid a specific model prey appearance and then performed a generalisation test with new mimics that shared one dimension with the model. I found that colour mimics were strongly avoided whereas pattern and shape mimics were attacked. This showed that the birds primarily attended to a single feature, colour, and thus generalised between models and mimics. In an additional experiment I found that the birds also learned the colour dimension significantly quicker than pattern and shape, showing that colour is a significantly more salient trait to them in terms of learning and categorisation.

S33.4 Optimization of eggs crypsis: a substrate choice experiment in Japanese quail

Camille Duval, University Of Birmingham

Eggshell colour primary role is maintaining eggs crypsis and enhancing clutch survival. The nest-crypsis hypothesis proposes that predators would detect conspicuous nests before eggs, thus no selection for egg crypsis would exist. However, ground-nesting species would lay eggs that match nest background. Using artificially colored eggs, many studies have failed to show any role of egg crypsis contrary to others that found a positive relationship between clutch survival and naturally pigmented eggs. Predation risk and egg rejection are the two main behaviors tested in the context of egg crypsis, but only few studies have looked at how eggshell patterns match nest background.

The aim of this study is to investigate whether females make a choice of the substrate they lay on, in an experimental design using the Japanese quail (*Coturnix coturnix japonica*), a species that lay brown spotted eggs and where eggshell appearance remains constant, despite female condition variations. Adult females were individually housed and given the choice of 8 plain or patterned substrates (mimicking eggshell background or spots appearance) to lay on for one week. Here I discuss how photography from eggs and substrates helps understanding potential eggs crypsis optimization by females Japanese quail.

S33.5 Distance-Dependent Defensive Colouration

James Barnett, University Of Bristol
Innes Cuthill

Camouflage and warning colouration are usually viewed as alternative defensive strategies at the opposite ends of the conspicuousness continuum. As such, they entail different costs and suit different life-history strategies; for example, crypsis constrains habitat choice and mobility, aposematism bears the cost of ineffectiveness against ignorant, hasty or nutritionally stressed predators. However, it is possible that crypsis and warning coloration can be combined, and their costs reduced, by the use of patterns that are detectable at different distances. This hypothesis finds support in experiments on humans searching for natural and manipulated photographs of insects on computer screens.

Using a technique developed in computer graphics, that of spatial frequency blending, we show that such distance-dependent defences are effective under field conditions against natural, avian, predators. Artificial moth-like prey that match the colour and texture of bark at a distance, but with yellow-and-black stripes that are conspicuous close-up, are predated at lower rates than prey with either colour pattern alone. Suitable controls, and search experiments using humans under the same conditions, isolate the mechanisms as concealment-at-a-distance and avoidance-close-up. Supporting the argument that animal colour patterns need not be optimised for one particular defensive strategy, and that signals may change with viewing conditions.

S33.6 A Nest Depredation Simulation Experiment Indicates That Birds Do Not See Their Eggs

Kim Derrickson, Loyola University Maryland

The proximate mechanism by which birds detect that their nest has been depredated is unknown. Nest failure is common and selection should favor rapid detection. Birds are extremely visual but behavioral responses reported here indicate vision is not used. I monitored behavior before and after clutch removal in 10 Wood Thrushes (*Hylocichla mustelina*). Females returned to and incubated empty nests 2.3 times on average, seven returning multiple times. The interval from landing on the rim to stepping into the cup did not differ between pre- and post-depredation visits. Incubation bouts (averaged 68.6 min for the 10 females pre-treatment) dropped to an overall average of 17.3 min but in a stepwise fashion with each subsequent visit getting shorter. The reverse occurred with incubation breaks (pre-depredation, 11.4 min; post-depredation, 79.6 min) again typically in a stepwise

fashion with subsequent breaks increasing in duration. Females moved within the cup (17.4 fold increase) and onto the rim (17.0 fold increase) significantly more post-depredation. Females also made these movements significantly earlier post-depredation. Unexpectedly, stereotypical nest building movements, never seen during normal incubation, occurred while incubating an empty nest. Two American Robins (*Turdus migratorius*) behaved similarly. Videos will show these dramatic, completely unanticipated changes in behavior.

BEHAVIOUR 2013

Concurrent Abstracts

C1: Behavioural flexibility

C1.1 Environmental tolerance in Urban Birds : a Synanthropic Adaptation?

Zina Skandrani, Museum National D'His

Understanding species' adaptation to anthropic habitats and the factors influencing the success or failure of species allows determining the most effective way to maintain high levels of biodiversity in human landscapes. Urban environments being characterized by human and domestic animal proximity, synanthropic species generally have broad environmental and human tolerance, in the form of behavioral flexibility (low neophobia and high innovation) and risk taking. These behavioral characteristics allow animals to adjust rapidly to circumstances of unpredictability and can therefore be an advantage for species when dealing with variable habitats. It remains however an open question whether they are the cause or the consequence of species' establishment in anthropic habitats.

The present study investigates whether environmental tolerance in urbanized birds is due to a genetical pre-adaptation, whether it is favored by cities' specific complex environmental conditions, whether it is the result of further adaptation to the urban context which we term "synanthropic adaptation". We tested these hypotheses by conducting comparative experiments in the field and in captivity, choosing urban and non-urban species which are either closely related but experience different ecological demands and vice-versa: feral pigeons, domestic homer pigeons, in captivity raised offspring of wild-caught feral pigeons and urban crows.

C1.2 When a male changes his ways: sex differences in feeding behaviour in the Pied Flycatcher

Raivo Mand, University Of Tartu
Elo Rasmann, Marko Magi

Although sexual dimorphism is a well known phenomenon, several aspects of it remain unresolved. For example, it is not clear how environmental conditions influence sexual dimorphism, especially in behavioural traits. In a study of Pied Flycatchers we tested whether there are differences in the composition of food brought to young by the different parents, and whether such sex differences are dependent on the hunger level of nestlings. We found that in normal feeding

conditions, female parents provisioned nestlings with relatively more food collected from the tree canopy (caterpillars), while males brought more food caught in flight (adult Lepidoptera).

To imitate a temporary worsening of environmental conditions, we experimentally increased the hunger level of nestlings. Male parents responded to this manipulation by changing their foraging behaviour such that the sex difference in provisioning behaviour diminished. Possible explanations for the observed sex differences are discussed. This result is in accordance with the general pattern previously found for sex differences in animal size and certain other traits – namely that sex differences tend to diminish in harsh environmental conditions. It is possible that a decrease in sex differences in harsh conditions represents a more general pattern than previously assumed.

C1.3 What makes an object novel?

Alison Greggor, University Of Cambridge
Alex Thornton

Object neophobia, the fear of novel things, is regarded to differ among species, to contribute towards temperament, and to inhibit exploratory and innovative behaviour. Yet, little is known about which components of an object elicit neophobic responses. Do these components function consistently across contexts, populations, and environments? How much exposure to a stimulus is needed before it is no longer perceived as novel? We investigated these relationships through a series of studies on object neophobia in jackdaws (*Corvus monedula*) at feeding and nest sites, in both urban and rural settings. Jackdaws often conflict with human interests, yet are able to exploit diverse environments where similar objects may provide different cues based upon their context. Object properties and the context of presentations were varied to uncover what makes an object novel. Our results highlight the specificity of novelty based upon experience, and indicate why neophobia needs to be considered in discussions of behavioural plasticity across environments. These results have implications across applied fields where neophobia and avoidance behaviour can be manipulated to reduce human/animal conflict.

C1.4 Population and seasonal variation in response to prey cues by an eavesdropping bat

Patricia Jones, University Of Texas At Austin
Michael Ryan, Rachel Page

The frog-eating bat, *Trachops cirrhosus*, hunts frogs and insects by approaching these prey's sexual advertisement calls. Previous research has demonstrated that *T. cirrhosus* can rapidly learn to associate novel acoustic stimuli with food rewards. It is unknown how this plasticity is related to natural foraging behavior. We examined population and seasonal variation in bat response to prey calls. Wild-caught adult bats from two populations that differ in available prey species (Soberanía, Panama and La Selva, Costa Rica) were presented with frog calls, katydid calls, and control stimuli. We found significant differences between populations in bat response to the calls of some prey species including the túngara frog, *Physalaemus pustulosus*, and katydid calls, but no significant differences in response to control stimuli.

To compare seasons, bats were captured in Soberanía in dry and wet seasons and presented with the calls of a dry season breeding frog (*Smilisca sila*), a wet season breeding frog (*P. pustulosus*), and four katydid species. We found significant seasonal differences in response to *S. sila* but not *P. pustulosus* or the katydid calls. Our data indicate plasticity in the foraging behavior of this eavesdropping predator, but response to prey cues is not dictated solely by prey availability.

C1.5 Risk-dependent predatory behaviour of an araneophagic assassin bug

Phil Taylor, Macquarie University
Fernando Soley

Web building spiders are formidable predators of insects, with venom and webs that afford them comparably formidable defence. Despite the obvious risks, *Stenolemus giraffa* assassin bugs have 'turned the tables' on web-building spiders, routinely hunting them ('araneophagy') by walking onto the web or by leaning into the web to grasp the resident from adjacent vantage points. Webs transmit even minute vibrations to resident spiders, and we here discuss how *S. giraffa* circumvents this highly sensitive early warning system to approach spiders undetected.

To investigate whether and how *S. giraffa* matches its hunting decisions to detection risk, we manipulated the predatory routes available in pursuits of spider species that build very different web types. For each prey spider species, *S. giraffa* tended to take routes that minimized contact with the web and its support lines. *Stenolemus giraffa* usually resorted to stepping onto the web to pursue spiders only once alternative routes had been

explored, but even then they avoided the dangerous capture area. Hunting routes closely reflected risks of detection, indicating a predatory strategy that is closely linked to the perceptual world of the well-defended prey.

C2: Evolutionary trade-offs

C2.1 Does extra-pair mating select for male philopatry in birds?

Caitlin Stern, University Of North Carolina At Chapel Hill

Janis Dickinson, Kern Reeve

Selection for male philopatry in birds is likely influenced by the costs and benefits of cooperation and competition with kin. However, a general explanation for why birds usually show female-biased natal dispersal as opposed to the male-biased dispersal of other taxa remains elusive. In socially monogamous mating systems with extra-pair paternity (EPP), common in birds, male philopatry can lead to competition among related males over extra-pair matings. Using a game theoretic "tug-of-war" model, we examine the tensions between the costs of competing with relatives for paternity and the potential inclusive fitness benefits of losing paternity to relatives rather than nonrelatives, asking how kin competition over paternity affects selection for male philopatry. The model predicts that selection on coevolving investments in competition results in reduced intensity of competition over EPP between kin compared to non-kin, leading to comparatively reduced fitness costs of kin competition.

Our results suggest a novel explanation for widespread female-biased dispersal in birds, indicating that the relatively high costs of competing with non-kin versus kin over EPP can select for male philopatry. The recently-revealed prevalence of kin structure in populations without known kin-directed cooperative behaviors is consistent with an inclusive fitness advantage to kin competition.

C2.2 The role of auxiliary males in bowerbird courtship

Jess Isden, University Of Exeter
Andrew Griffiths, Caroline Dingle, Carmen Panayi,
Joah Madden

Males may tolerate the presence of competing rivals when the cost of suppressing them is higher than the cost of tolerance. Alternatively, males may gain direct or indirect (genetic) benefits from the

presence of rivals. In male spotted bowerbirds, *Ptilonorhynchus maculatus*, bower owners appear to tolerate the repeated presence of particular males at their bowers which are sites of sexual display.

We describe these males as auxiliaries. Owners risk cuckoldry, especially if auxiliaries are unrelated, or suffer interference to their displays. However, owners may benefit directly from improvement to their sexual display through contributions towards bower maintenance, and added protection from marauding neighbours.

We analysed relatedness between owners and their auxiliaries and their behaviour across multiple breeding seasons. We found that owners were not more related to the auxiliaries at their bowers. We discuss how auxiliary presence influenced bower maintenance, rates of marauding and owner mating success. We also explored potential benefits to auxiliaries. Auxiliaries may gain experience in bower-building and display, and can inherit bowers from owners. This unusual example of joint sexual display presents an excellent opportunity to explore evolutionary trade-offs in multi-male sexual display.

C2.3 Whole organism performance in spiders: relations with morphology and among performance measures

John Prenter, St Mary's University College Belfast
Rowan McGinley, Phillip Taylor

Investigations of whole organism performance link behaviour, morphology and fitness. Invertebrates are popular models for studies of behaviour but not studies of performance.

We examined four performance traits in a jumping spider (running speed, climbing speed, endurance and pulling force) and explored relationships among traits and their association with morphological measures (body size, relative leg length and relative body mass / condition) expected to influence maximum performance capacity and fitness-related activities such as success in foraging, predator avoidance and contests. We identified performance advantages for large size, long legs and high relative mass in male spiders. Running speed, climbing speed and pulling force were all positively related, suggesting overlaps in underlying mechanism and evolutionary synergy. In contrast, endurance capacity was negatively related with running speed and climbing speed, suggesting conflict in mechanism and evolutionary tradeoff. These associations among performance measures cannot

be explained simply as correlates of morphology. Large size conferred greater running speed, climbing speed, and pulling force, but was not associated with endurance. Relative leg length was linked to pulling force, but not to any other performance measure, and relative mass was linked to climbing speed and endurance, but not running speed or pulling force.

C2.4 The influence of cyto-nuclear interactions on behaviour

Hanne Lovlie, Linköping University
Emil Gustavsson, Goran Arnqvist

Despite the longstanding perception of the selective neutrality of mitochondrial genes, there is a growing awareness of their influence on life-history traits via interaction with the nuclear genome. Due to their effect on traits such as metabolism and growth rates, cyto-nuclear interactions are affecting variation predicted to explain the evolution of behavioural types or personalities (i.e. behavioural variation that is consistent within individuals, but differs among individuals). However, while cyto-nuclear interactions have significant potential to explain variation in behaviours, this line of research remains poorly explored.

We used nine cyto-nuclear introgression lines, where three cytoplasmic genomes were introgressed into three nuclear backgrounds, to disentangle genetic effects on both life-history traits and behavioural variation in the seed beetle (*Callosobruchus maculatus*). We show that life-span, but also activity of individuals in behavioural assays are influenced by the interaction of nuclear and cytoplasmic genes. Variation in activity level is consistent among individual beetles, suggesting that intergenomic interactions can also explain variation in animal personality.

These results advance our understanding of the functionality of mitochondrial genes and their non-neutrality, and highlight the importance of cyto-nuclear interactions in explaining variation in behaviour and personality.

C2.5 Should I stay or should I go? Ecological trade-offs and migratory behaviour in a freshwater fish

Ben Chapman, Lund University
Anders Nilsson, Kaj Hulthen, Henrik Baktoft, Jakob Brodersen, Christer Bronmark, Christian Hansson, Christian Skov

Behavioural polymorphisms are widespread in nature, and there has been much discussion about what forces maintain their existence within animal populations. One idea is that ecological trade-offs act to balance the costs and benefits of different behavioural strategies. In my system I study migratory dimorphism in a freshwater fish, the roach. Populations of roach are commonly composed of both migrants and residents, a phenomenon known as partial migration.

I have previously speculated that an ecological trade-off between predation risk and growth potential is important in shaping migratory dynamics in this system, but empirical evidence in support of this idea has been lacking. Here I present data from two studies which show (a) a predation cost to residency and (b) a feeding cost to migration. These data support a predation/growth trade-off model of migration, and may provide important clues as to the forces that maintain migratory dimorphism in nature.

C3: Language & Communication

C3.1 Dialects in short songs of yellow-rumped (*Cacicus cela*) and red-rumped caciques (*Cacicus haemorrhous*): evolution and discrimination at the colony level

Helene Thielges, Ethologie Animale Et Humaine
Laurence Henry, Veronique Biquand, Sarah DuBosq,
Maxime Herve, Pierre Deleporte

A field study has been conducted in French Guiana since 2005, by recording "short songs" of male yellow-rumped and red-rumped caciques. This is a rare field study on Neotropical birdsong, focusing on the Icterid family, a very good model to study the evolution of birdsong in relation with sociality. Short songs are involved in male-male communication in these two colonial multi-male / multi-female species. We found dialects characterized by time and frequency parameters in male short songs in both species. This is the first description for such song and dialect in male red-rumped caciques. We analyzed the temporal evolution of these songs in the two species, over seven years at the same localities. We find dialects each year but the short songs' frequency and time parameters vary from year to year. Playback experiments were also made at different colonies in 2012 for yellow-rumped caciques. We observed in reaction to the stimuli (familiar or unfamiliar song) neither alarm calls or flight, nor aggressive behavior toward the loudspeaker. We discuss the results in relation with

hypotheses for the evolution of bird dialects, with a special focus on social influences on song plasticity.

C3.2 Propagation-induced sound degradation and information coding: a neuroethological analysis of the individual signature in propagated communication calls

Solveig Mouterde, University Jean Monnet
Frederic Theunissen, Julie Elie, Nicolas Mathevon

The detection and recognition of communication signals in natural soundscapes is a difficult task that animals and birds in particular excel at. We have used a neuroethological approach to quantify the recognition performance for propagated communication signals in the zebra finch, specifically regarding the information about individual identity.

We analyzed propagated signals using discriminant function analyses on a set of analytical parameters as well as a complete spectrographic representation of the signals. We found that while call duration and pitch are important parameters at short distances, frequency modulation gains become critical at longer distances. Operant conditioning experiments showed that female zebra finches were able to discriminate male calls at up to 128m but not at 256m, except when trained on the same pair of stimuli for 4 consecutive days. Finally, neurophysiological recordings showed high neural discrimination for calls at short distances and a decline of this ability with the degradation of information as a function of distance. We are currently analyzing the tuning properties of neurons that showed the most invariant responses to propagated sounds and hypothesized that these will be tuned to the parameters that we found were the most informative in the discriminant function analysis.

C3.3 From associative learning to unsupervised learning of complex patterns and of language: can one model do it all?

Oren Kolodny, Tel Aviv University
Shimon Edelman, Arnon Lotem

To study the evolution of advanced cognitive abilities from simple principles, we developed a model (implemented as a computer program) that uses basic elements of associative learning, but can be modified incrementally to facilitate unsupervised learning of complex environmental regularities. The program receives strings of data as input, and

constructs a weighted network that represents associations of items in time and space. It can also segment data sequences, assess their statistical significance, and cluster them into higher hierarchies. We use the same program both to study basic forms of unsupervised learning in animals and to successfully reproduce experimental results of language acquisition by humans. Testing the model in agent-based simulations of animal foraging demonstrates that unsupervised learning is more adaptive than simple reinforcement learning when the environment includes statistical dependencies among non-food items, and when food is relatively rare and time for learning is limited. We show that the model's ability to infer useful foraging paths is equivalent to its ability to construct grammatically correct sentences, based on learning of strings from child-directed speech. Thus, testing the program in increasingly complex foraging environments offers a useful framework for studying the evolution of advanced cognitive abilities from associative principles.

C3.4 Animal vocal sequences: a cross-taxa comparison of their statistical properties

Arik Kershenbaum, National Institute For Mathematical And Biological Synthesis

Many animal species produce vocalisations that are made up of a sequence of stereotyped elements, or "syllables". In some species, the sequences consist of a small number of motifs that are repeated over and over with slight variation. In other species, the vocal sequences seem to vary almost randomly. Understanding the statistical and corresponding neurological processes from which these sequences are generated can shed light both on the proximal role of sequences in inter-individual signalling, and on the ultimate (evolutionary) process of syntactic cognition – an essential precursor of linguistic ability. I present a statistical comparison of the vocal sequences of species from widely varying taxa, including Bengalese finches (*Lonchura striata*), free-tailed bats (*Tadarida brasiliensis*), and rock hyraxes (*Procapra capensis*). Different statistical analyses uncover different features of the properties of the signal sequence, and different statistical models vary greatly in their ability to predict the observed sequences. For many species, the most commonly used model of vocal sequence production, the Markov chain, poorly describes the sequence repertoire, whereas other models such as the renewal process better capture the statistical properties of the sequence. From this, we can draw conclusions about the mechanisms of information encoding and decoding in animal vocal cognition.

C3.5 Wordy warnings: great tits use discrete, graded and combinatorial variation in alarm calls to communicate predator type

Toshitaka Suzuki, The Graduate University For Advanced Studies

Many animals use variation in alarm calls to warn others about different predatory threats. Information about predators can be encoded by producing discrete types of alarm calls and/or through graded variation in a single call type (i.e. calling rate or note repetitions). By combining different calls or notes, animals may be able to convey further complex information. However, little is known about how individuals use discrete, graded and combinatorial variation in alarm calls to denote specific risks. Here, I show that Japanese great tits communicate predator type by using production specificity, graded features and note combinations of alarm calls.

Great tits produce acoustically discrete alarm calls for different nest predators: 'jar' calls for snakes, and 'chicka' calls for crows and martens. Discrete alarm calls elicited different adaptive responses in both adults and nestlings. The tits further discriminate between crows and martens by altering the calling rate and note number of 'chicka' calls. They also use variation in note combinations of 'chicka' calls to denote predator type and caller's identity. Further analysis showed such variation produces a greater potential of information encoding than written English.

This study demonstrates a previously unexpected degree of variation and structural complexity in animal signals.

C3.6 Network analyses provide new insights into song organization: a study on the singing of Common Nightingales (*Luscinia megarhynchos*)

Silke Kipper, Free University Berlin
Henrike Hultsch, Constance Scharff, Michael Weiss

Animals often present their communicative signals in long, heterotype sequences. This complexity has inspired inquiries into similarities of such communication systems to human language. For example, birds often sing their songs in sequences with syntax-like structures. This sequential order has traditionally been described with transition matrices and Markov chain analyses. Here, we present data proving that network analysis provides a powerful

new tool to characterize the order in song sequences.

We analysed long nocturnal song sequences of Common nightingales (*Luscinia megarhynchos*) and translated these sequences into networks of song types with song transitions as connectors (N=19). We compared conventional measures to describe song sequences with network measures. Furthermore, we conducted a playback experiment (N=12) with song types of certain transition properties [those that opened a song sequence to more variety (branches), and those that narrowed sequences to passages of less variety (bottlenecks)]. Male nightingales adjusted their singing depending on the playback, providing first evidence that transition properties of song types might indeed play a role in male-male singing interactions. We conclude that network approaches and measures provide biologically meaningful data to describe the song structure in species with large repertoires and complex rules of song retrieval.

C4: Foraging & Economic Decisions

C4.1 Blob breaks bank: an amoeboid organism's strategy for solving the Two-Armed Bandit problem

Chris Reid, New Jersey Institute Of Technology
Tanya Latty, Hannelore MacDonald, Simon Garnier

Foraging organisms must compromise between sampling the environment to find the best foraging areas, and focusing their efforts on the area of highest return. This is known as the exploration-exploitation tradeoff, and equates to the classical 'Two-Armed Bandit' problem. To solve this problem, a player aims to maximize their gain when faced with two slot machines, each with a distinct but unknown reward rate. An optimal solution to the problem has been established with an algorithm called the Gittins Index, and several taxa (e.g. pigeons and great tits) have been found to optimally balance exploration/exploitation in such foraging experiments. Studies thus far have only been undertaken in organisms with brains, yet the exploration-exploitation tradeoff also applies to unicellular foragers, which must tackle the problem without the aid of neurons. We tested the slime mold *Physarum polycephalum*, which behaves as a self-organized collective system, with the Two-Armed Bandit problem by assessing the effect of sampling on foraging patch choice in a Y-maze. We then used the Gittins Index to assess the optimality of the amoeba's strategy, and thus how well it performs in the exploration-exploitation tradeoff. Our study challenges the common view that

neurological hardware is required to solve complex problems.

C4.2 Waiting For What Comes Later: Capuchin Monkeys Show Self-Control Even For Nonvisible Delayed Rewards

Bonnie Perdue, Georgia State University
Theodore Evans, Jessica Bramlett, Michael Beran

Self control tasks in nonhuman animals typically involve the choice between an immediate option and a delayed, but more preferred option. However, in many self-control scenarios, not only does the more impulsive option come sooner in time, it is often more concrete than the delayed option. For example, studies have presented children with the option of eating a visible marshmallow immediately, or foregoing it for a better reward that can only be seen later. We tested 8 capuchin monkeys to better understand this potential effect by manipulating the visibility of the response options. Subjects observed two food items (20g or 5g piece of banana) each being placed either on top of or inside of one of two opaque holders attached to a revolving tray apparatus. Trials ended when subjects removed a reward from the rotating tray. To demonstrate self control, subjects should have allowed the smaller piece of food to pass if the larger piece was forthcoming. Overall, subjects were successful on the task, allowing a smaller, visible piece of banana to pass from reach in order to access the larger, nonvisible banana piece. This finding suggests that capuchin monkeys succeed on self-control tasks even when the delayed option is also more abstract than the immediate one – a situation likely faced by primates in everyday life.

C4.3 Choice impulsiveness and the producer-scrummer game: modulated representations of food value in the nucleus accumbens of the domestic chicks

Toshiya Matsushima, Hokkaido University
Chentao Wen, Hidetoshi Amita

Impatience might be a beneficial trait in the context of scramble kleptoparasitism. Actually, in week-old domestic chicks, competitive foraging experiences enhanced impulsiveness measured by inter-temporal choice paradigm, so that immediate food option was chosen more frequently even though the expected profitability was unchanged. Nucleus accumbens (NAc) has so far been assumed to play a pivotal role in the accompanying temporal discounting, as localized lesion caused chicks to

make impulsive choices (Izawa et al. 2003). We therefore examined whether neuronal activities in NAc could be contextually modified by competitive foraging. Single unit activities were recorded in freely behaving chicks in cue color discrimination task reinforced by delayed food. The NAc neurons showed activities in 3 periods of the task, namely (1) *cue* period when the food was anticipated, (2) *delay* period after the decision was made, and (3) *reward* period when food was finally delivered. Even though the food was not scrounged, pseudo-competition suppressed the *cue* and *reward* activities, whereas the *delay* activities did not change. The suppression of reward values in NAc could underlie the social modulation of impulsiveness in domestic chicks, although direct causal links remain to be shown.

C4.4 Do monkeys and great apes like risk?

Attraction of gains drives gambling behaviour

Amelie Romain, University de Strasbourg
Marie-Helene Broihanne, Bernard Thierry, Josep Call, Valerie Dufour

Trading has often been considered a hallmark of human behaviour, but nonhuman primates can also demonstrate bartering skills. Humans are expected to rationalise their decision (bartering or not) according to risk inherent to the transaction. However, they sometimes deviate from rationality and are influenced by their own perception of risk (being risk-prone or risk-averse). Here we investigate whether similar deviations can be found in six primate species. We test two monkey species, capuchins and Tonkean macaques, and great apes, orang-utans, gorillas, bonobos and chimpanzees. We involve subjects in a risky situation using a food gambling task, where gains and losses are at stake. Subjects can predict the odds of losing or gaining by viewing the possible rewards but they have no certainty about which one they will receive. Results show that subjects adapt their gambling according to the odds of gain, although they do not demonstrate perfect accuracy. Most of the monkeys and great apes appear to be risk prone rather than risk averse. Interestingly, in all species, the odds of gains have the strongest effect in decision-making, leading subjects to gamble. Our study shows that attitudes towards risk might influence decision-making in nonhuman primates, like in humans.

C4.5 Animals searching for food should discount hyperbolically, not exponentially

Benja Fallenstein, University Of Bristol

Laboratory experiments on impulsive behavior suggest that animals value delayed rewards according to hyperbolic discounting, but adaptive explanations based on the possibility of interruptions (such as by predators) normally predict exponential discounting instead. A common feature of these accounts is that they assume that delays are deterministic. In nature, however, delays while searching for food are likely to be variable and exponentially distributed. Here I consider the optimal behavior of an animal that has evolved to expect variable delays. I show that if the animal uses the deterministic delay in an experiment to estimate the rate of finding food items, then optimal behavior follows hyperbolic discounting. I propose a mathematical model in which animals treat the beginning of each trial as finding a promising patch, and the end of each trial as being interrupted while foraging in this patch. This proposal combines features of the two main adaptive explanations for hyperbolic discounting: random interruptions and maximization of the rate of energy intake. I discuss how the model can account for several findings from behavioral experiments as well as from studies of discounting in the dopaminergic reward system.

C4.6 Starlings uphold principles of economic rationality

Marco Vasconcelos, University Of Oxford & University Of Minho
Tiago Monteiro, Alex Kacelnik

According to both microeconomic and optimality models, rational decision makers should not show circular preferences, or alter relative preference between alternatives depending on the presence of other options. These principles of rationality are important for economists to predict individual behaviour and its consequences for markets, and for biologists to apply evolutionary logic to understand behaviour assuming the maximisation of Darwinian fitness. Reported violations of rationality in non-humans include intransitivity (i.e., circular preferences) and lack of independence of irrelevant alternatives (changes in relative preference between options when embedded in different choice sets), but the extent to which these observations truly represent breaches of rationality is debatable. We tested both principles with starlings (*Sturnus vulgaris*), training subjects either with 5 options differing in food delay (Exp. 1) or with 6 options differing in reward probability (Exp. 2), before letting them choose repeatedly one option out of several binary and trinary sets of options. The

starlings conformed to economic rationality on both tests, showing strong stochastic transitivity and no violation of the independence principle. The results endorse both axiomatic microeconomics and optimality assumptions in behavioural ecology.

C5: Applied Ethology

C5.1 Emotional valence: Is it reflected in call types and in acoustic properties of piglet vocalizations?

Marek Spinka, Institute Of Animal Science Prague
Celine Tallet, Pavel Linhart

How emotional valence is encoded in mammalian vocalizations is a prominent question in animal-welfare-oriented bioacoustics. We assessed this question using 1513 calls produced by 84 piglets in 11 situations. The negativity of the situations was ranked based on judgments of 28 pig behaviour experts. The acoustic quality of calls was described with 8 acoustic parameters. K-means clustering method was used to classify the calls into 5 call types. Statistics were calculated based on situation means (N=11, P adjusted for multiple testing). More negative situations were associated with longer calls ($r_s = -0.80$, $P = 0.025$) but no other acoustic parameter was associated with the experts' ranking of situations. The proportion of high-pitched, stable frequency "scream" calls was higher in more negative situations ($b = -0.55$, $P = 0.012$) while medium-pitched tonal "croaking" calls were increasing in more positive situations ($b = 0.34$, $P = 0.012$). Thus the acoustic quality and the call types were related to the expert-ranked negativity of the situation but not as much as expected. The experts might have overrated negativity of some human-induced situations (eg, brief isolation) and underrated negativity pig-induced situations such as fighting for teats. Emotional valence is encoded in piglet vocalizations but animal-based measures of the situations' negativity are needed to assess the relationship precisely.

C5.2 Chronic noise affects predator avoidance behaviour via trade-offs in resource use

Sophie Holles, University Of Bristol
Stephen Simpson, Erica Morley, Andrew Radford

Trade-offs in resource allocation are vital to survival through developmental stages. Many recent studies have revealed impacts of anthropogenic noise on a wide variety of taxa including birds, mammals and fish varying from stress responses, to disruption of vital cue detection via distraction and masking. In this study we investigated the impact of chronic

noise through early stages of development in an economically important vulnerable species where recruitment is vital for population dynamics; Atlantic cod (*Gadus morhua*).

Three experiments revealed that 1) acute exposure to ship noise playback caused startle responses; 2) chronic exposure to ship noise playback lead to reduced body condition and 3) reduced body condition was linked with reduced survival time in a predator avoidance experiment. We propose two mechanisms where trade-offs may affect body condition and as a result, predator avoidance behaviour: a cognitive trade-off in the allocation of attention to noise versus foraging, affecting resource acquisition; and a physiological trade-off in resource allocation to growth and development versus the metabolic load incurred by chronic adrenal activation.

These experiments reveal that anthropogenic noise has the potential to impact behaviour, survival, population dynamics and selection through trade-offs in resource allocation during developmental stages.

C5.3 Simple environmental enrichments improve reproductive success in a model captive carnivore, the American mink (*Neovison vison*)

Rebecca Meagher, University Of Guelph / University Of British Columbia
Jamie Dallaire, Dana Campbell, Maria Diez-Leon, Misha Buob, Georgia Mason

Unstimulating enclosures typically reduce welfare, and some hypothesise that they impair reproduction (e.g. in breeding centres/zoos). We tested this hypothesis via a large-scale experiment on three mink farms. We selected two 3-month-old male-female pairs from each of 260 families, providing one pair/family with balls and a hose or chain. Temperament (in "stick tests") and play were assessed two-three months later; and fur-chewing scored in the c. 60% subjects "pelted" at 7 months. Enrichments increased play, and reduced fearfulness (plus aggression on one farm) and fur-chewing. As adults (9-10 months), faecal cortisol metabolites (FCM) and locomotor stereotypies (e.g. pacing) were assessed; mating observed in a male sub-sample; and 380 new age-matched individuals recruited (half enriched). Enrichments did not reduce stereotypies, and only reduced FCM on one farm. However, enriched males copulated for longer than controls, and life-long enriched females had reduced infertility. Once litters were born, c. 20% of females were given elevated shelves for resting.

These reduced nursing females' stereotypy and their infants' mortality. The "balls-and-chain" group's new recruits also had reduced infant mortality (suggesting novelty enhances enrichment effects). These benefits combined additively, increasing numbers of infants weaned by over 25%. Enrichments can thus enhance reproduction as well as welfare.

C5.4 An agent-based model of tail biting behaviour in pigs

Iris Boumans, Wageningen University
Gert Jan Hofstede, Imke de Boer, Eddie Bokkers

Tail biting in pigs is an abnormal behaviour frequently observed in pig husbandry, because housing systems often do not provide enough stimuli to fulfil pigs' needs to forage and explore. The aim of this study was to investigate the suitability of an agent-based approach for modelling tail biting behaviour of pigs. Based on empirical pig behaviour studies, a spatially explicit agent-based model was constructed in Netlogo to simulate the behaviour of group housed pigs. Key behaviours of the agents (pigs) in the model were determined by internal states of agents and environmental stimuli. The effects of enrichment and group density on internal states, behavioural patterns, the frequency of tail bites, and pigs changing into victims, biters, or both biter and victim of tail biting were studied. Results showed that at a high group density and in a barren environment the frequency of tail biting behaviour on group level could increase exponentially, which corresponds to empirical data in literature. The model allows to further study behaviour of pigs in different environmental settings and the effect of farmers' interventions. We, therefore, believe that agent-based modelling is a suitable technique to contribute to developing novel housing systems that better meet pigs' needs.

C5.5 Species differences in behaviourally plastic responses to a novel environment

Mary Montague, School Of Biological Sciences
Hansjoerg Kunc

Behavioural plasticity is the ability of an individual to adjust its behaviour to changing environmental conditions. Bird song is a plastic trait and only species with sufficient acoustic behavioural plasticity may be able to adjust their signals to the environmental change caused by anthropogenic noise. As bird song is sexually selected and contributes to breeding success, this could facilitate

species persistence in urban habitat. Previous studies have shown that birds sing higher pitched songs in areas with high levels of anthropogenic noise. This difference is likely to be due to the behaviourally plastic adjustment of song to changes in the acoustic environment. Therefore, species might differ in their ability to adjust to novel environmental conditions.

To test whether species differ in their behavioural plasticity in response to changing environmental conditions, we conducted noise exposure experiments on nine passerine species. We found a consistent response in the direction of the adjustment of song. However, patterns of adjustment diverged between species. These divergent song adjustments may correspond to species-specific differences in behavioural plasticity.

Our results suggest that novel environments modify the plastic expression of sexually selected traits across species differently.

C5.6 Individual housing impairs reversal learning and novel object recognition in dairy calves

Daniel Weary, University Of British Columbia
Charlotte Gaillard, Ruan Daros, Marina von Keyserlingk

Early social housing is thought to benefit cognitive development in animals. Dairy calves are typically housed alone but no work to date has addressed the effect of this practice on cognition. The aim of this study was to determine the effects of housing on two measures: reversal learning and novel object recognition.

Calves were housed individually in a standard calf pen (n=8) or kept in pairs using a double pen (n=10) and trained in a Y-maze to discriminate two colours (black/white) until they reached 80% correct responses over three consecutive sessions. Training stimuli were then reversed and training continued until calves once again reached this criterion. Calves from both treatments learned the initial discrimination at similar rates, but the individually-housed calves made more incorrect responses before they reached the criterion in the reversal task ($F_{1,14}=7.33$, $P=0.018$). Calves were exposed to a novel object (a red bin) 8 times over a 48-h period. Pair-housed calves reduced exploration with repeated testing ($F_{1,61}=10.25$, $P=0.002$), but the individually-reared calves responded similarly each time they were tested ($F_{1,55}=0.08$, $P>0.05$), suggesting they were unable to recognize the object.

Together, these results provide the first evidence that individual housing impairs cognitive performance in calves.

C6: Vigilance & Anti-Predator Behaviour

C6.1 Costs and benefits: The role of predation in ladybird laying strategies

Sarah Paul, University Of Exeter
Martin Stevens, Jason Baverstock, Judith Pell, Jon Blount

Chemical defence is widespread across taxa and in many cases toxins are passed from mother to offspring via the egg, protecting what is often the most vulnerable stage in the life cycle. Toxin production or sequestration can be costly, and consequently mothers may face a trade-off in the allocation of resources to maximise offspring number versus offspring quality (i.e. levels of chemical defence). If so, in environments where the risk of predation is high, mothers may be predicted to produce fewer, robustly defended offspring. Alternatively, in such environments mothers may withhold investment in egg production altogether, in order to maximise future reproduction when conditions are more favourable (i.e. 'bet hedging'). In this study, we tested these predictions using the UK native 2-spot ladybird (*Adalia bipunctata*) and the invasive alien harlequin ladybird (*Harmonia axyridis*) – a significant intraguild predator – as a study system. Results show differing investment in egg production depending on predation risk and are discussed in the context of potential reproductive trade-offs and consequences for our understanding of intraguild interactions in these important pest control species.

C6.2 Geometry of Collective Detection in Zebrafish (*Danio rerio*)

Delia Shelton, Indiana University
Brittany C. Price, Erik Wegner-Clemens, Emília P. Martins

By living in groups, animals can benefit from enhanced detection of food patches, suitable habitat and predators. Certain spatial arrangements can create super-sensory systems that detect disturbances faster than could any solitary individual. The spatial orientation of a group can also reduce individual vigilance time thereby reducing the total time any one individual is vigilant. Here, we investigated individual and collective geometry of zebrafish (*Danio rerio*) in response to weak water flows. By varying the flow rate, we

asked 1) whether groups vary their spatial arrangements in ways likely to enhance detection in and 2) if individuals exhibit behavioral variation consistent with relying on group dynamics to reduce individual vigilance.

We found that groups of zebrafish responded to increasing flow rates by elongating and remaining oriented perpendicular to the water flow thereby potentially enhancing the ability of the group as a whole to detect disturbances. In contrast, individual fish oriented randomly in the water column showing no evidence of placing themselves to maximize detection using the lateral-line system. Taken together, the results suggest that zebrafish use group behavior to enhance detection and allow for greater individual behavioral flexibility for members.

C6.3 Living in a landscape of fear: responses of primates to spatial variation in predation risk

Russell Hill, Durham University

Predation is a key selective force driving animal evolution with almost all species engaged in some form of predator-prey interaction. How animals manage the risk of predation is a central issue in ecology, but also one of the most challenging to study. Here I take a landscape of fear approach to examine the impact of predators on their diurnal primate prey, drawing on behavioural data from my Primate & Predator Project for vervet monkeys (*Cercopithecus aethiops*) and samango monkeys (*Cercopithecus mitis erythrarchus*) in South Africa.

Despite differences in substrate use by the two species, the results suggest that predation risk is more significant than other ecological factors such as food availability in determining range use for both primates, although the primary predator varies. Furthermore, for samango monkeys, the landscape of fear also leads to predictable spatial variation in vigilance behaviour. Through adopting a spatial approach to predation risk that incorporates the independent effects of different predator guilds we can start to understand the precise significance of predation in shaping animal behaviour.

C6.4 Using intraflock association patterns to understand why different bird species join mixed-species flocks

Hari Sridhar, Centre For Ecological Sciences, Indian Institute Of Science
Kartik Shanker

Birds join mixed-species flocks (flocks hereon) either for direct foraging or anti-predation benefits. In this study, conducted in an Indian tropical evergreen forest, we developed and used a novel approach based on intra-flock association patterns to obtain a community-wide assessment of flock participation benefits. The rationale of our approach is as follows. To obtain direct foraging benefits (flushed prey, kleptoparasitism or copied foraging locations), individuals need to be physically proximate to particular heterospecific individuals within flocks. Alternatively, for anti-predation benefits, physical proximity to particular heterospecifics is not required, i.e. just being within the flock will suffice. Therefore, based on species' choice of within-flock locations, we can infer whether they are obtaining direct foraging or anti-predation benefits. Using this approach (2385 focal observations across 29 species in 370 flocks), we found that only a small subset of the bird community (5/29 species), composed of all members of the sallying guild, showed non-random physical proximity to heterospecifics within flocks. Majority of species (24/29) chose within-flock locations randomly with respect to heterospecifics. Our findings suggest that only a minority of species (all sallying species) obtain direct foraging benefits in flocks while the majority (all non-sallying species) joins flocks for anti-predatory benefits.

C6.5 Sentinel behavior: Between anti-predator mechanism and social information gathering

Yitzchak Ben Mocha, Tel Aviv University

The role of sentinel behavior is still contested. The presented study is based on eight consecutive months of intensive observations on six social groups of Arabian babblers (*Turdoides squamiceps*), each including at least two competing males. It found that, in accordance with empirical evidence and theoretically grounded predictions, predator presence has a significant positive effect on the duration of sentinel behavior. However, in contrast to those predictions, this effect is short-lived. On the other hand, social factors such as the presence of foreigner conspecifics have a stronger effect. Moreover, differences, within the same individual and among social ranks, were observed in relation to the group's location within the territory. Beta males - whose reproductive options within the group are restricted and who therefore face the dilemma whether to stay in their group or whether to disperse - were found to increase their sentinel effort at the border of the territory, where the social information that is needed for the above described

decision is available. This suggests that they seize the sentinel position to collect and/or convey social information.

The study thus indicates that there are other functions, of social nature, which explain an additional portion of the phenomena of sentinel behavior.

C6.6 Can defense behavioral patterns explain the population depletion of *Tayassu pecari*?

Selene Nogueira, Universidade Estadual De Santa Cruz

Aline Reis, Stefane Marsaro, Viviana Moreto, Sergio Nogueira-Filho

We aimed to test the hypothesis that differences in defense behavioral traits explain why two sympatric species, *Tayassu pecari* (WLP) and *Pecari tajacu* - (CP), show different conservation status: WLP is a near-threatened species and CP is of least concern. To this end, we compared the behavioral responses of 10 WLPs and 10 CPs, five males and five females of each species, through a modified mouse defense test battery - (MDTB). Behavioral responses were analyzed using PCA followed by t-Student tests to compare both species' factor scores. We also compared their plasmatic cortisol concentration before and after MDTB. We differentiated WLPs from CPs in six out of seven tests. WLPs were related to confident behavioral patterns, such as exploring new environment ($r=0.78$) and threatening the predator model ($r=0.85$), while CPs were related to alert ($r=0.67$) and retreat ($r=0.92$) fear patterns. WLPs showed higher plasmatic cortisol concentrations than CPs ($P<0.05$), both before (0.63 vs 0.45 ng/dL) and after (0.93 vs 0.75 ng/dL) battery tests, independent of sex. Therefore, CP awareness may help to prevent its population decrease in overhunted areas, while WLP boldness, besides habitat deforestation, may contribute to including this species in the near-threatened category.

C7: Olfaction

C7.1 Influences of relatedness and the social environment on family odors in the European earwig

Janine Wong, University Of Basel

Joel Meunier, Christophe Lucas, Mathias Kölliker

Relatedness can increase the level of cooperation between group members and, thus, result in inclusive fitness benefits via kin selection. However,

gregarious species also face the risk of kin competition and inbreeding. Kin recognition mechanisms simultaneously enable cooperation between kin and inbreeding avoidance. Recognition cues can be determined genetically or environmentally. The European earwig (*Forficula auricularia*) displays group living and social behavior throughout its life-cycle and previous research showed detrimental effects of inbreeding on fitness. Our experiment aimed to disentangle the contributions of heritable variation and the social environment on the putative recognition cues in *F. auricularia*.

We experimentally manipulated the number of male mates and reared the offspring in pure versus mixed family groups to adulthood. We subsequently extracted and analyzed the cuticular hydrocarbons (CHC), which have known functions in earwig social interactions, and as kin recognition cues in other social insects. We found family specific CHC-profiles. The accuracy of assigning individuals to their family decreased with higher genetic diversity. Furthermore, the likelihood of correctly assigning individuals to their family was higher for individuals raised with only their siblings compared to individuals that were raised in groups originating from mixed families. Our results show that in *F. auricularia*, individuals exhibit family specific CHC-profiles that have a heritable component, but they are also influenced by the social environment.

C7.2 Olfactory Ecology of the Syrphid, *Episyrphus balteatus*

Daniel Reed, Newcastle University
Colin Tosh, Gordon Port

The ability of pollinators to detect plant odours and species specific scent marks has been well studied but almost all of this work has concentrated on species of bees.

We investigated the syrphid *Episyrphus balteatus* and its ability to detect and learn to associate these odours with a reward. In field trials we used previously bagged and previously unbagged flowers to test visitation rates. Both bees and syrphids showed a significant preference for the previously bagged flowers. This provided good evidence that bees and syrphids could detect a reward without landing on the flower. We followed this with laboratory trials in which visitation behaviour of syrphids was recorded. We presented different odours and associated these with rewarding or unrewarding artificial flowers to discover if they were able to learn odour cues when making short

range foraging decisions. *E. balteatus* consistently learned and responded to both *Bombus* scent marks and a plant volatile (1-hexanol). The syrphids were able to develop short term memory based on exposure to these odours and learned to avoid scented artificial flowers when reward in both scented and unscented flower was equalised. We discuss possible applications of this finding and implications for pollinator and pest control management.

C7.3 Reward value plays different role in olfactory learning by sexual and unisexual *Trichogramma brassicae*

Hossein Kishani Farahani, University Of Tehran
Ahmad Ashouri, Martin Shapiro, Seyed Hossein Goldansaz

During an associative conditioning process, conditioned responses can be modified by rewards of different value which are offered. Effects of reward value, host age, were studied in learning type and memory duration of sexual and asexual strains of *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae). Two types of host eggs were used as reward: Fresh host eggs (one day old) as high value reward and old host eggs (45 days old) as low value reward. According to our observations, asexual wasps showed associative learning when they exposed to fresh and old host eggs whereas sexual strain showed associative learning when they were exposed to fresh host eggs. Sexual wasps showed aversive learning when they were offered by old host eggs. Memory lasted 20 h and 12 h for sexual and asexual strains when they were exposed to fresh eggs respectively. Asexual wasps showed a 10 h memory duration when they were offered by old eggs. As our result showed, sexual and unisexual strains showed a completely different behavior in response to reward value.

C7.4 Olfactory mediated social networks in fish

Tanja Kleinhappel, University Of Lincoln
Oliver Burman, Anna Wilkinson, Libby John, Tom Pike

The structure of animal groups, such as shoals of fish, can be highly complex, with studies suggesting that these interactions are far from random. In three-spined sticklebacks (*Gasterosteus aculeatus*), conspecific odour cues are used to inform shoal choice and maintain shoal cohesion, yet nothing is known about how these cues might mediate intra-shoal interactions. We investigated whether the social network structure of stickleback shoals, in

same and mixed species contexts, could be mediated by olfactory cues.

Sympatric three- and nine-spined sticklebacks (*Pungitius pungitius*), fed with diets based on Chironomid larvae or *Daphnia*, were used to generate replicated social networks. Depending on the condition, shoal members differed in diet and/or species.

Results across species show that not only is the network structure of stickleback shoals non-random, but interactions can be mediated by association preferences for fish from the same diet treatment (irrespective of species), most likely through diet-derived odour cues. A difference in the amino acid composition of urinary secretions between fish on the two diet treatments indicates a possible mechanism mediating the observed social interactions.

These findings provide detailed insights into the mechanisms underlying intra-group interactions in shoaling fish.

C7.5 Can parrots sniff each other out?

Milla Mihailova, Deakin University
Mathew Berg, Kate Buchanan, Jacqui Adcock, Andy Bennett

Recently, there is growing evidence that birds use odour for a range of functions. Several studies have investigated olfactory abilities in Psittaciformes, but only a handful have investigated the role that olfaction plays in communication. The crimson rosella (*Platycercus elegans*), a parrot species complex of south-eastern Australia, is an excellent candidate for studying olfactory signalling. It is a highly variable species, featuring populations that differ dramatically in plumage colour and genetics. It also produces a strong, distinct plumage odour, which to our knowledge has never been investigated. Combining field and lab experiments, and chemical analyses, we studied whether the crimson rosella was able to discriminate the odour of conspecifics and whether the chemical composition of the plumage odour conveyed information about individual genetic diversity, subspecies, sex, age and parasite infection. In both the field and the lab, we tested for evidence that individuals discriminate their own species-specific odour.

Our analysis on the chemical composition of the plumage odour tested for differences across sexes, subspecies and parasite infection. In conclusion, our

study shows that bird species may use odour as a signal for species recognition and that certain chemical compounds may provide information on individual identity, genetics, sex, subspecies and health.

C7.6 Olfactory Imprinting in Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead (*O. mykiss*) embryos

David Noakes, Oregon State University
Andy Dittman, Ryan Couture, Joseph O'Neil

Adult Pacific salmon use chemical cues to return to their freshwater spawning locations, from imprinting as juvenile smolts. If they imprint on the chemical features of their water during embryonic development, artificially imprinting hatchery salmon will be technically feasible from a management perspective.

We reared Chinook salmon and steelhead trout in different sources of river water or well water. We tested all fish against all possible water sources, in pair-wise combinations. Each fish was tested once soon after yolk depletion. Fish were tested in Plexiglas Y-maze tanks in the dark to minimize any visual cues. At the end of each trial, we recorded the location of each fish and designated odor choice as the arm with more fish at the end of the trial. All fish preferred river water compared to well water, regardless of their rearing water, suggesting an intrinsic attraction of "surface" water. Fish responded equally to different sources of river water, suggesting they have similar chemical signals. Fish reared in well water showed an increased attraction to well water, suggesting that early learning occurs. We discuss the implications for rearing water sources and imprinting for hatchery and wild salmon.

C8: Reproductive Decisions

C8.1 Being on time: attendance patterns provide a key to reproductive success

Kristine Meise, University Of Bielefeld
Fritz Trillmich

In polygynous species, males maximize reproductive success by monopolizing access to females. Large body size is predicted to correlate with dominance and mating success. Alternatively males may enhance mating success by attendance in proximity to females. However, if female oestrus occurs asynchronous, males are unable to attend colonies for entire breeding seasons. In Galápagos sea lions

(*Zalophus wollebaeki*) the reproductive season is exceptionally long (>5 months).

Do males of different sizes attend the colony at different times to reduce competitive interactions? Colony attendance rather than territoriality was the best predictor of male mating success. Accordingly, attendance is expected to increase at peak breeding time. Only small males, unlikely to reproduce in the presence of competitive rivals, should decrease attendance to avoid harassment by other males. Territorial males were sighted most often. Size of non-territorial males did not affect attendance at the beginning of the season, but during the peak breeding season the percentage of days sighted increased with body size. For non-territorial males, reproductive success was positively correlated with male attendance. This correlation only held for the beginning of the season, suggesting that non-territorial males may benefit from the less competitive situation at the beginning of the season.

C8.2 Getting late: laying dates and density dependence

Rudy Jonker, Bielefeld University
Nayden Chakarov, Holger Schielzeth, Tim Schmoll, Oliver Krueger

The ability of individuals to respond to a changing environment is crucial in times of rapid environmental change and the influence of climate change on laying dates has been shown in many bird species. With increasing spring temperatures, the peak of food availability advances, making adjustment of laying dates important to raise offspring successfully. However, competition for food is also thought to affect laying dates. Here we show how temperature and density affect individually-based laying dates of common buzzards, which have delayed breeding by 7 days over the 23 year study period. We show that this delay in laying dates is mostly influenced by an increasing population density and hardly by the opposite effect of increasing temperatures. We also show that over time, selection on early breeding has become weaker, and there seems to be selection for synchronized breeding, which is very unusual in a strictly territorial raptor species. Moreover, individuals that bred more than one year bred more synchronized than single-time breeders, which suggests that either these individuals gradually learn to synchronize, or that the synchronizing individuals have intrinsically higher chances of surviving to the next year.

C8.3 Experimental manipulation of hatching asynchrony magnitude influences sibling competition run and outcome

Thomas Merklung, University Of Toulouse
Lena Agdere, Elise Albert, Romain Durieux, Scott A. Hatch, Etienne Danchin, Pierrick Blanchard

In unpredictable environments, any tactic that affords avian parents greater control over food distribution in order to adjust brood size according to environmental conditions should be favoured. Hatching asynchrony, which occurs whenever incubation commences before clutch completion, has been suggested to be such a tactic among birds. For instance, the sibling rivalry hypothesis states that the natural hierarchy establishment, concomitant to hatching asynchrony, should reduce sibling competition and allow parents to preferentially feed the older chick, with the younger eventually dying from starvation when conditions are poor. Some studies have tested this hypothesis, but none of them investigated the effect of an upward and downward manipulation of hatching asynchrony on chick behaviour, growth and survival. We conducted such an experiment on the black-legged kittiwake (*Rissa tridactyla*). In accordance with the hypothesis, synchronous hatching increased aggression and feeding rates, but the reverse was true for begging rates. Moreover, with increasing hatching asynchrony the younger chick was attacked and begged proportionally more often, had slower growth and was more likely to die than its sibling.

Altogether, our results suggest that the natural magnitude of hatching asynchrony may be adaptive as it moderates sibling competition and chick losses

C8.4 Selfish mothers? An empirical test of parent-offspring conflict over extended parental care

Anindita Bhadra Indian Institute Of Science
Education And Research
Kolkata Sreejani, Sen Majumder, Manabi Paul

Parent-offspring conflict (POC) theory is an interesting conceptual framework for understanding the dynamics of parental care. However, this theory is not easy to test empirically, as exact measures of parental investment in an experimental set-up are difficult to obtain. We have used free-ranging dogs *Canis familiaris* in India, to study POC in the context of extended parental care. We observed females and their pups in their natural habitat for the mother's tendency to share food given by humans with her pups in the weaning and post-weaning

stage. Since these dogs are scavengers, and depend largely on human provided food for their sustenance, voluntary sharing of food by the mother with her pups is a good surrogate for extended parental care. Our behavioural observations convincingly demonstrate an increase of conflict and decrease of cooperation by the mother with her offspring over given food within a span of 4-6 weeks. We also demonstrate that though the competition among the pups in a litter scales with litter size, the conflict shown by the mother is independent of the size of her litter.

C8.5 Paternal investment in a polygynous cooperative breeder is both fixed and biased

Arne Jungwirth, University Of Bern
Michael Taborsky

Polygamous animals can increase their reproductive effort with every additional partner, thereby compromising future fitness; or they divide a fixed amount of effort by the number of partners, either equitably, or in a biased way reflecting partner preference. In polygynous cooperative breeders, not only mate quality but also the quality of mates' resources may vary, for instance the quantity and quality of brood care helpers assisting female breeders. In the highly social cichlid *Neolamprologus pulcher* males defend a varying number of breeding territories, each containing a female breeder and a diverse number of differently sized helpers.

We compared time allocation and behavior in the field between males paired with 1-6 females. The more territories a male monopolized, the less time it spent feeding and the more effort was allocated to conspecific aggression, whereas total parental investment was unaffected. Nevertheless, males distributed investment unevenly among mates, so that certain harem members received as much paternal effort as monogamous partners. Apparently polygynous males (1) keep parental effort constant regardless of the number of mates, but (2) they bias time and effort allocation towards preferred groups. Raised intraspecific competition is paid by reduced feeding time, which may ultimately diminish residual reproductive value.

C9: Social Learning

C9.1 Do zebra finches copy?

Lauren Guillette, University Of St Andrews
Kate Morgan, Zach Hall, Ida Bailey, Susan Healy

As a social species it might be expected that zebra finches would copy food choices of more experienced conspecifics. Copying is typically tested by presenting observers with two demonstrator birds that differ in some way (e.g., sex, familiarity, leg-band colour, postnatal condition), each feeding on a different colour food (or food hopper). However, using this paradigm, if the observer exhibits a preference, it remains unclear whether the observer is copying the choice of one individual or avoiding the choice of the other bird.

Furthermore, observers are never tested for possible pre-existing preferences for one colour over the other. Therefore we presented the observer bird with only one demonstrator eating from only one of two coloured food hoppers. We found that observers in same-sex dyads tended to avoid the colour of demonstrators while observers in mixed-sex dyads either copied or avoided colour choice of demonstrators. We also determined whether birds without demonstrators preferred to eat from one or other coloured hopper. Most of these control birds strongly preferred one or other coloured hopper. These pre-existing colour preferences could explain the apparent copying data and, indeed, may explain all the apparent evidence for copying in zebra finches in the literature.

C9.2 Social foraging strategies and acquisition of novel foraging skills in wild, cooperative breeding, Arabian babblers

Oded Keynan, Tel Aviv University
Arnon Lotem, Amanda. R Ridley

Social foraging strategies and their interaction with learning and innovation abilities have been studied extensively in flocking birds, but their importance for cooperatively breeding birds has been relatively unexplored. We studied social foraging strategies and the acquisition of a novel foraging skill in 17 groups of wild, cooperatively breeding, Arabian babblers (*Turdoides squamiceps*). We used a foraging grid of 96 feeding wells that was provided to the birds in the field, allowing them to search for food (produce) or join other birds (scrounge). Young males scrounged significantly more than dominant males and females. However, scrounging was not related to poor learning ability or neophobia, because almost all individuals who learned a new foraging skill in the second experiment (removing a rubber lid to reach food) were young (<2 years). In this second experiment young individuals spent longer time on the grid than adults, suggesting that their ability to acquire a new skill may be related to higher motivation, which is in line with the

"necessity drives innovation" hypothesis. Finally, birds that didn't learn scrounged on the feeding wells opened by young, suggesting that the ability of young helpers to solve novel tasks may benefit the group.

C9.3 Experimental evidence for social learning and for the importance of self-experience in mediating its success in house sparrow fledglings

Noa Truskanov, Tel-Aviv University
Arnon Lotem

Studies of small passerines and pigeons suggest that joining conspecifics and scrounging on their food findings may block learning of food related cues, thus hindering social learning. Here we show, however, that hand-raised house sparrow (*Passer domesticus*) fledglings that are imprinted on a mother model and scrounge on her food findings, can readily learn to use the sand color chosen by the mother as a cue for the presence of food during independent foraging. Our experiment also demonstrates that such social learning may indeed be less effective when it is not mediated by self-learning: Fledglings in our experiment were assigned into two groups. In the first, the mother exposed the seeds and allowed fledglings to approach them directly; in the second, she merely pointed to the location of the seeds, coercing the fledglings to dig actively in the sand. Although fledglings of both groups learned to prefer the color chosen by the mother, this preference was significantly stronger in the second group. Furthermore, a step-by-step analysis of the learning process suggests that fledglings gave more weight to successes that resulted from active search than from finding seeds exposed by the mother.

C9.4 Observational learning in Great Tits

Anders Brodin, Brodin Lund University
A. Utku Urhan

Even though pilfering of other individuals' caches is reasonably common among scatter hoarding birds, the ability to memorize positions of caches made by others in order to retrieve the food later seems occur only in some species of corvids. In smaller birds such as parids (titmice and chickadees) observational learning of this type has not been found. The great tit, *Parus major*, is a non-storing parid. Observations of great tit behaviour at bird feeders made us hypothesize that it could possess this ability. In a laboratory experiment we allowed caged great tits to observe caching marsh tits in a

typical set up for caching studies. The great tits remembered caching locations both one and 24 hours after observation. This is the first time observational spatial learning of this type has been demonstrated in such a small bird species. We argue that this ability is rare because it might be cognitively more advanced than the memorization hoarders make of their own caches. The reason is that it requires understanding of allocentric space, for example, angles and distances will differ between observation and recovery sessions. Furthermore the close inspection of the cache that hoarders do after caching will usually not be possible.

C9.4 The local enhancement conundrum: in search of the adaptive value of a social learning mechanism

Michal Arbilly, University Of St Andrews
Kevin Laland

Mechanisms of social learning (the acquisition of information through others) vary in their degree of complexity as well as in their prevalence in nature. Local enhancement (LE) is learning about a specific stimulus at a specific location, and stimulus enhancement (SE) is learning the properties of a stimulus that generalize to similar stimuli at other locations. While the latter appears more useful to an animal, empirical evidence suggests that the former is much more widespread. Simulating populations engaged in a producer-scrounger game, we used mathematical models to identify the adaptive benefits of reliance on LE and/or SE, and the alternative conditions favoring their evolution. Surprisingly, we found that while SE readily evolves, LE is advantageous only under highly restricted conditions: when generalization of information was made unreliable or when error in social learning was high. Our results generate a conundrum over how seemingly conflicting empirical and theoretical findings can be reconciled. Perhaps the prevalence of LE in nature is due to costs of SE independent of the learning task itself (e.g. predation risk), perhaps natural habitats are often characterized by unreliable cues, or perhaps LE occurs less frequently, and SE more frequently, than widely believed.

C9.5 Guppies rapidly learn both who to learn from and when to employ social information

Simon Reader, McGill University
Gregory Kohn, Michelle Spierings

Animals may employ so-called 'social learning strategies' to maximise the utility of social information, information produced by the behaviour of others. However, the origins of social learning strategies remain controversial. In a series of four experiments, we demonstrate that guppies *Poecilia reticulata*, small tropical fish, learn the value of social cues. In Experiments 1-2, subjects observed trained fish ('demonstrators') foraging while we manipulated perceived foraging success, creating 'successful' and 'unsuccessful' demonstrators. After this training, large but not small subjects remembered and preferentially learned from the successful individual, resulting in 'directed' social learning. In Experiments 3-4, subjects observed groups of demonstrators that either led them to or away from a food reward depending on the prevailing context cues. After this training, subjects were exposed one-by-one to demonstrators in the two contexts. Subjects followed demonstrators in the context where demonstrators had previously led them to food, but avoided demonstrators in the opposite context. Associative learning provides a parsimonious explanation for these acquired preferences to preferentially learn from successful conspecifics and to favour social information under particular circumstances. We argue that social learning strategies, such as 'copy-successful-individuals', need not require adaptively-specialized cognitive mechanisms, and may thus be widespread across the animal kingdom.

C10: Parental Care

C10.1 Tadpole transport logistics in the Neotropical frog *Allobates femoralis*

Eva Ringler, Department Of Integrative Zoology, University Of Vienna

Andrius Pasukonis, Magdalena Erich, Walter HÄ¶dl, Max Ringler

The evolutionary transition from aquatic to terrestrial egg deposition has enforced the development of various parental behaviours, in order to protect eggs from external threats and ensure the final development of aquatic larvae.

Poison-dart frogs have evolved a remarkable variation in courtship and parental behaviours, and forms of parental care are present in almost the entire family. Beside the knowledge that tadpole transport is obligatory in almost all dendrobatid frogs, very little is known about the underlying movement patterns and distribution strategies. We investigated the tadpole deposition behaviour in a natural population of *A. femoralis* in French Guiana

over five years, and used microsatellite markers to identify the actual parents of the transported larvae. While in the vast majority of cases the tadpoles were carried by males, we also observed 10 females performing this task. The fact that frogs carried on average 8.43 tadpoles on their back, given the average clutch size of 20 eggs, indicates that frogs do not transport entire clutches at once and/or that they distribute their larvae across several water bodies. The distance males were observed apart from their home territories during tadpole transport significantly correlated with the number of tadpoles on their back.

C10.2 Allolactation in a non-communal breeder: what factors influence the likelihood of allonursing in the meerkat?

Kirsty MacLeod, University Of Cambridge
Tim Clutton-Brock

Allolactation, the nursing of another female's offspring, occurs most commonly where females nest or raise young communally. Little is known, however, about this costly form of allomaternal care in species where breeding is not communal. In the cooperatively breeding meerkat (*Suricata suricatta*), one dominant female monopolizes reproduction. Subordinate female helpers frequently nurse the dominant female's litters, typically when not concurrently nursing a litter of their own. In this study, using analysis of a long-term dataset, we investigated factors influencing whether or not meerkat females invest in allonursing. All females were more likely to allolactate if they were or had recently been pregnant; this effect was stronger if they were also highly related to the litter's mother. More subordinate females allolactated if they had recently returned to the group following eviction. We suggest that allolactation may persist, despite its costs, as a way of evacuating excess milk following abortion, and as a currency allowing allosucklers renewed access to the group. Our results, therefore, may indicate adaptive benefits for the dominant female of evicting subordinate females that have not been previously considered.

C10.3 Sharing the load: flexible maternal care behaviour in an African murid rodent

Tasmin Rymer, James Cook University
Neville Pillay

The development and expression of parental care behaviour is influenced by interactions between parents and offspring during the early postnatal

period (organisational effects) and experience during adulthood (activational effects). We investigated whether the expression of maternal care behaviour in biparental striped mice

Rhabdomys pumilio is organised during the early post-natal period and/or activated during adulthood. Maternal care was unaffected by whether females were raised by their mothers alone or by both parents: daughters showed consistently high levels of maternal care, which contrasts with their brothers that respond by increasing parental care behaviour when raised by their mothers only. Individual experience, as well as their mate's parental care experience, caused females to alter their maternal behaviour: experienced females decreased their level of investment, regardless of whether they raised young alone or with a mate, while inexperienced females only decreased investment when raising young with a parentally experienced male. Our study demonstrates that female striped mice alter their behaviour in response to their own internal state, their own maternal care experience and their mate's motivation to provide paternal care.

We suggest that the maternal care phenotype is behaviourally flexible, being strongly influenced by activational effects, and modulated by prevailing social conditions.

C10.4 Relating testosterone, parental care and paternity loss in a monogamous song bird

Camila Villavicencio, Max Planck Institute For Ornithology
Beate Apfelbeck, Bart Kempenaers, Wolfgang Goymann

It has been proposed that in birds with biparental care males may trade-off between taking care of the young and seeking for extra-pair partners. As reproductive behaviours are influenced by hormones, testosterone has been suggested to mediate this trade-off between parental and mating effort.

Testosterone levels are high during the mating phase, but remain low during the paternal phase to avoid interference with parental care. In addition, testosterone has been suggested to increase the likelihood of males to show extra-pair behaviour. So far, few studies have investigated the relationship between natural variation of testosterone, parental care and paternity. Here we investigate this relationship in the male black redstart (*Phoenicurus ochrurus*), a socially monogamous bird. We found

no relation between feeding rate and paternity loss of males. Testosterone levels were higher during the mating phase than during feeding of the second brood, but there was no correlation between testosterone levels and parental behaviour. However, we found that males showing paternity loss had lower testosterone levels than males not losing paternity.

Our results suggest no trade off-between parental care and mating effort. Thus, testosterone might not act as a proximate mediator, but it may influence the likelihood to experience loss in paternity.

C10.5 A confused paternity or a shared maternal duty: what is the best strategy to prevent infanticide?

Yannick Auclair, University Of Zurich
Barbara Koenig, Anna Lindholm

Infanticide, the killing of dependent conspecific offspring, has evolved to maximize the reproductive success of its perpetrator while reducing that of its victim. To improve the survival of their offspring, females have developed counterstrategies to limit infanticide.

The literature abounds of studies reporting the benefits of cooperation between breeding individuals to repel infanticidal conspecifics, or of mating strategies like polyandry to confuse offspring paternity and inhibit males from killing. However, how these two strategies interact and whether females rely on both or on one exclusively remains unknown. Using long-term data from a wild population of house mice we analysed whether offspring survival after birth was improved by polyandry as reflected by multiple paternity within litters, and by whether or not females reared their litters cooperatively in communal nests. Our results showed that offspring survival was higher in communally than solitarily-reared litters. Moreover, polyandry improved offspring survival in solitarily-reared litters whereas it had no effect in communally-reared litters. Cooperation between breeding females may improve offspring protection in infanticidal species, and suggests that social traits may have evolved to allow social mate choice. Alternatively, polyandry may compensate the extra offspring mortality suffered by the females for whom cooperation was not possible.

C10.6 Avoiding exploitation and signalling quality as alternative selection pressures for reduced parental care

Kate Lessells, Neth Inst Ecol (NIOO-KNAW)

There is ample evidence that parents 'negotiate' over biparental care, but our understanding of how the underlying sexual conflict is evolutionarily resolved is still incomplete. I will present two models of negotiation over parental care: in the first (Lessells & McNamara 2012), there is no within-sex variation in parental quality, and negotiation is mediated by the state of the offspring before each bout of investment. The second model is a signalling model in which one sex varies in parental quality, and can potentially signal its quality via its level of investment in the first of two bouts of care. The other parent can modify its investment in the second bout in relation to this signal. In both models the evolutionary stable level of investment is reduced by negotiation, but for different reasons: in the first model, parents reduce care in early bouts to avoid exploitation, whereas in the second, the parent of the variable-quality sex reduces care to honestly signal its quality. Thus there are two different sets of selection pressures that can lead evolutionarily to a reduction in investment when parents negotiate over parental care.

C11: Conspecific Recognition

C11.1 Who's your neighbour? Acoustic cues to individual identity in red squirrel (*Tamiasciurus hudsonicus*) rattle calls.

Shannon Digweed, Grant MacEwan University
Drew Rendall, Teana Imbeau

North American red squirrels produce a territorial rattle call when conspecifics enter or invade a territory. Previous playback experiments suggest that calls may indicate an invader's identity as squirrels responded more intensely to calls played from strangers than to calls from neighbors. This dear-enemy effect is well known in a variety of bird and mammal species and functions to reduce aggressive interactions between known neighbours. However, although previous experiments suggest individual differentiation and thus recognition, detailed acoustic analysis of potential acoustic cues in rattle calls have not been conducted. If calls function to aid in conspecific identification in order to mitigate aggressive territorial interactions, we would expect that individual recognition cues would be acoustically represented. Our work provides a detailed analysis of acoustic cues to identity within rattle calls. A total of 225

calls across 32 individual squirrels from Sheep River Provincial Park, Kananaskis, AB, Canada, were analyzed for potential acoustic cues to individual identity. Analysis of calls revealed a reliable acoustic differentiation across individuals. Further analysis of clusters of neighbouring squirrels indicated that calls were assigned correctly to specific squirrels (55-75%); in other words squirrels have distinct voices that should allow for identification and discrimination by conspecifics.

11.2 Genetic kin recognition in communally-nesting female house mice

Jonathan Green, University Of Liverpool
Andrew Holmes, Amanda Davidson, Robert Beynon,
Steve Paterson, Paula Stockley, Jane Hurst

Alloparental care, the provision of care to non-offspring, is common in many rodent species. Inclusive fitness theory predicts that benefits of alloparental care will be maximised where individuals are able to direct care towards relatives. One mechanism for recognising relatives is the use of polymorphic genetic markers, which could permit recognition of kin based on phenotypic similarity to themselves or to known familiar relatives. Female house mice (*Mus musculus domesticus*) frequently rear young in communal nests, with both females providing milk to their own and their partner's offspring. Previous research using laboratory mice has assessed the ability to discriminate putative recognition markers on a constant genetic background; however, the use of these animals in tests of kin recognition is highly constrained by the absence of normal genetic variation. Here, we present the results of experiments testing kin recognition in wild-derived mice with natural levels of genetic variation.

Using a breeding design that allows us to manipulate putative recognition markers independently of relatedness, we test whether females prefer communal nesting partners sharing markers at the highly polymorphic Major Histocompatibility Complex (MHC) and/or at the Major Urinary Protein (MUP) gene cluster, both of which have been implicated in inbreeding avoidance in mice.

C11.3 Multisensory representation of social familiarity in the songbird brain

Isabelle George, Universite de Rennes
Hugo Cousillas, Laurence Henry, Martine Hausberger

Social skills and preferences are thought to emerge from greater exposure to and hence familiarity with some social signals rather than others. The ability to differentiate and categorize familiar and unfamiliar individuals and to build a multisensory representation of known individuals emerges from successive social interactions, in particular with adult, experienced models. In different species, adults have been shown to shape the social behavior of young by promoting selective attention to multisensory cues. The question of what representation of known conspecifics adult-deprived animals may build therefore arises. Here we show that starlings raised with no experience with adults fail to develop a multisensory representation of familiar starlings.

Electrophysiological recordings of neuronal activity throughout the primary auditory area of these birds, while they were exposed to audio-only or audiovisual familiar and unfamiliar cues, showed that visual stimuli did, as in wild-caught starlings, modulate auditory responses but that, unlike what was observed in wild-caught birds, this modulation was not influenced by familiarity. Thus, adult-deprived starlings seem to fail to discriminate between familiar and unfamiliar individuals. This suggests that adults may shape multisensory representation of known individuals in the brain, possibly by focusing the young's attention on relevant, multisensory cues.

C11.4 Conspecific visual recognition in Zebra finch females

Shirly Fleischman, Tel Aviv University
Joseph Terkel, Anat Barnea

Zebra finches are social songbirds, dwelling in large flocks that can number up to 300 members. Although there is evidence regarding their ability to recognize other conspecifics based on their song and different calls, little is known about visual recognition in this very social species. We hypothesized that visual intra-species recognition exists in Zebra finches and that this ability is strongest between mates, and probably less strong between both closer and more distant members of the flock. Captive adult female Zebra finches were trained, using food rewards, to peck on a digital screen when presented with photographs of their mates vs. strangers, in flocks of up to 10 individuals. We thus examined whether females are able to distinguish between the photographs of different individuals, and thus possess conspecific visual recognition.

To date, we have found strong evidence for female visual recognition of their mates, and also for their ability to visually identify other close flock members. We are now investigating whether this ability is also retained in larger flocks.

C11.5 Memory of social interactions in sibling competition

Amelie Dreiss, University Of Lausanne
Charlene Ruppli, Sevrine Antille, Alexandre Roulin

Memory is essential to adjust behavior according to past experience. In societies where animals interact on numerous occasions, memory of previous social interactions may help optimize investment in competition. In the barn owl (*Tyto alba*) nestlings vocally compete for priority of access to the next indivisible food item brought by a parent. We tested to what extent young owlets remember the displayed hunger level of siblings and modulate their vocal investment accordingly.

How long information about the resource holding potential and motivation to compete of conspecifics is retained depends on how fast the value of this information fades. Because asymmetry in hunger level between siblings fluctuates over time depending on parental feeding rates, we predict memory retention to be relatively short. Playback experiments showed that owlets memorized an eavesdropped vocal interaction taking place between two siblings for at least 30 minutes, but only if the interaction was witnessed on a sufficient number of occasions. This suggests that even at young ages, actions performed by an individual at a given time point can durably influence its competitors. Taking into account memory ability is important to understand how family members adjust their competitive investment over parental resources.

C11.6 Kin recognition in *Drosophila*: the importance of ecology and gut microbiota

Anne Lize, University Of Liverpool
Raegan McKay, Zenobia Lewis

The animal gut commonly contains a large reservoir of symbiotic microbes. Whilst these microbes have obvious functions in digestion and immune defence, gut microbes can also affect behaviour. Here, we explore whether gut microbiota plays a role in kin recognition by altering the scent of their host individual.

We assessed whether relatedness, familiarity and food eaten during development, which affects gut microbiota composition, altered copulation investment in three species of *Drosophila* with diverse ecologies. We found that a monandrous species exhibited true kin recognition, whereas familiarity determined kin recognition in a species living in dense aggregations. Finally, in a food generalist species, food eaten during development masked kin recognition; when gut bacteria were removed via antibiotics, the effect of food on copulation investment disappeared.

Our results provide the first evidence that varied ecologically determined mechanisms of kin recognition occur in *Drosophila*, and that gut bacteria can have strong impacts on kin recognition.

C12: Brain Size, Cognition and Evolution

C12.1 Did tool-use evolve with enhanced physical cognitive abilities?

Sabine Tebbich, University Of Vienna
Claudia Wascher, Madeleine Scriba, Auguste von Bayern, Venessa Huml, Irmgard Teschke

The use and manufacture of tools has been considered to be cognitively demanding and thus a possible driving factor in the evolution of intelligence. In our study we tested the hypothesis that enhanced physical cognitive abilities evolved in conjunction with the use of tools, by comparing the performance of naturally tool-using and non-tool-using species in a suite of physical and general learning tasks. We predicted that the habitually tool-using species, New Caledonian crows and Galápagos woodpecker finches, should outperform their non-tool-using relatives, the small tree finches and the carrion crows in a physical problem but not in general learning tasks. We only found a divergence in the predicted direction for corvids. That only one of our comparisons supports the predictions under this hypothesis might be attributable to different complexities of tool use in the two tool using species.

C12.2 Nest construction in birds: Building the neural circuits

Zachary Hall, University Of St. Andrews
Marion Bertin, Ida Bailey, Simone Meddle, Susan Healy

Nest construction in birds typically involves a sequence of behaviour (nest material collection and deposition in the nest) that offers a unique model

for addressing how the brain sequences motor actions. In this study, we identified brain regions involved in nest construction in male and female zebra finches (*Taeniopygia guttata*). We used Fos immunohistochemistry to quantify expression of the immediate early gene *c-fos* (a molecular indicator of neuronal activity) in brain regions and correlated this expression with the variation in nest construction behaviour. Using this technique, we identified the neural circuitry involved in motor sequencing, social behaviour, and reward and motivation as involved in nest construction. Within nesting birds, we found that the number of times a male picked up nesting material and the amount a female visited the nest (quantified as either time spent in the nest or the number of visits to the nest) were positively related to and significantly explained the variation in Fos expression in the anterior motor pathway, social behaviour network, and dopaminergic reward circuit. Identifying which regions and circuits of the brain are involved in the control of nest construction may contribute to the debate on the role of cognition in nest building.

C12.3 Cognition of different length by *Physarum polycephalum*: Weber's law in an amoeboid organism

Yoshihisa Mori, Teikyo University Of Science
Asami Koaze

A true slime mould, the plasmodium of *Physarum polycephalum* has the ability to find the shortest route between two points in a labyrinth. To find the shortest route between two points, detection of the difference in lengths can be made from two aspects: the absolute difference between the lengths or the ratio of them. We found that the ratio of two lengths, rather than the absolute difference between the two lengths, was important in discriminating the difference in the two lengths by *P. polycephalum*. This finding indicates that an amoeboid organism detects differences in stimulus intensity as though it is constrained by Weber's law, suggesting that Weber's law is not reliant on the presence of a neural system and is used widely even in Amoebozoa.

C12.4 Finding the function of brain lateralization

Nele Zickert, University Of Groningen
Tess Beking, Reint Geuze

Brain lateralization (the differential control of functions by the two hemispheres) is now known to be a fundamental property of the organization of

brain and behaviour but its function is poorly understood. One hypothesis postulates enhancement of cognitive performance by lateralized processing, due to hemispheric specialization and increased scope for parallel processing when two tasks are each processed in a different hemisphere.

We tested this in human subjects by examining the performance of two cognitive tasks in a single and dual (i.e. simultaneous) condition in relation to strength and direction of lateralization of these functions. Language function (left hemispheric dominance) was tested by a word generation task whereas visuo-spatial functioning (right hemispheric dominance) was tested by a mental rotation task. Strength and direction of both functions were established independent of performance by using functional transcranial Doppler (fTCD), measuring blood flow to both hemispheres. Interestingly, many subjects did not show lateralization patterns according to text books. Nevertheless, in both the single and dual condition, strength of lateralization was indeed positively related to performance.

These results provide for the first time evidence that human brain lateralization is advantageous for cognitive performance and thus relevant for understanding the evolution of brain lateralization.

C12.5 The lateralisation of emotion in the spotted hyena

Adam Milligan, University Of Stirling
Sarah-Jane Vick, Stephen Glickman

Studies in several classes of vertebrates have suggested that emotional contexts profoundly influence behavioural lateralisation and that the hemispheric specialisation of emotion is manifested by lateral biases during social interactions. However, key issues arise from the existing literature on this topic. Firstly, although there are two competing hypotheses for the hemispheric lateralisation of emotion, these are differentiated by the direction of laterality of only positive and not negative emotion. Past studies have almost exclusively focused on negative emotional scenarios and therefore cannot distinguish between these two hypotheses. Furthermore, close examination of the methods employed by past studies suggests that their evidence of population-level behavioural lateralisation may be overstated. This study was the first to investigate laterality in a hyena species (*Crocuta crocuta*) and addressed the issues identified from previous emotional laterality research by implementing a more accurate method.

Furthermore, by considering negative and positive emotional contexts a more thorough comparison of the two competing hypotheses was possible. Through this approach, this study evidenced a left side behavioural bias at the population level across all emotional contexts; thereby providing the first evidence of lateralisation in Africa's most abundant predator and, most significantly, demonstrating that the right hemisphere controls emotion.

Robert Barton

C12.6 Human frontal lobes are not relatively large

Robert , Barton Durham University
Chris Venditti

One of the most pervasive assumptions about human brain evolution is that it involved relative enlargement of the frontal lobes. We show that this assumption is without foundation.

Analysis of six independent data sets using correctly scaled measures and phylogenetic methods reveals that the size of human frontal lobes, and of specific frontal regions such as prefrontal cortex, are as expected relative to the size of other brain structures. Furthermore, using a recently developed method for detecting shifts in evolutionary rates, we find that the rate of change in relative frontal cortex volume along the phylogenetic branch leading to humans was unremarkable, and that other branches showed significantly faster rates of change.

Although absolute and proportional frontal region size increased rapidly in humans, this change was tightly correlated with corresponding size increases in other areas and whole brain size, and with decreases in frontal neuron densities. The search for the neural basis of human cognitive uniqueness should therefore focus less on the frontal lobes in isolation and more on distributed neural networks.

C13: Communication

C13.1 Investigating state-attribution in non-human animals: how do male jays know what food their mate desires?

Ljerka Ostojic, University Of Cambridge
Rachael Shaw, Lucy Cheke, Edward Legg, Nicola Clayton

As part of their courtship behaviour, male Eurasian jays (*Garrulus glandarius*) share food with their female partner. This behaviour provides a novel means to investigate whether non-human animals might be capable of ascribing to others

psychological, internal states, such as desires or beliefs. Using a specific satiety paradigm, we were able to manipulate the females' desires towards different food types: after pre-feeding her one type of food, her subsequent desire for that food decreased such that she preferred the other, non-pre-fed food. After watching the female being pre-fed on one type of food, male jays were subsequently capable of flexibly adjusting their food sharing behaviour according to the female's decreased desire for the pre-fed food. We will discuss the critical finding that the males' sharing pattern was not simply a response to their mate's behaviour while they were sharing with her: males needed to watch the female while she was being pre-fed to later share with her the food that she desired. We further report results of studies investigating the information males might be extracting during watching the female eating and discuss whether these findings can bring us a step closer to understanding state-attribution in these birds.

C13.2 Corncrake males acquire new signal meanings during aggressive interactions

Pawel Rek, Adam Mickiewicz University

For many animals, the repertoires of songs or calls are relatively small and static during a lifetime. One reason for this is that there are physiological limitations in the respiratory, phonatory and filter systems due to different evolutionary histories. Nevertheless, learning does not have to be associated exclusively with the acquisition of new vocalisations; individuals may recombine a limited number of elements already present in an individual's repertoire into new sequences. Here, I tested the possibility of learning of the timing of calls in the corncrake, a non-passerine bird with a low repertoire of calls. I tested whether male corncrakes are able to comprehend and use a new pattern by connecting known syntax with a new meaning through experience.

Experiments demonstrated that males were able to comprehend a new temporal pattern only after a few minutes of exposure to the pattern. Additionally, apart from comprehending, males began signalling their aggressive motivation with a new pattern. These results indicate that corncrakes' innate call structures and lack of complex and variable songs allow them to learn the temporal distribution of their calls. This suggests a much broader application of contextual learning for the evolution of simple acoustic signalling systems.

C13.3 Ouch that hurts! Using facial expressions to assess pain in rodents and rabbits

Matthew Leach, Newcastle University

Paul Flecknell, Stephanie Keating

Pain in animals is of considerable public concern. Pain compromises not only animal welfare, but also raises considerable ethical concern. To alleviate pain, we must be able to assess its severity and duration effectively. Although we have made considerable advances in assessing animal pain, there remain limitations to many of the currently used methods. These include being time consuming to develop and implement, only offering an 'direct' measure of an animals' physical reaction to pain rather than how it makes them 'feel', and often being subtle and difficult to detect. Facial expressions are routinely used to assess pain and other emotional states in humans, particularly in those who are unable to communicate verbally (e.g. newborn babies).

There is now an increasing body of literature demonstrating that facial expressions change in response to painful procedures in rodents and rabbits (Langford et al. 2010, Sotocinal et al. 2011, Leach et al. 2012, Keating et al. 2012). If these expressions are a direct response to pain, then this may offer a new method of assessing pain in animals. In this presentation I will detail our work to develop and validate facial expressions as a means of assessing post-procedural pain in rodents and rabbits.

C13.4 Syntactic rules for non-vocal sound production in a songbird

Masayo Soma, Hokkaido University

Vocal learning is an essential cognitive function for language acquisition. Previous studies on vocal learners such as songbirds and parrots have revealed how animals learn and produce syntactically structured vocalizations. Moreover, recent discoveries have suggested that vocal learning capacity is linked to abilities of rhythmic body movement, i.e. synchronization to musical beat. However, little is known about regulation and learnability of ritualized body movements in the context of naturally occurring communications in songbirds.

The courtship display of the Java sparrow involves multiple behavioral elements such as singing, bill clicking, dancing and straw handling, of which songs

and bill sounds are recorded to analyzed syntactic rules in this study. Java sparrow males have a repertoire of one song, which is characterized by the note repertoire and the types of note-to-note transitions.

I found that each male had a syntactic rule not only for note-ordering but also for bill clicking patterns. Specifically, bill click sounds are produced in fixed positions in the note sequence. In addition, at least some birds learned this bill clicking patterns from their social (foster) fathers, suggesting a possibility that ritualized body movements can be socially learned.

C13.5 Acoustic communication in noise: signal plasticity and vocal constraints in bird song

Henrik Brumm, Max Planck Institute For Ornithology

This world is a noisy place - in addition to all kinds of biotic and abiotic noise sources present in every habitat, many places are becoming more and more noisy due to human activity. Because of their tractability in the lab, their complex vocal repertoires, and their elaborate signaling systems, birds have proven valuable models for understanding the effects of noise on acoustic communication. Moreover, variation in communication success is likely to have major fitness consequences for a singing bird because the function of song is closely linked to sexual selection. Recent bioacoustic research has revealed that bird songs are remarkably plastic and that individual song adjustments are used to reduce masking from background noise. However, bird songs are limited in their ability to respond to noise due to physical constraints during sound production. I will focus on vocal production and individual song adjustments, and review latest advances in our understanding of how singing birds get their messages across in noisy environments. Data from field, lab and modelling studies will be considered as well new insights into how urban birds cope with anthropogenic noise.

C13.6 Multicomponent and multimodal signals: what factors lead to their evolution?

James Higham, New York University

Much animal communication occurs using multiple signals, often expressed in multiple modalities. Despite a growing number of empirical studies involving such communication, there has been less theoretical work on the advantages it confers. Here I

ask: why should animals communicate with multiple signals?

I tackle this question by considering game theoretic techniques, in particular highlighting models developed in the economic signaling literature that might offer insight into biological problems. I investigate signal honesty under two paradigms of honest communication - costly signaling and cheap talk. In both paradigms, without further constraint, it has been shown that anything that can be achieved with multiple signals can be achieved with one, and that there are no fitness advantages to sending multiple signals. I present a range of constraints that when applied to these models make communication with multiple (including multimodal) signals strictly preferable, and hence more likely to evolve. These include constraints on cost functions and bandwidths, orthogonal noise structures across modalities, the use of strategically distinct signaling nodes, the communication of multiple qualities, and the presence of multiple signalers, and of multiple audiences. Such circumstances all provide biologically plausible scenarios that theoretically favor multiple signaling generally, and often multimodal signaling specifically.

C14: Social behaviour in ants

C14.1 Social homeostasis following fission and fusion in ant colonies

Nathalie Stroeymeyt, University Of Lausanne

Social insects form highly complex cooperative societies whose success crucially depends on efficient division of labour and information transfer within colonies. Colonies can experience considerable changes in size and composition over their life cycle, and face the important challenge of maintaining functional social organisation in the face of those changes. We investigated how such social homeostasis may be achieved following the major, abrupt modifications in colony structure caused by fission (fragmentation into several nests) and fusion (merging of several nests into one) in a seasonally polydomous ant, *Camponotus kiusiensis*. Using an automated tracking system, we monitored the spatial location and social interactions of all individually-tagged workers in 8 colonies before and after fission and fusion events took place. Overall division of labour and individual specialization on tasks were little affected by fission or fusion. By contrast, the structure and functioning of social interaction networks showed important modifications and revealed the presence of key individuals connecting well-separated communities

in the multi-nest situation. Overall, our results suggest that work organisation is maintained through fission and fusion events, even though the spatial structure and social organization of the colony may drastically change.

C14.2 Tracking individuals shows spatial fidelity is a key regulator of ant social organization

Danielle Mersch, University Of Lausanne
Alessandro Crespi, Laurent Keller

Ants live in organized societies with a marked division of labor among workers, but little is known about how this is generated. We use a tracking system to continuously monitor individually-tagged workers in six colonies of the ant *Camponotus fellah* over 41 days. Network analyses of over 9 million interactions revealed three distinct groups that differ in behavioral repertoires. Each group represents a functional behavioral unit with workers moving from one group to the next as they age. The rate of interactions was much higher within- than between groups. The precise information on spatial and temporal distribution of all individuals permitted calculation of the expected rates of within- and between-group interactions. These values suggest that the network of interaction within colonies is primarily mediated by age-induced changes in the spatial location of workers.

C14.3 Temporal organization of traffic on army ant trails

Simon Garnier, New Jersey Institute Of Technology
Matthew Lutz, Edward Hurme, Simon Leblanc, Iain Couzin

While foraging, the nomadic army ant *Eciton burchellii* forms long trails of workers that can extend over hundreds of meters into the rainforest. The foraging success of the colony depends largely upon the organization of the intense, high-speed traffic along these trails. For instance, army ants form separate traffic lanes that reduce interactions between workers moving in opposite directions. They also build living bridges to facilitate the movement of workers over irregular terrain. In a recent study, we showed that the traffic on the trail experiences regular oscillations. Such oscillations are often associated with decreased traffic efficiency in studies of car and pedestrian traffic. Using field experiments and computer modeling, we investigated the origin of these oscillations on army ant trails. In particular we looked at the effect of traffic intensity and bidirectionality on the intensity

and frequency of the oscillations. We also studied the traffic dynamics at trail forks and its role in shaping traffic oscillations. Finally we evaluated the impact of these oscillations on the amount of food successfully transported to the bivouac. The results of our study broaden our understanding of the temporal organization of traffic in social insects and other social species.

C14.4 Social prophylaxis through short-term specialisation and spatial segregation of corpse-carrying ants

Lise Diez, Université Libre De Bruxelles
Helene Le Borgne, Claire Detrain

The division of labour plays a major role in the success of social insects. In the case of prophylactic behaviors such as corpse removal, specialization of some ant individuals may not only increase task performance, but may also reduce the number of workers in contact with hazardous pathogens, thus diminishing risks of spreading diseases. We characterize workers involved in necrophoresis in the common red ant, *Myrmica rubra*. Corpse-carrying ants spend most of their time outside the nest, and when inside the nest, they stand closer to nest entrance with a lower probability of touching larvae than other nestmates. These ants do not show any medium-term strict specialization in corpse management, as they can concurrently perform other tasks outside the nest such as foraging. Some corpse-carrying individuals can however develop a short-term specialization as shown by their increased probability of making several successive corpse transports in less than one hour. Unlike other ant species, *M. rubra* does not possess a highly specialized group of workers involved in corpse management. Instead, the common red ant has developed a flexible strategy in which ants outside the nest can either perform foraging tasks or can quickly handle corpses and deal with sanitary issues.

C14.5 Do ant colonies transport resources efficiently?

Zoe Cook, University Of York
Peter Gass, Daniel Durstewitz, Barbara Vollmayr

Transportation of resources is an essential behaviour for many animals. In social insect colonies many individuals do not leave the nest to forage for themselves and so rely on efficient transport of resources to the nest. In polydomous ant colonies, which consist of two or more spatially separated but

socially connected nests, resources must also be transported between nests, making these species ideal model systems for studying resource transport behaviour. Transportation between nests usually takes place on a network of trails formed by interactions between many individuals. To determine whether ant colonies create efficient trail systems we analyse the structure of the transportation networks in eight polydomous ant colonies. In contrast to previous laboratory studies, the natural colonies in our study do not minimise the total distance of trails. We find nests are most likely to connect to their nearest neighbours, however the network structure is not entirely determined by these spatial associations. Our results suggest that the ant colony networks have small-world properties, making them both locally and globally efficient. I will discuss the possible mechanisms by which ant colonies create and maintain these networks, and how they allow the effective distribution of resources throughout the ant colony.

C14.6 One is solitude, two is company - the effect of social interaction on individual behaviour in ants

Ana Sendova-Franks, University Of The West Of England

Thomas Harris, Daphna Gottlieb, Nigel Franks

A fundamental issue in collective behaviour is the effect of group size on individual patterns of activity (and vice versa). Here we cut through this complexity by performing experiments to determine if the behaviour of individual ants changes when they are alone or in a pair. We used a balanced design to compare the behaviour of the two ants tracked continuously over periods of 3 hours both when they were alone and together (replicated for three such pairs from each of five colonies). We tested for the effect of condition (solitary/paired), original social role in their colony (internal nest worker or outside worker), location (nest/arena) and order of condition (first/second) on the movement characteristics of each individual. Both internal and external ants had lower activity (especially outside the nest) when they were together but only if they had first been solitary. Nevertheless, as in their original colony, external ants spent more time outside the nest than internal ants. These experiments show that individual ants behave differently in solitude than in the company of a single nestmate but even when alone they retain the relative differences in behaviour that are the building blocks of the division of labour in their societies.

C15: Mate Choice 1

C5.1 Benefits of social and sexual mating choice in blue-black grassquits (*Voaltinia jacarina*)

Jeff Graves, University Of St Andrews

Lilian Manica, Jeffrey Podos, Regina Macedo

Females in socially monogamous species may benefit from multiple mating. In the socially monogamous and sexually polygamous blue-black grassquit males exhibit repeated complex multimodal displays that integrate motor (vertical flights, "leaps") and acoustics (short vocalizations). We predicted 1) the height and rate of male leap displays would positively correlate with male reproductive success within-pair and/or extra-pair; and 2) extra-pair young would be in better body condition than their within-pair half-sibs. We also explored female preference for song traits that could potentially reveal a male's vocal performance and thus his quality.

We assigned parentage for 174 nests over 3 years with microsatellites. Extra-pair paternity ranged from 8.2% to 34.2% over the 3 years. The motor and acoustic display components had different impacts upon mating decisions of females: males with higher leaps were more likely to form a social bond, and males with shorter songs lost less paternity in their social nest. Extra-pair and within-pair young did not differ in condition.

We did not find any direct benefit of extra-pair copulations for the female, but we did find support for indirect benefits through "good genes" since females chose males with better motor performance in their displays, i.e., those that had higher leaps.

C15.2 Substrate-borne vibratory communication during courtship in *Drosophila melanogaster*

Caroline Fabre, University Of Cambridge

Berthold Hedwig, Graham Conduit, Peter Lawrence, Stephen Goodwin, Jose Casal

Courtship in *Drosophila melanogaster* consists of a series of stereotyped actions by the male to first assess the female's suitability and then elicit her acceptance of copulation, which is signaled by her ceasing to walk. The male and female communicate via vision, air-borne sounds and by pheromones, but it remained unclear what cues trigger female immobility. We describe a further component of *Drosophila* courtship behaviour that has, surprisingly, been overlooked. We show by video

recordings and laser vibrometry that the abdomen of the male vibrates rhythmically ("quivers") to generate substrate-borne vibrations that have a repetition rate of about 6 pulses per second. We present evidence that the female stops walking and becomes receptive mainly because she senses these vibrations and not, as had previously been suggested, as a response to the air-borne song produced when the male extends and flutters one wing. We also show that the neural circuits expressing the sex determination genes fruitless and doublesex are required for the quivering behaviour. Moreover, we show that these abdominal quivers and associated vibrations, as well as their presumed effect on female receptivity, are conserved in other *Drosophila* species. Substrate-borne vibrations are an ancient form of communication that is widespread in invertebrates and vertebrates. We are now also investigating the neuromuscular circuitry responsible for the generation of these substrate-borne signals and the sensory systems needed for their reception.

C15.3 What females want: physiology, performance and the costs of courtship

Sophie Mowles, The University Of Nottingham

Males typically attempt to convince females to mate by performing displays that demonstrate some aspect of their quality. While some displays are elaborate and spectacular in appearance, others involve simple repetitive actions. Dynamic repeated displays may advertise a signaller's stamina, which may be informative in mate choice as it communicates i) the general health and energy reserves of the signaller or ii) its ability to perform well in other ecologically relevant activities. Here, I describe a combination of physiological and whole-organism performance indicators that can reveal the relevance of stamina to courtship. For example, courting male field crickets, *Gryllus bimaculatus*, experience heightened levels of haemolymph lactic acid indicative of anaerobic respiration, and the wing-raising courtship display of the Cuban burrowing cockroach, *Byrsotria fumigata*, significantly handicaps its stamina on a racetrack in performance capacity trials. Thus, simple repetitive courtship actions are informative in providing females with information about a male's stamina, allowing females to select physically fit, good-quality mates.

C15.4 Why are guarded females popular among males in spider mites?

Keiko Oku, Wageningen University
Erik Poelman, Peter de Jong, Marcel Dicke

In general, male reproductive success increases with the number of mates, whereas it does not apply to females. Therefore, intrasexual selection favours males that have traits to ensure their reproductive success. On the other hand, females should choose their mates to obtain their own benefits. In some species, it is known that females incite male combat and then mate with a winner of the combat. In spider mites (Acari: Tetranychidae), only the first mating results in fertilization. Consequently, males guard quiescent deutonymph females, the stage immediately before adult emergence and sexual maturation. Because quiescent deutonymph females are immobile, it was believed that females would not choose their mate, whereas males could do. However, we found that when males had a chance to choose between a guarded female and a solitary female on the same leaf, males significantly preferred the former female over the latter one. When more than one male attempts to guard a female, male combat often occurs. Here, we present a proximate factor to attract male attention and a possibility of female mate choice during precopulatory mate guarding in spider mites.

C15.5 Visual Tricks used by Great Bowerbirds during courtship displays

John A. Endler, Deakin University
Laura Kelley

Great Bowerbirds (*Ptilonorhynchus nuchalis*) construct and decorate a bower consisting of a 0.6-1m thatched avenue opening onto two 1m courts. If females are interested they watch the male display from inside the avenue, seeing part of the display through the avenue opening. The courts are lined with uncoloured objects (Gesso) with some coloured objects placed on and near the courts. Males use 3 visual tricks during courtship. The size of the gesso objects increases with distance, and this creates a forced perspective illusion which has several visual effects and better ones favour mating success. Coloured objects are mostly outside the female's field of view until the male picks them up and waves them in front of her, alternating with his lilac nuchal crest. This creates a flash of colour over the gray court background. Males "paint" the inside of the avenue walls with reddish plant material and females stay inside the avenue long enough to become light adapted to the reddish light, making green displayed objects more chromatic.

C16: Early-life stress

C16.1 Starlings subjected to early life nutritional stress strategically consume toxic prey to defend their state

Ben Brilot, Newcastle University
Michael Emmerson, Göke Ergün-a-ztürk, Daniel Nettle, Melissa Bateson

Early-life stressors, such as poor nutrition, are implicated in negative health outcomes for humans in later life (e.g. obesity and diabetes). Rodent models of pre-natal nutritional stress suggest that post-natal feeding behaviour is shifted towards hyperphagia, particularly directed towards high fat content foods. We present data from an alternative animal model: the European starling (*Sturnus vulgaris*), a wild and relatively long-lived species. We created nutritionally stressed starlings in a cross-fostering experiment: artificially causing starlings to be reared with either one other nest mate (two brood) or six other nest mates (seven brood). We subsequently examined the willingness of birds from each group to consume toxic prey (mealworm larvae injected with 1% quinine solution). We found that there was little relationship between body condition (mass controlling for skeletal size) and willingness to consume toxic prey for birds that were reared in two broods. However, there was a clear positive relationship between these two measures for birds reared in seven broods: 'fatter' early life nutritional stress birds were most willing to consume toxic prey. We suggest that early-life nutritionally stressed starlings may be more sensitive to their adult nutritional status: willingly consuming toxic prey with the payoff of maintaining optimal condition.

C16.2 Effect of nutritional stress at different developmental periods on HPA axis and cognition in the zebra finch

Buddhamas Kriengwatana, University Of Western Ontario
James Brooymans-Quinn, Haruka Wada, Kim Schmidt, Matthew Taves, Kiran Soma, Scott MacDougall-Shackleton

Developmental environments can have long-term effects on cognition. Elevated glucocorticoids could be the mechanism by which developmental stress affects cognition. We investigated the effects of nutritional stress at different stages of development on HPA axis, song, and associative learning in a songbird. Zebra finches (*Taeniopygia guttata*) were raised in consistently high (HH) or low (LL) food

conditions until post-hatch day (PHD) 62, or were switched from high to low conditions (HL) or vice versa (LH) at PHD 34. A standardized restraint stress protocol was used to measure corticosterone (CORT) at PHD 30 and 60. Adrenocorticotropic hormone (ACTH) and dexamethasone (DEX) challenges were used to assess HPA axis function in adulthood. Song and associative learning were measured in adulthood. We found that nutritional stress increased stress-induced CORT levels of LH and HL groups at PHD 30 and 60, respectively. However, there were no differences between baseline CORT of any treatment groups during development or in adulthood. There was also no effect of treatment on DEX-induced negative feedback, but LL conditions lowered maximum ACTH-induced CORT levels in adulthood. Although LH conditions impaired learning ability of females, none of the nutritional manipulations affected song learning or vocal performance of males.

C16.3 Decision Making and Judgement Bias in low and normal birth-weight pigs

Eimear Murphy, Utrecht University
Rebecca Nordquist, Franz Josef van der Staay

Low birth weight (LBW) in children is associated with cognitive and emotional deficits. In pigs, LBW is common. We studied cognition, through decision making, and emotion, through judgement bias, in LWB (n=8) and normal birth weight (NBW; n=8) pigs. We developed a two-choice decision making task for pigs (P-IGT) based on the Iowa Gambling Task. In six blocks of 20 trials, pigs chose freely between a 'disadvantageous' option (large rewards, low probability of reward) and an 'advantageous' option (small rewards, high probability of reward). For judgement bias, pigs learned to discriminate a positive tone-cue from a negative tone-cue, signalling availability of large or small rewards respectively, in two distinct locations. Next, pigs' responses to ambiguous tone-cues were scored as optimistic or pessimistic depending upon whether the pig responded in the location of the large or small reward. In the P-IGT, birth weight did not affect advantageous choices ($F_{1,14}=1.54$, $P=0.234$), which increased in both groups over time ($F_{1,14}=5.84$, $P=0.009$). LBW pigs showed fewer optimistic judgements than NBW pigs ($t_{14}=2.95$; $P=0.010$). There was no relationship between P-IGT and judgement bias performance ($r=-0.18$; $P=0.499$). We find that LBW pigs do not show altered decision making, but are more pessimistic than NBW pigs.

C16.4 Long-term effects of early social and predation experience on the behaviour of cooperatively breeding cichlids

Stefan Fischer, University Of Bern
Cecilia Wikström, Barbara Taborsky

The environment experienced during early development has often strong and persistent influences on the future behaviour and life history of animals. It is largely unknown, however, how animals integrate experiences made in different ecological contexts when coping with multiple ecological challenges later in life. In the cooperatively breeding cichlid *Neolamprologus pulcher*, the composition of social groups and predation threat critically determine survival. We performed a 2-way factorial rearing experiment to test whether early social experience and predator exposure interactively affect later social competence and predator evasion abilities in these fish. Forty-two experimental groups were reared for two months either with or without parents and a helper, and with or without repeated presentation of a predator. During the treatment phase, behaviour was affected by both social and predator experience. Tests performed after the treatment during the juvenile and adult stages showed that the ability to cope with social challenges later in life is interactively shaped by early social and predator experience. In contrast predator avoidance ability was only affected by early predator exposure. Our results show that developmental experiences across different ecological contexts have to be accounted for, if we aim to understand the performance of animals in natural environments.

C16.5 Early growth affects adult reversal learning in zebra finches

Vera Brust, Bielefeld University
Yvonne Wuerz, Oliver Krüger

Conditions early in life are known to have long-term consequences on morphological, reproductive and behavioural traits in zebra finches. However, not much evidence exists for influences on cognitive traits like associative learning or behavioural flexibility. We raised zebra finches under high/ low quality of nutritional provision (HQT and LQT treatment) during their first 35 days of life and tested them in a reversal learning task four years later. Besides a significantly lower growth rate of LQT birds during the treatment phase, the LQT birds were also slower to associate a colour cue with the reward in the learning task. Interestingly, an additional, but indirect, treatment effect was

present: birds that had gained more weight during the treatment phase learned the association faster while they were at the same time slower to reverse their choice. Experiences made early during ontogeny thus seem to have lifelong influences on associative learning and behavioural flexibility too, leading to different cognitive types.

C16.6 Stress causes trans-generational epigenetic effects on chicken behaviour

Per Jensen, Linköping University

Behaviour is a corner-stone in animal welfare assessment. This is largely dependent on the genetic setup of an animal, i.e. DNA-sequence variation. However, also epigenetic factors, regulating the orchestration of the genome, can affect behaviour and welfare. Here I report on a series of experiments investigating this in chickens, with a focus on understanding domestication effects and responses to stress. We found that chronic stress modified brain gene expression and caused deterioration in spatial learning. Both the gene expression profile and the modified learning was mirrored in the offspring, showing trans-generational effects in both. Furthermore, chronic stress caused what appeared to be an adaptive modification of foraging strategies and social dominance, again mirrored in a similar behaviour in the offspring. We also found that early stress, during the first weeks of life, caused chronic modifications in both physiological and behavioural stress coping, and similar effects were seen in the offspring. Comparing brain gene expression and DNA-methylation of Red Junglefowl and domestic chickens, we found hundreds of differentially expressed and differentially methylated genes and the pattern of breed differences was highly correlated over generations. This indicates that selection on epigenetic variation may have been an important of chicken domestication.

C17: Predators & their consequences

C17.1 When to shout and when to shush: Social Aspects of Anti Predator Behaviour in Common Ravens (*Corvus Corax*)

Christian Blum, Department Of Cognitive Biology, University Of Vienna
Thomas Bugnyar

Mobbing is a viable anti-predator strategy often found in animals that come in frequent contact with predators and have the cognitive abilities for identification and coordinated action. Previous

studies on wild American crows focused on mobbing responses to artificially introduced predators, i.e. masked humans that were catching crows. Here we applied a similar paradigm but precisely controlled the number of 'predator' encounters in our captive colony of subadult ravens (n=16). We tested mobbing responses of birds to masked human experimenters in a "neutral" and "dangerous" condition, both in the group and in individual isolation. During the first five tests the person with a "dangerous" mask carried a dead raven while passing the aviaries, whereas the person with a "neutral" mask did not; afterwards, tests were always performed without a dead raven. We were interested in how quickly ravens learned to mob the "dangerous" mask, how long they showed a selective response and which social factors influenced their participation in mobbing. Results showed that most birds quickly learned to differentiate between masks and continued to do so for over a year. Participation in mobbing was influenced by kin, dominance and group constellation, indicating that particular individuals may take over given roles.

C17.2 Evolutionary history of predation risk influences consistency and plasticity of cooperative behavior in wild Trinidadian guppies

Mathew Edenbrow, University Of Exeter
Bronwyn Bleakley, Safi Darden, Indar Ramnarine,
Croft Darren

Animal personality research has recently integrated individual-level plasticity and consistency into an adaptive framework. Studies implicate predation risk as an important ecological determinant in behavioral correlations across contexts, yet we know little regarding the interacting roles of risk and social landscape for consistent vs. plastic behavior. We address this limitation by investigating wild Trinidadian guppies from eight populations differing in predation risk (four high/four low). We assayed cooperative behavior repeatedly during predator inspection and investigate consistency/plasticity across populations differing in their selection regime. Individuals were assayed twice in a standardized mirror assay and with two live partners. Using random regression modeling we find individual variation, but not individual plasticity, best explained the data within each social context (mirror/live), highlighting consistent individual differences. Individual variation within mirror assays also predicted individual variation in live partner assays, however, patterns varied by river drainage and population. Considering plasticity across test

contexts (mirror/live) we document individual plasticity variation, suggesting socially mediated adjustment of cooperative behavior. Interestingly, individual cross-context plasticity variation differed by river drainage and predation regime. We discuss these results in relation to the evolution of cooperation and highlight that additional ecological influences require further study to understand personality in wild organisms.

C17.3 Predators and social evolution: integrating behavioural mechanisms, ecology and evolutionary dynamics

Daniel Van Der Post, University Of Groningen
Rineke Verbrugge, Charlotte Hemelrijk
Alison Dunn, Lesley Morrell

We focus on how social evolution depends on (i) local decision-making mechanisms, and (ii) on the inter-relation between multiple social phenomena. These questions are not addressed in evolutionary theory that focuses on single social phenomena, without explicit local decision-making. We use multi-scale models to study how socio-ecological patterns and Darwinian fitness self-organize. In our model, foragers compete for food, use vigilance to avoid predators, and evolve to live in groups. We find that multiple social phenomena interact and affect evolutionary dynamics: (i) Coordinated travel generates constraints on group size evolution; (ii) Group size co-evolves with joint detection of predators, where a within-group selection cycle leads to larger groups and less vigilance. This is periodically reversed by between-group selection for small groups with vigilance, generated by an emergent assortment. This evolution depends on the details of decision-making. How additional social phenomena, and increased cognitive sophistication will affect evolution, is therefore an open question, but crucial for interpreting models where interactions are artificially excluded.

C17.4 How prey group size affects detection by olfactory predators and prey survival

Asa Johannesen, University Of Leeds
Arend Hintze, Fred Dyer, David Knoester, Christoph Adami

Prey aggregation is a beneficial anti-predator behaviour when avoiding a visual predator. However, how prey survival is affected by group size when the predator uses olfaction to detect prey is not well understood. We investigated the effect of prey aggregation on prey survival, search time and

likelihood of being located by an olfactory predator. We used two different predators; three spined sticklebacks (a primarily visual species) and *Gammarus pulex* (a primarily olfactory species) and carried out a series of prey detection and foraging trials using chironomid larvae as prey. We found that *G. pulex* search time decreased asymptotically with increasing prey group size. However, we also found that risk of location was not linearly related to prey group size. In foraging trials with sticklebacks, we found that aggregated prey survived for longer than dispersed prey in stickleback foraging trials. As olfactory predators may increase foraging effort in areas with high olfactory prey cue concentration, prey may suffer negative trait mediated effects by prolonged predator presence. While aggregating in large groups may lead to decreased consumptive risk, the optimal strategy may be to minimise available olfactory cue while maintaining group sizes large enough to dilute risk if discovered.

C17.5 Using digital models of evolution to study how animal behavior evolves: a case study with the predator confusion effect

Randal Olson, Michigan State University

Studying the evolution of animal behavior is a difficult problem because there is no "fossil record" of animal behavior and because it is difficult to infer the selection pressures acting on ancestral populations. We present a framework using a digital model of evolution to study the forces that may have shaped grouping behavior in animals. Within this framework, we can experimentally manipulate the genetic as well as environmental factors that influence the course of evolution. As a case study, we used this framework to test the hypothesis that predator confusion impacts the evolution of swarming behavior in prey. We demonstrate that the predator confusion effect could (1) provide a sufficient selective advantage for prey to evolve swarming behavior in response to predation, (2) in turn select for a more focused visual system in predators that feed on swarming prey, and (3) change the shape of the functional response curve describing the predator's consumption rate as prey density increases. Thus, by considering the predator confusion effect in an evolutionary context, we show that predator confusion could have pervasive evolutionary effects on prey behavior, predator sensory mechanisms, and the ecological interactions between predators and prey.

C17.6 Evolving the selfish herd: evolutionary consequences of variation in predator attack

Lesley Morrell, University Of Hull

Recently, evidence has emerged that patterns of collective behaviour in grouping animals are governed by interactions between small numbers of individuals within the group. These findings contrast with study of the 'selfish herd', where increasingly complex individual-level movement rules have been proposed to explain the rapid increase in aggregation observed when prey groups are startled by or detect a predator. While individuals using simple rules take into account the position of only a few neighbours, those using complex rules incorporate multiple neighbours, and their relative distance, to determine their movement direction. Here, I simulate the evolution of selfish herd behaviour to assess the conditions under which simple and complex movement rules might evolve. I find that complex rules outperform simple ones under a range of predator attack strategies, but that simple rules can fix in populations particularly when they are already in the majority. In addition, I explore whether a movement rule derived from studies of collective behaviour (where individuals use the position of 7 neighbours to determine movement direction) performs as successfully as more complex rules.

C18: Spatial cognition

C18.1 Homing behaviour in intertidal gobies: Linking brains, behaviour and ecology

Culum Brown, Macquarie University
Gemma White

The ecological cognition hypothesis postulates that the brains and behaviour of animals are shaped by the challenges they face in their every-day lives. Here we examined the site fidelity, homing behaviour and brains of five species of intertidal fishes in Sydney.

Three of the species we examined are intertidal residents spending their entire lives in rockpools, while the other two species temporarily inhabit rockpools during early ontogeny before shifting to alternative habitats. Our data revealed that rockpool residents show very high site fidelity compared to non-residents, with most resident individuals still present in their home pool 42 days after tagging. Fish were subsequently displaced distances up to 30m from their home pool and we monitored homing behaviour. Resident fish show very high rates of homing behaviour with the

majority of displaced fish returning to the home pool. Non-residents, however, showed much poorer homing abilities. Examination of the brains using a range of imaging techniques revealed that resident species had relatively larger telencephalons compared with non-resident species. This brain region is known to be involved in spatial learning in fishes. Evolution has clearly favoured enhanced spatial learning in intertidal rockpool species and this ability is underlined by the appropriate cognitive hardware.

C18.2 From Multitudes to Movement - Exploring how robins (*Petroica longipes*) react to number and animacy in native New Zealand forest

Alexis Garland, Victoria University Of Wellington
Jason Low, K.C. Burns

Food caching in naïve robins of New Zealand offers a unique opportunity to key in to behaviour that may shed some light on how core cognitive mechanisms work in the wild.

A series of experiments were conducted exploring this wild songbird's behavioural response to numerosity and agency by using Violation of Expectancy (VoE) and choice tasks. Testing visuospatial memory of hidden food caches, spatially distributed quantity discrimination and simple computation were explored using mealworm prey (*Tenebrio molitor*). This songbird's unusual habit of storing perishable hunted prey – and the subsequent use of living prey as experimental items lead to unique questions surrounding robins' cross-species perception of agency, specifically in human experimenters and insect prey. These trials demonstrate that *Petroica longipes* displays many behaviours indicative of the fundamental hallmarks of these representation systems, but reveal unique patterns of response when compared to other species.

Our findings engender further questions about the behaviour of this isolated island species and what it could potentially contribute to our broader understand of evolution, adaptation and development.

C18.3 Smelling home in the wind. The relation of petrels' homing behaviour to wind conditions at the nest

Gaia Dell'Araccia, CEFE-CNRS
Marianne Gabriot, Aurelie Celerier, Pauline Palmas,
Jerome Mardon, Francesco Bonadonna

Petrels need a functional sense of smell to successfully home at night, evidencing that odours emanating from the burrow are a key cue for nest finding. In air, wind dynamics directly affect the distribution of odorant molecules in space and time, as well as the flying behaviour of petrels. Thus, petrels have to adopt peculiar homing behaviours to take advantage of both chemical and air dynamic information in order to move toward the nest burrow.

To explore homing olfactory guidance, we related wind conditions near the burrow to resultant homing behaviour in different petrel species. In particular, we tracked with high resolution GPS-loggers 20 Cory's shearwaters (*Calonectris borealis*), 8 Scopoli's shearwaters (*C. diomedea*) and 7 Blue Petrels (*Halobaena caerulea*) in different colonies, reconstructing their homing paths at 1 fix/sec. Simultaneously, we recorded with an anemometer the wind conditions at the nest. We characterized hovering behaviour around the nest, and analysed a number of parameters (i.e. loops number and length, nest approaching direction and flight direction changings) in relation to wind intensity and direction, in order to link behavioural responses to environmental conditions. In addition, we compared the different behavioural responses of Cory's shearwaters when homing by night and by day.

C18.4 The representation of three-dimensional space in fish

Robert Holbrook, University Of Oxford
Vicki Davis, Theresa Burt de Perera

There are many challenges associated with navigating through three-dimensional space, yet previous research has focused on how individuals find their way horizontally. Terrestrial animals are constrained to surfaces most of the time, whereas many aerial and aquatic animals are free to move through three-dimensional space. These different forms of movement might influence how space is learned, remembered and used. By using experimental and theoretical approaches, we consider how fish deal with the problem of three-dimensional navigation.

We show that in a fish's representation of space, the vertical and horizontal components are stored separately, with fish demonstrating a preference for using the vertical. We theorise that this preference is because the vertical axis contains particularly salient spatial cues, including hydrostatic pressure. We also demonstrate that freely swimming fish are

able to correctly encode metric information in a volume, and do so with similar accuracy in each dimension.

Together, our results reveal that the vertical component of the representation of space is vitally important to fish. By comparing our results to studies on surface-bound animals, we hypothesise that the representation of space in the brain of a vertebrate might be shaped by the degrees of freedom of movement that binds the animal.

C18.5 Memory in an avian brood parasite: Testing the adaptive specialization hypothesis

Melanie Guigueno, Western University
Scott MacDougall-Shackleton, David Sherry

The adaptive specialization hypothesis (ASH) proposes that cognition and the brain are adaptively specialized to serve specific ecological functions. Brown-headed cowbirds (*Molothrus ater*) are an ideal species for testing the ASH because they show seasonal and sex differences in spatial behaviour. Cowbirds are brood parasites, only females search for host nests, and breeding females have a larger hippocampus than males. We therefore predicted that females would outperform males on a spatial memory task, especially during breeding. We tested cowbirds on spatial and colour memory operant tasks on touchscreens in breeding and non-breeding conditions. There was no overall sex difference in performance on either task. On the spatial task, males actually performed better than females at the shortest retention interval, although non-breeding females were better able to handle successive increases in retention interval compared to non-breeding males. On the color task, females performed much better when in breeding condition than in non-breeding condition. The most straightforward prediction from the ASH of better spatial memory in females is not supported by these results. However, a number of more subtle and unexpected sex differences, and effects of breeding condition, were found to occur in spatial and non-spatial memory in cowbirds.

C18.6 Consolidation and reconsolidation of memory for cache sites in Black-capped chickadees

David F Sherry, University Of Western Ontario
Matthew C Barrett

Black-capped chickadees (*Poecile atricapillus*) are able to remember which of their caches they have emptied of food and which ones they have left

intact. Consolidation is the protein-synthesis dependent process that establishes long-term memory. The theory of reconsolidation proposes that when information is retrieved from memory, it becomes labile and must be reconsolidated back into long-term memory by a protein-synthesis dependent process. We hypothesized that if cache sites are retrieved from memory as a batch during search for caches, those sites not actually emptied may require reconsolidation back into long-term memory.

We used anisomycin to disrupt protein synthesis following caching and search for caches. We found that anisomycin disrupted initial consolidation of memory for caches, but did not affect memory for sites that were left intact following a bout of searching. Anisomycin did, however, disrupt birds' ability to avoid revisiting sites they had visited and emptied. Protein synthesis is thus required for consolidation of cache sites into long-term memory and for tagging some sites as empty. It is not necessary for reconsolidation, possibly because cache sites are retrieved from memory one at a time and not as a batch, or because memory for cache sites in chickadees does not undergo reconsolidation.

C19: Avian vocal communication

C19.1 Socially guided song learning in the zebra finch: effects at multiple time scales

Otilia Menyhart, Cornell University
Raymond Chou, Michael Goldstein, Timothy DeVoogd

Vocal development of juvenile songbirds and human infants requires interactions with adults to develop its proper form and function. What mechanisms drive the superior learning performance associated with live interactions? Young learners can elicit contingent responses from adult social companions in different modalities that reinforce learning and promote more advanced vocalizations.

We studied vocal development in the Zebra finch to assess relations between vocal precursors in juveniles and contingent responses from the parents. Eight families were recorded between 30-75 days, and social interactions surrounding juvenile or adult song were analyzed. Juvenile and father song were compared when juveniles reached song maturation.

We find that both parents contribute to juvenile song learning. Juveniles whose immature song received more contingent song from their fathers copied their father's song sequence more

accurately. Non-vocal feedback from mothers also predicts song learning. The number of maternal fluff-ups around juvenile song positively correlated with later sequential similarity between adult and juvenile males, and female wing strokes were associated with real time changes in the dominant frequency of the juvenile song syllables. Our findings imply that the mechanisms underlying the development of vocal communication may be best understood when studied in the context of a communication system.

C19.2 Feel your stress: Acoustic emotional contagion between mates in a songbird, the zebra finch

Emilie C. Perez, Macquarie University, Université Jean Monnet

Julie E. Elie, Ingrid C. A. Boucaud, Thomas Crouchet, Christophe Soulage, HEdi A. Soula, Frederic Theunissen, Clémentine Vignal

Vocalizations carry stable information such as the emitter's identity, but they can also carry labile information about the emotional state of the sender. Empathy, as the capacity to feel the emotions of another individual, has been proposed as a proximate basis for group-living and altruistic behaviours, but has mainly been described in mammals. Zebra finches *Taeniopygia guttata* are gregarious songbirds that form lifelong pair bonds; because males were recently shown to express their stress through modulations of their vocalisations, we hypothesized that they could also transmit their stress to their mate using acoustic cues. We thus performed playback experiments on females separated from their partner. While mate's stressed-calls increase females' vigilance, enhance their vocal response and provoke a physiological stress, non-stressed control calls only trigger high vocal reaction. These effects seem to be mate-specific as both stressed calls and non-stressed calls from unfamiliar males modify neither the females' behaviour nor their physiological stress. Our results demonstrate the existence of emotional contagion based on acoustic cues in a songbird. Our study thus suggests new research opportunities in this model system for studying vocal signalling and perception of emotions in vertebrates.

C19.3 Dinner's ready! Ravens join feedings when affiliates are calling

Georgine Szípl, Department Of Cognitive Biology, University Of Vienna

Markus Boeckle, Michela Spreafico, Claudia Wascher, Thomas Bugnyar

Upon discovering food, ravens (*Corvus corax*) produce far-reaching yells that contain information about food availability and sender identity. Here, we investigated if receivers use information about sender identity for deciding whether or not to approach feeding sites. In a paired playback design, we tested reactions to food calls in a group of individually marked, free-ranging ravens. We simultaneously played back sequences of food calls in two different locations and varied the factors sex and familiarity (known or unknown to local birds). Ravens reacted significantly more to food calls of known females by approaching the area around the speaker where the female stimuli were played. These patterns reflect observed behaviour during daily feeding, where mainly female ravens produced food calls. The results further showed that individuals that were known to have affiliate relationships to the stimuli birds were approaching the respective speaker. Our findings indicate that ravens extract information within food calls to recognise conspecifics on a class level (familiarity and sex) and likely also on an individual level. The results support the idea that ravens have detailed knowledge of their own relationships to others, and that they use this knowledge to avoid given conspecifics and to join social allies.

C19.4 Individual contributions to cooperative territorial defence under experimentally manipulated levels of threat

Jenny York, University Of Exeter
Andrew Young

The collaborative defence of territory is among the most widespread forms of animal cooperation, but remains remarkably poorly understood. Cooperative contributions to defence are of particular interest as they may entail risk to self but yield collective benefits, leaving them susceptible to erosion by selection for free-loading. Here we investigate the causes of individual variation in contributions to territorial defence in white-browed sparrow weaver, *Plocepasser mahali*, societies. Using simulated territorial intrusions, we first show that the dominant breeding pair contribute significantly more to cooperative defence than their subordinates (responding first, initiating more synchronized song and conducting more aggressive grass waving) and that the sexes contribute similarly. Second, we utilize the widespread dear-enemy phenomenon to experimentally investigate how dominants and subordinates adjust their

cooperative contributions under two levels of territorial threat. Both dominants and subordinates significantly and similarly increased their cooperative contributions to defence under the higher threat treatment, resulting in a stronger collective response by the group. Our findings demonstrate that, while dominants do invest most heavily in cooperative territorial defence, subordinates increase their contributions when they are needed most, suggesting that potential collective action problems arising from free-loading by subordinates may be largely overcome by fitness payoffs to contributors.

C19.5 Song learning beyond imitation: coordinated singing activity in zebra finch social groups

Julia Hyland Bruno, Hunter College And The Graduate Center Of The City University Of New York (CUNY)

Christina Roeske, Ofer Tchernichovski

In the crowded auditory environment of a songbird colony, learning when to sing is not less important than learning what to sing. Social patterns of singing, such as duets and counter-singing, were studied in adult birds, but it is not known how social interactions during development might adaptively shape patterns of singing interactions and coordination. To study the development of coordinated singing patterns, we raised zebra finches in a controlled social environment, with ten juveniles in separate cages encircling a single adult tutor. We recorded video and audio during song development and analyzed singing interactions. As adult pairs, these birds exhibited striking coordinated singing behaviors. Some pairs developed a “unisong”: their imitations of the tutor were virtually identical and their song syllables were delivered simultaneously, with an accuracy of milliseconds, throughout the joined song bout. Other birds developed complex patterns of turn-taking, where one bird would sing for several bouts or minutes, and then let the other bird sing without interruption. Other birds performed canon singing and rhythmic song-call synchronization. These findings indicate that birds can learn to perceive and coordinate song performance on multiple timescales. Further, these data now allow us to investigate how those patterns come about.

C19.6 Not for parents only: Begging calls allow sibling recognition in juvenile zebra finches

Clementine Vignal, University Of Saint-Etienne
Severine Ligout, Fabrice Dentressangle, Nicolas Mathevon

The benefits of kin recognition may range from inbreeding avoidance to cooperative behaviours. In birds, kin recognition has almost exclusively been studied between parents and offspring. Yet, sibling recognition could be of special importance in fledglings for nest location or detection of feeding opportunities by recognition of the begging calls produced by siblings on the return of a parent. We studied sibling recognition based on begging calls in fledglings of domestic zebra finches (*Taeniopygia guttata*), a gregarious songbird in which fledglings may gather in crèches and are fed by parents during 20 days. Using playback tests, we showed that chicks displayed stronger responses to the begging calls of their siblings than to the calls of unrelated familiar individuals. The response was influenced neither by the subject’s sex nor by the brood size, but chicks answered more to male than to female calls. Discriminant function analysis based on acoustic parameters showed that begging calls carry an individual signature as well as a brood signature which might account for such sibling discrimination. As the zebra finch has become a model species for the study of acoustic communication, our results offer new opportunities of research on mechanisms and evolution of kin recognition.

C20: Personality 1

C20.1 Assessing the frequency distribution of behavioural phenotypes and their relationship to physiological traits

Rodrigo Vasquez, IEB, University Of Chile
Carolina Saavedra, Nasrim Butler, Pablo Sabat

Intra-specific variability is the raw material on which natural selection acts to shape evolutionary change. However, few studies have assessed behavioural variability within species, and only recently this area has been growing due to the increase in personality research. Intra-specific behavioural variability can have important ecological and micro-evolutionary consequences, particularly since different behavioural phenotypes can be adaptive under different ecological and social scenarios. We have been studying behavioural variability in the caviomorph rodent *Octodon degus*, a diurnal and highly social rodent that exhibits social foraging, bi-parental care, communal living, and complex vocalizations. Experimental evidence shows that degus use learning to gather information about food sources as well as in social interactions, particularly in kin and non-kin related interactions. We assessed within population variability in exploratory behaviour, and we found that (i) the population is

characterized by having two different phenotypes, exploratory and non-exploratory animals, and (ii) exploratory behaviour is negatively correlated with trapping capture success. Furthermore, we found that basal metabolism is significantly lower among non-exploratory animals, suggesting different levels of stress. These results have important behavioural, neurobiological, ecological, evolutionary, and conservation implications, making the species an exciting model for an integrative study of behaviour. (ICM-P05-002, PFB-23-CONICYT)

C20.2 The nutritional modulation of adult personality

Jose Noguera, University Of Glasgow
Neil Metcalfe, Pat Monaghan

Periods of poor nutrition have been shown to affect a variety of life history traits either during early development or at sexual maturity. Nevertheless, very few studies have investigated how nutrition can affect an important aspect of an organism's phenotype: the development of its personality. In this study we manipulated the availability of the main antioxidants present in the diet of zebra finches during their early development or during their sexual maturation. The availability of antioxidants during development influenced the aggressiveness and fear responses of adult birds but in a sex-specific manner: amongst birds that received a low antioxidant diet during early development, females were more aggressive (and less fearful) than males. In contrast, males that had received a high antioxidant diet during early development were not only bolder than females but also than males fed with a low antioxidant diet. Nutrition during the period of sexual maturity had a similar effect on adult aggressiveness. Furthermore, both sexes were calmer when they received a low antioxidant diet during sexual maturity. Overall, our results emphasise the importance of the availability of essential nutrients in the development of male and female personalities which could significantly influence their future fitness.

C20.3 Personality drives physiological differences between individuals

Allert Bijleveld, Nioz
Georgina Massourakis, Annemarie van der Marel,
Anne Dekinga, Bernard Spaans, Jan van Gils, Theunis Piersma

Recent models explaining the origin and maintenance of personality variations assume that

variations in metabolic machinery cause variations in personality. Here we challenge this assumption, as well as the notion that the size of an individual's metabolic machinery is associated with reduced survival. We found that exploratory behaviour of captive *Calidris canutus* correlated with digestive organ (gizzard) mass while free-living ($r = -0.52$). We then manipulated gizzard mass and found that individual exploration scores were unaffected ($P = 0.52$). Mark-recapture analyses of a long-term dataset showed that apparent survival of free-living birds was unaffected by gizzard mass, but resighting probability was positively correlated with gizzard mass. Our results show that consistent behavioural differences cause variations in metabolic machinery, rather than vice versa, and that survival costs of increased exploratory behaviour are compensated for by physiological adaptations. These results necessitate reconsideration of models explaining personality variations based on metabolic machinery.

C20.4 Personality and cognition: influence of personality in complex cognitive tasks

Josefina Zidar, Linköping University
Alexandra Balogh, Anna Favati, Hanne Lövlie

Cognitive abilities of birds are comparable to, or even exceed those of many mammals. While this has stimulated a lot of research, few studies have looked at individual variation in cognition. We therefore investigated individual cognitive differences in red junglefowl chicks in two learning tasks: (i) associative learning, and (ii) reversal-learning, the latter consisting of both re-learning and extinction of the previously learned association. Not surprisingly, individuals vary in their ability to learn an association. However, we found no correlation between individuals' performance in the two different tasks. Contrarily, extinction rates in the reversal-learning task were negatively correlated with individuals' latency to explore alternatives after an absent reward in the reversal task. Thus, birds that re-learned quickly, investigated the previously correct option thoroughly before investigating alternative options. These results fit well with the speed-accuracy trade-off hypothesis, where proactive individuals are expected to be fast and inaccurate, while reactive individuals are more thorough. Our preliminary results therefore indicate that variation in personality can be associated with more challenging cognitive tasks, and will be further investigated in additional cognitive tests and personality essays.

C20.5 How does variation in the environment and individual cognition explain the existence of consistent behavioral differences?

Petri Niemelä, University Of Oulu

Anssi Vainikka, Jukka Forsman, Olli Loukola, Raine Kortet

According to recent studies on animal personalities, the level of behavioral plasticity varies among individuals, populations, and species. Still, it is conceptually unclear how the interaction between environmental variation and variation in animal cognition affect the evolution of behavioral plasticity and expression of animal personalities. Here, we (1) use literature to review how environmental variation and individual variation in cognition explain population and individual level expression of behavioral plasticity and (2) draw together empirically yet nontested, conceptual framework to clarify how these factors affect the evolution and expression of individually consistent behavior in nature. Along the lines of the evolution of cognition, we predict that environments with moderate variation favor behavioral plasticity. This occurs since in those environments costs of cognition are covered by being able to recognize and use information effectively. Similarly, non-plastic, stereotypic behaviors may be favored in environments that are either invariable or highly variable, since in those environments cognition does not give any benefits to cover the costs or cognition is not able to keep up with environmental change, respectively. Therefore, expression of consistent behavioral differences may depend on environment so that invariable or highly variable environments favor the existence of stereotypic animal personalities.

C20.6 Population level consistency versus individual personality

Sarah Dalesman, University Of Exeter

The pond snail, *Lymnaea stagnalis*, demonstrates differences among but consistency within populations in their ability to form memory. Following an identical training regime some populations form memory lasting 3 to 6 hours ('standard' populations), whereas others demonstrate memory lasting 5 to 6 days ('smart' populations). This variability is consistent across generations and independent of whether they are wild caught or laboratory reared. Memory phenotype also correlates with how the population responds to several environmental stressors, for

example social isolation, calcium availability and pollutants. Whilst there is a high level of consistency in the average response to training, within populations there are frequently a few individuals that demonstrate the alternate memory phenotype. This raises the question, is there a similar relationship between memory phenotype and stress response at an individual level as found at a population level, i.e. does population level consistency reflect individual personality? The consequences of this variation will be discussed in terms of population level adaptation to environmental stress.

C21: Collective behaviour

C21.1 Construction of physical trails in the leaf-cutting ant *Atta laevigata* (F. Smith, 1858) (Hymenoptera: Formicidae): is it worth the effort?

Sofia Bouchebti, Université Toulouse 3

Luiz Carlos Forti, Vincent Fourcassié

Leaf cutting ants of the genus *Atta* build physical trails that can exceed 200m in length and that are used during several weeks. Since these trails are costly to build and maintain, the question arises of their benefit for the colonies. We studied the building of physical trails in *A. laevigata* colonies living in pastures of South East Brazil. Five stages of trail construction were defined. The first stage corresponded to the creation of a chemical trail, before the initiation of trail construction, and the last stage to the complete removal of vegetation (green and dry) and obstacles along the trails. At each stage we measured on a sample of 50 laden individuals the speed of the ants, their weight, and the weight of the leaf fragment they carried. Our results show that the formation of a physical trail had a strong impact on foraging efficiency. Transport efficiency (ant speed x weight of leaf fragment carried) increased by a 3 fold factor between the first and last stage of trail construction. Nevertheless, there was no further increase in transport efficiency after all the green grass blades along the trail had been cut, thus questioning the function of the remaining work.

C21.2 Group decision-making in flocks of homing pigeons

Benjamin Pettit, University Of Oxford

Andrea Perna, David Sumpter, Dora Biro

Group decisions can increase accuracy and reduce risk by combining information from multiple

individuals. Models have demonstrated the effectiveness of self-organized mechanisms for reaching consensus, in which each individual balances its personal information against a tendency to follow neighbours. Key questions to ask of empirical data are how individuals integrate social information from many conspecifics, and how this in turn affects information pooling and leadership within the group as a whole. In this study, we use high-resolution GPS tracking to analyse how pigeons respond to each other while reaching a consensus homing route, in groups of two to five birds. Each pigeon had previously established a preferred homing route when flying alone. By comparing flock and solo routes, we estimate each bird's relative influence in the group decision. In larger groups, individuals with outlying preferences were disproportionately less likely to dominate the decision, and instead they followed the majority. Furthermore, we fitted various classes of model to the pigeons' momentary turning behaviour and tested how well the models predicted global features of decision-making across a range of group sizes. Our results demonstrate how flocking behaviour affects collective information processing in a navigational context.

C21.3 The impact of stallion removal on the social structure of a family group and the dynamic of collective movements

Léa Briard, IPHC - DEPE, UMR 7178, CNRS - UoS
Jean-Louis Deneubourg, Richard Bon, Odile Petit

We investigated the social structure and the dynamic of collective movements in a family group, with and without the stallion. The aim was to determine whether the stallion played a specific role, as suggested in previous studies. Removing the stallion led to a modification of the group's affiliative social network. Three subgroups were identified when the stallion was present, but hierarchical cluster analysis revealed only two subgroups of different composition in its absence. Moreover, in both conditions, a different individual was excluded from all subgroups. Analysis of collective movements did not reveal personal leadership to be concentrated on the stallion. In fact, nine out of ten individuals, including the stallion, had initiated at least one collective movement. This suggests a distributed leadership that persisted when the stallion was removed from the group. Stallion removal also revealed a specific joining order among the mares that was correlated with their affiliative social network. However, we

did not identify any specific joining order when the stallion was present.

This suggests that the presence of the stallion disturbs the collective movements dynamic rather than acting as a catalyser, and that its specific role during these phenomena is not linked to leadership.

C21.4 Collective motion in sheep, information transfer in large groups

Sylvain Toulet, Université Paul Sabatier
Richard Bon

When an individual leaves its group and initiates a collective move, individual mechanisms are required to maintain group cohesion. Numerous studies have revealed that collective motions depend on interactions between individuals and have proposed models allowing reproducing observed collective patterns. However most of these studies infer the individual behaviour from the collective observations. Recently, a social model simulating the following behaviour in sheep (*Ovis aries*) was formalized thanks to experimental data collected at the individual level. It reveals that after an initiation in small groups, the individual following probability depends both on the number of conspecifics already departed and the number of non-departed individuals. This model relies on the hypothesis that in small groups, all individuals can monitor each other and that their response is independent from their positions.

Here, we applied the protocol used previously to build the model but with increased group sizes and applied the social model with the results we obtained experimentally. The social model is pertinent in groups of 8 and 16 individuals, but not in groups of 32. We propose that in large groups, the information propagates and we show that the decision making to follow depends on individuals' position relatively to the initiator.

C21.5 Previous social feedback critically affects coordinated movement and leadership in a changing social environment in three-spined sticklebacks

Jolle Jolles, University Of Cambridge
Adeline Wilson, Shinnosuke Nakayama, Rufus Johnstone, Andrea Manica

Studies of collective behaviour have shown that, in many animal groups, certain individuals are

consistently more likely to initiate and direct group movement. Recent studies have shown that it is often bold individuals that take the lead and that positive social feedback plays a fundamental role. It remains unclear however how leadership might be affected by previous social feedback as a result of social dynamics within groups. To investigate this we subjected individual three-spined sticklebacks (*Gasterosteus aculeatus*) to a boldness task and subsequently paired them with two consecutive partners. We found that, conform previous studies, leadership emerged through the effects of social feedback with bold individuals inducing followership and shy individuals leadership in their partners. Next to that, the boldness of the previous partner and the resulting social feedback affected this behaviour of both individuals in the 2nd pairing. Importantly, individuals differed considerably in the way they were affected by this changing social feedback; bold individuals were relatively consistent whereas shy individuals were much more plastic in their behaviour. Together these findings demonstrate that in a changing social environment both current and previous social feedback affect leadership and thereby critically influence group movements.

C21.6 Both competition and predation dynamically influence collective decision-making in the wild

Damien Farine, University Of Oxford
Ben Sheldon

The social decisions made by individuals living in groups are influenced by a clear trade-off: large groups provide greater protection from predators, but also incur greater competition for resources. The emergent social structure in populations should therefore arise as a consequence of the collective decisions made by individuals in response to these opposing pressures. We tested experimentally how predation pressure and competition influenced the rules of collective decision-making in mixed-species fission-fusion flocks of tits *Parus*, using automated data-collection in the wild. Whilst individuals continued to exhibit collective feeding throughout all treatments, in treatments where access to food was limited they shifted towards leaving more dense sites and arriving at less dense sites within patches. This pattern was reversed in treatments where individuals were exposed to model predators. Fitting a model of collective decision-making in animal groups suggested that competition significantly influenced the conspecific rather than heterospecific component of collective decision-making. However, these components did not differ under control or predation treatments implying that

all species contribute to herding effects. Together, these findings suggest that the competition and anti-predation effects are interlinked, and that fission-fusion population structure emerges from an integration of environmental and within- and between-species social conditions.

C22: Social behaviour & social networks

C22.1 Pathogen exposure alters behavioural networks in ant societies

Sylvia Cremer, IST Austria
Line Ugelvig, Carsten Marr, Fabian Theis

Social interaction networks in insect societies are shaped by colony-intrinsic factors such as density, age and task performance of the interacting individuals. In addition, extrinsic factors like pathogen exposure are known to change the behaviour of the sick individuals, as well as their nestmates. Ants react to fungal pathogen exposure by hygienic grooming behaviour, either directed towards themselves (selfgrooming), or towards other colony members (allogrooming). Grooming reduces the risk of infection of the exposed ant, but bears the risk of cross-infection to the previously healthy allogroomers. We analysed how individual selfgrooming and social allogrooming of all group members changes when a single ant per colony is exposed to a fungal pathogen. We found that self- and allogrooming frequencies were altered in both the pathogen-exposed ant and its nestmates, leading to a change of the social interaction network in the colony. Epidemiological modelling revealed that these behavioural changes are adaptive, limiting disease transmission in the colony. Interestingly, it is particularly the alteration of the social grooming between individuals that has highest effect on disease dynamics in ant colonies.

C22.2 Inter-group intruder familiarity predicts levels of post-conflict affiliation in a cooperative cichlid

Rick Bruintjes, University Of Bristol, UK
Andrew Radford

Conflict between individual group members in social species is often followed by affiliative behaviour, such as grooming in primates. In social species, conflict between groups can be of paramount importance for its members when resources such as mates or territories are at stake. However, experimental studies examining the link between inter-group and intra-group behaviour are extremely rare. By experimentally staging conflicts

between resident groups and their neighbours or unknown groups, we studied whether inter-group intruder familiarity influences defence rates and whether it predicts levels of post-conflict affiliation, submission and aggression in the highly social fish *Neolamprologus pulcher*. Our results show that groups exhibit higher levels of aggressive defence against unknown groups than towards their neighbours. Contrary to predictions, resident groups showed an increased level of affiliation after intrusion from their neighbours compared to from unknown groups, potentially signalling the strength of social group cohesion to their neighbours. Neither post-conflict submission nor aggression among group members differed between treatments. This is the first study to employ inter-group intrusions to study post-conflict behaviour in any animal, shedding light on the interaction between inter-group and intra-group behaviour and allows a fuller comprehension of the evolution of group dynamics and cooperation.

C22.3 Facebook For Geese: What Are The Causes And Consequences Of Differences In Social Strategy In A Fission-Fusion Social System?

Matthew Silk, University Of Exeter
Andrew Jackson, Darren Croft, Stuart Bearhop

Light-bellied brent geese (*Branta bernicla hrota*) have a fluid fission-fusion social system during non-breeding periods. There has been negligible research on fission-fusion sociality in avian systems, and little is known about the causes and consequences of variation in an individual's social environment in unstable social systems more generally. We use social network analysis to examine social structure in staging populations of this species and determine whether there are individual differences in social position. We can then use supplementary behavioural, body condition and reproductive data to investigate the correlates of different social strategies, and whether these differ across the annual cycle. Firstly, I will demonstrate the validity of using social network approaches to make inferences about sociality at an individual level in colour-ringing studies. I will then discuss our knowledge of the factors contributing to population-level social structure and individual social position in this study system, together with some evidence for variation in social position having important consequences at an individual level. Understanding how an individual's social environment interacts with its phenotype and condition has important implications for understanding social behaviour and decision making in this system, as well as making

predictions about social structure in migratory bird species more generally.

C22.4 Dynamics of third-party intervention in male Przewalski horses

Konstanze Krueger, Nuertingen-Geislingen University
Gudrun Schneider, Birgit Flauger, Juergen Heinze

Conflict among group members poses severe threats to the cohesion and integrity of animal societies. One mechanism to resolve such conflict is third party intervention, i.e., the interruption of dyadic interactions by a third individual through direct physical contact, interposition or threats. Several functions of intervention behaviour have been proposed, such as kin protection, coalition formation, and the promotion of group cohesion. Still, empirical research on the function of intervention behaviour is rare, particularly in ungulates, in which intervention behaviour has been described in several species. We studied intervention behaviour in a semi-wild bachelor group of six to ten male horses (*Equus ferus przewalskii*) in basic social situations, and in high aggression situations when a new horse joined the group. Contrary to earlier suggestions, the stallions did not intervene to support kin and did not have a higher social rank than horses they intervened against, at least in high aggression situations. Stallions may have intervened primarily for coalition formation and to maintain group cohesion. In high aggression situations, one or two horses intervened on any one occasion and thus displayed so-called 'social control roles'.

C22.5 Information Transfer Combines with Intra-specific Competition to Explain Colony Specific Habitat Use in a Long-Distance Forager

Thomas Bodey, University Of Exeter
Adam Kane, Stephen Votier, Keith Hamer, Andrew Jackson, Samantha Patrick, Ewan Wakefield, Stuart Bearhop

Colonial breeding is a widespread phenomenon, and there is increasing evidence that colonies of non-related individuals, including seabirds, maintain broadly discrete foraging ranges despite an absence of territoriality. Mechanisms to explain this are poorly developed, but central-place foraging provides a number of opportunities for individuals to gather information on the foraging success of others. However, there is a time-limited tradeoff for individuals between observing others versus actively

searching, and there is an additional tradeoff between increasing public information use and increasing competition. These tradeoffs between the use of information types, and their impact on competitive interactions, are predicted to greatly impact on spatial foraging patterns. Here we empirically demonstrate through the use of tracking data from 70 Northern Gannets *Morus bassanus* at 5 colonies that colony specific foraging occurs. We then demonstrate mechanistically that intra-specific competition and public information transfer combine to facilitate colony separation. We show that public information transfer both at-sea and at-colony is key to the population-level patterns observed. This supports the potential for cultural transmission of foraging locations. Such separation of foraging grounds by colony may occur in many central-place foragers, and has important implications for the ecology and conservation of numerous charismatic species.

C22.6 The sublime secrets of red deer sisterhoods: social bonds in red deer females

Kathreen Ruckstuhl, University Of Calgary
Josephine Pemberton, Fiona Guinness

Social network analysis is used to infer relationships between pairs of individuals in groups. Benefits of close associations range from decreased stress levels, to increased survival and reproductive success. We investigated to what extent social connections affect red deer female fitness, by examining a 35-year data set from Rum, Scotland. Females closely associated with their close relatives for most of their lives. Matrilineal groups had high clustering coefficients (measure of cliquishness), and daughters' degree centrality (number of direct ties to other animals in the network) closely matched those of their mothers. Clustering coefficient, degree centrality, and matriline ID were strongly correlated with lifetime reproductive success. Matriline ID, the birth weight, and the year a calf was born in were strong predictors of calf survival. In the year after their mother died, sisters significantly increased their degree of association. If a female lost her sister, she did not change the degree of association with her other associates. However, if a mother or sister died there was a substantial increase in the chances of a female dying within the first year after the deaths. We discuss environmental and genetic factors as potential drivers of survival and reproductive success in females.

C23: Mate choice 2

C23.1 Facial symmetry predicts physical fitness in older men: The role of DNA methylation in the paired box 3 (PAX3) gene

William Brown, University Of Bedfordshire
Meishan Raal-Nunes, Hannah Dugdale, Alexander Ross, Tom Sully, Peter Herbert, Nick Sculthorpe, Fergal Grace

Developmental stability -- the capacity to buffer ontogenetic perturbations -- could underlie symmetry maintenance during senescence. Despite fluctuating asymmetry predicting behaviours linked to natural and sexual selection, molecular epigenetic markers are not isolated. One candidate is *PAX3* transcriptional regulation, a homeobox gene important for skeletal muscle formation, facial development and training-responsiveness. *PAX3* is epigenetically regulated (i.e., heritable alterations of expression without DNA sequence changes). Whether DNA methylation -- an epigenetic modification -- of *PAX3* plays a role in facial asymmetry or training-responsiveness is unknown. We predicted that age-matched physically fit older men [i.e., behaviourally and physiologically categorised "master athletes" aged 61.23 ± 5.12 years, $n=13$] would be more symmetrical than sedentary controls [aged 63.06 ± 5.66 years; $n=17$]. Artec MH scanner captured 3D facial topography. Procrustes-based geometric morphometrics obtained measures of asymmetry. Master athletes were significantly leaner and symmetrical compared to sedentary controls. *PAX3* DNA methylation (high resolution melt analysis real-time PCR) from blood samples revealed that master athletes had significantly lower *PAX3* methylation than sedentary men. Thirteen younger men (21.53 ± 2.37 years) had significantly lower *PAX3* methylation compared to sedentary older men, but not master athletes. *PAX3* methylation predicted facial asymmetry regardless of age, suggesting that epigenetic dysregulation may indicate developmental instability.

C23.2 Basking experience alters scent mark composition in male lizards: an opportunity for female choice?

Robert Heathcote, University Of Oxford
Emily Bell, Patrizia D'Ettorre, Geoffrey While, Tobias Uller

Signals used in mate choice should honestly advertise the benefits that males can provide females, with direct benefits often argued as being more important for female fitness than indirect benefits. However, the nature of direct benefits in

species without paternal care or nuptial gifts, such as lizards, is poorly understood. Previous studies on lizards have suggested that scent marks by territorial males are used by females in making mating and home range settlement decisions. Because access to high-quality thermal resources such as basking sites is crucial for feeding and reproduction, females may be able to detect and exploit thermal-induced variation in the chemical composition of male scent marks when assessing the quality of his territory. In this talk I show that the amount of time male wall lizards are allowed to bask significantly affects the chemical composition of their femoral secretions, which are used in scent marking. The direction of the change is consistent with adaptive plasticity to maintain signalling efficacy under warmer conditions. The compounds affected also included those argued to be important in previous studies on female choice and male-male competition in lizards. However, whilst female lizards could discriminate between scent marks of males with different basking experience, they did not appear to preferentially associate with the scent from males from high-quality thermal conditions. We believe this is the first study to show that olfactory cues involved in signalling are plastic in response to the thermal environment in an ectothermic vertebrate. These results may have important implications for within- and between-population variation in chemical signals, and suggest a neglected environmental effect on olfactory communication given the often crucial importance of thermal resources in reptile biology.

C23.3 Genetic and phenotypic influences on social status and pairing patterns in a tropical monogamous bird species, the Zenaida dove, *Zenaida aurita*

Aur lie Quinard, University Of Burgundy
C zilly Frank, Dechaume-Moncharmont Fran ois-Xavier

In monogamous species with biparental care, mutual mate choice is expected to occur for phenotypic and/or genetic characters which are related to individual fitness. Such a phenomenon can result in various mating patterns depending on whether individual quality is absolute or relative, and also depending on whether individual quality is related to the same characters in both sexes. Here we analyse mating patterns in a socially monogamous tropical bird species, the Zenaida dove, *Zenaida aurita*. Populations of this species are mainly composed of individuals that defend territories year-round, alone or in pairs, and a few floaters. We first analyze the effects of wing length (as a measure of body size and competitive ability)

and heterozygosity (as a measure of genetic quality) on social status (floaters vs. unpaired territorial individuals vs. paired territorial individuals). We then assess mating patterns in relation to body size, heterozygosity, and genetic dissimilarity between mates. We discuss our results in relation to mate choice and long-term social monogamy in a tropical environment.

C23.4 Influence of life history and swelling status on social behaviors in free-ranging female bonobos (*Pan paniscus*)

Heungjin Ryu, Primate Research Institute, Kyoto University
David Hill, Takeshi Furuichi

Perineal sexual skin swelling in relation to menstrual cycle occurs in a variety of primate taxa. However, exaggerated sexual swelling is only found in some Old World monkeys and apes. Although several hypotheses have been proposed to explain the significance of exaggerated sexual swelling, the species in which it is found vary greatly in terms of social organization, so it seems unlikely that a single hypothesis can account for the significance of exaggerated swelling in all species. Therefore, it is useful to try to understand this phenomenon in the context of the social system of each species. In this study it was found that free-ranging female bonobos with maximal sexual swelling engaged in social interactions with other females (e.g. genito-genital rubbing, staying in close proximity and grooming) more frequently than females without maximal swelling. Together with solicitation of social interaction and approaching data, it seems that female with maximal swelling are attractive to other females for social interactions. The results also suggested that the benefits of maximal swelling may vary among females depending on their life-history stage. In particular, young females may get more benefits from maximal swelling through increased grooming reciprocation and staying in close proximity to other females.

C23.5 Scent marking enhances male reproductive success

Kerstin E. Thonhauser, Konrad Lorenz Institute Of Ethology
Shirely Raveh, Attila Hettyey, Helmut Beissmann, Dustin J. Penn

Scent marking is assumed to be a secondary sexual trait that enhances males' reproductive success, though direct evidence for this hypothesis is lacking.

We conducted a study with wild-derived house mice to test whether scent marking increases males' reproductive success when females could freely choose between two territorial males. We experimentally altered males' scent marking and male-male conflict by exchanging scent marked tiles between the neighboring males' territories (intrusion treatment) or by relocating males' tiles within their territory (control). All animals were tested twice and we examined whether individual males were consistent in their marking. We found that males marked significantly more in the intrusion treatment compared to controls and especially at their territorial border. We found high within and between individual variation in scent marking, and yet the sum of a male's marking over time was consistent in different trials. Genetic paternity analyses revealed that scent marking increased males' reproductive success in both intrusion and the controls. Surprisingly, however, males' scent marking did not increase females' attraction to their territories. These results provide direct evidence that scent marking enhances males' reproductive success when females can choose their mates, even if it does not increase the attractiveness of males' territories.

C24: Parasitism & disease

C24.1 Aggression as a behavioural defence trait against social parasites

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Evelien Jongepier, Tobias Pamminer, Mirjam Papenhagen, Susanne Foitzik

Animals often consistently vary in behaviour, a phenomenon known as animal personalities. In social insects not only individuals can vary in behaviour, but also entire colonies, leading to the concept of colony personalities. We could recently show that colonies of the ant *Temnothorax longispinosus* consistently vary in aggression against non-nestmate conspecifics and that the expression of this behavioural trait influences colony fitness. For example, more aggressive colonies occur under high density and fare better during invasions of *Protomognathus americanus* slavemaker queens, the main social parasite of *T. longispinosus*. Here, we show that more aggressive host colonies are also better able to defend themselves during slave raids, but high host aggression leads to more fatalities in intraspecific encounters, suggesting a trade-off: high aggression is selected for under high parasite pressure, but might be costly when parasites are absent. Following up on this hypothesis, we indeed demonstrate in a large scale study comparing 17

populations that host colonies from parasitized populations exhibit a more aggressive behavioral colony type. Moreover, host colonies from parasitized populations responded to invading slavemakers faster by evacuating their nest. Our studies reveal that colony personalities can be under selection and that selection regimes can vary with parasite pressure.

C24.2 Does behavioural thermoregulation prevents chytridiomycosis on frogs? The case of the heliothermic frog, *Dendropsophus labialis*

Ivan Camilo Beltran Arevalo, Los Andes University
Adolfo Amézquita Torres, Martha Cardena Toquica, Sandra Victoria Flechas

Chytridiomycosis, a disease caused by the chytrid fungus *Batrachochytrium dendrobatidis* (Bd), has been implicated in the amphibian population declines around the world. Efforts to control this disease in the field, focused mostly in natural defences of amphibians have had little success. It is known that high body temperatures are harmful for pathogens, a fact exploited by some ectotherms via behavioural thermoregulation. Little is known, however, regarding the interactions between behavioural thermoregulation and the inhibition of pathogens by frog skin's microbiota. We studied *Dendropsophus labialis*, a Colombian heliothermic anuran with low prevalence of chytridiomycosis compared with sympatric species. The study evaluates the relation between Bd infection and thermal preferences in *D. labialis*, and the effect of these variables on the composition of the cultivable skin bacterial community. Temperature selection experiments preliminary indicate that infected animals prefer higher temperatures and a reduction of the pathogenic load in infected animals which were allowed to thermoregulate. We also tested for differential association of bacterial morphotypes between infected and non infected frogs and for change in the bacterial diversity in individuals who thermoregulate. Understanding the host-pathogen-native microbiota relationships should allow progress in the control of this disease in the field.

C24.3 Beyond contact-based transmission networks: the role of geographical coincidence

Thomas Richardson, University Of Lausanne
Thomas Gorochoowski

For animals that live in societies, efficient communication is essential for group coordination. However as pathogens may hijack the same

pathways used to transmit information, a conflict exists between enhancing information flow and inhibiting pathogen spread. Transmission of such agents over the networks formed by direct 'same-place, same time' interactions (e.g. physical contacts) has been studied in human and animal societies, and all studies have found interaction networks inhibit spreading. However, indirect dissemination via the 'geographic coincidence' network - the set of spatial locations visited at different times by different individuals - has been ignored. Here we simulate the well-known Susceptible-Infected (SI) model of disease or information spread over a set of time-ordered and spatially explicit interaction networks obtained from video-recordings of ant colonies. The spatial component allows us to obtain a distribution of interaction strengths, extending from strong direct interactions to weak indirect interactions arising from historical geographic coincidence. These network parameter-spaces display regimes of both enhanced and inhibited spreading, resolving the conflict between dissemination of beneficial agents and inhibition of harmful agents. We show how this dual-function arises from the interaction between the weak ties arising from geographic coincidence and the temporal decay of the spreading agent.

C24.4 Show me your friends and I will tell you who you are: the role of social network analysis in understanding disease transmission in wildlife

Rodrigo Hamede, University Of Tasmania
Hamish McCallum, Jim Bashford, Menna Jones

Social network analysis has been increasingly used to study the relationship of animal behaviour and wildlife epidemiology. Nonetheless, few studies include contact heterogeneities and social behaviour when modelling disease outbreaks in wildlife. Using a novel technology – proximity sensing radio collars – we describe the contact network and social behaviour in a wild population of Tasmanian devils. We then use our empirical estimates of contact heterogeneities and network metrics to simulate outbreaks of devil facial tumour disease (DFTD), an extinction-threatening infectious cancer affecting Tasmanian devils. We incorporate tuneable algorithms and a range of DFTD transmission rates to grow networks capable of reproducing observed aspects of devil behavioural ecology, demographic and seasonal-based mixing preferences. The outputs of the network model are compared with a stochastic mean-field model, where every individual is equally likely to pass or acquire infection through time. Our network model

predicts a lower epidemic threshold for DFTD, faster devil extinction and higher DFTD extinction probabilities compared with the stochastic mean-field model. Our approach provides a template for using empirically obtained data on contact networks to develop models that explore the extent to which social behaviour and network structure influences transmission rates, epidemic behaviour or extinction probabilities for host and pathogens.

C24.5 Repeatability of antiparasitic behaviors across various temporal scales

Mark Hauber, Hunter College
Tomas Grim, Peter Samas

Hosts of avian brood parasites defend their nests predominantly by egg rejection. High consistency of egg rejection responses by potential host individuals is assumed by most theoretical models of brood parasite-host coevolution. Surprisingly, few studies have examined empirically how repeatable individual host responses are across various temporal scales, including within a breeding attempt (WBA), between breeding attempts within a breeding season (BBA), and between breeding attempts across different breeding seasons (BBS). Using experimental parasitism within and between nesting attempts, we found that the rejection of non-mimetic eggs (blue redstart type model) by Blackbirds (*Turdus merula*), was overall highly repeatable ($r \sim 0.70$). Although the repeatability was highest at the shortest temporal scale (WBA), the repeatability estimates remained high ($r \sim 0.6$) when the intervals between observations were longer (BBA and BBS). Repeatability of egg rejection did not vary with female age, although older females had a tendency to reject parasitic egg more often. Regarding the latency to ejection, another aspect of antiparasitic behaviors, we detected low repeatability ($r \sim 0.20$) across all time scales. These findings provide an impetus to study how sensitive theoretical models are to non-perfect repeatability of host behaviors against parasites. Funded by HFSP.

C25: Cooperative breeding

C25.1 Mean and variance in ecological conditions influence fitness consequences of group-living and communal rearing in the rodent *Octodon degus*

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Álvaro Villegas, Loren Hayes

Sociality and cooperation during offspring rearing may have evolved to face typical or mean conditions that are challenging to reproduction, or reduce

environmentally induced variance in fecundity. Examinations of these hypotheses come mostly from singularly breeding, bird studies. We examined fitness-ecology relationships in *Octodon degus*, a plural breeder rodent with offspring communal care. An 8-year field study was used to determine how mean and variance in food abundance, soil hardness, predation risk, ambient temperature, and precipitations predicted group size and number of breeding females (potential for breeding cooperation). Within years, mean (but not variance) food abundance and predation risk influenced group size but not breeding cooperation. Across years, variance (but not mean) in food abundance and precipitation influenced breeding cooperation. Increasing mean food abundance had a negative influence on the effects of increasing group size and number of breeding females on per capita offspring produced (PCOP). Increasing yearly mean maximum temperature had a positive influence on the effects of increasing group size on PCOP. Variance in food abundance had positive effects on PCOP of increasing group size. Thus, fitness consequences of sociality and communal rearing depend upon mean and variance in ecological conditions, possibly at different scales of social variation.

C25.2 Cooperation versus exploitation: communal nursing in house mice (*Mus musculus domesticus*)

Manuela Ferrari, University Of Zurich
Anna Lindholm, Barbara König

Understanding the evolution and maintenance of cooperative behaviour requires testing of the opportunity for exploitation. Female house mice show facultative communal nursing, in which two females raise their litters together and indiscriminately nurse all young. There is a risk of exploitation in situations where one of the females has a smaller litter, as both will invest the same amount of energy into the communal litter, but the pay-offs (number of weaned pups) will differ. Under laboratory conditions, we compared pairs of communally nursing females in which litter sizes were similar or different. We manipulated litter size based on a selfish genetic element (*t* haplotype) using a genotype dependent mating-design. The experimental manipulation of birth litter sizes allowed to test whether cooperative behaviour is modified when the risk of exploitation is enhanced. We found that the second female to give birth reduced the litter size of the other female while still pregnant (first born litters had lower survival probabilities), thereby minimizing the risk of being exploited. Furthermore, females showed a reduced

propensity to form communal nests in enhanced conflict situations. This study therefore provides evidence that communally nursing females compete over reproduction and modify their behaviour according to the conflict potential.

C25.3 The winner takes it all, the loser standing small: Evidence of winner and loser effects in a eusocial species

Alok Bang, Université Paris-Sud XI
Raghavendra Gadagkar

Many animal species, especially social species, establish and respect a social dominance hierarchy that has important implications on fitness and survival of individuals. What makes certain individuals more dominant than others? In answering this central question, factors like winner and loser effects (prior experience of winning or losing affecting current behaviour of individuals) born of social environment of individuals have been largely overlooked in general, and have never been attempted in a truly social species. We carried out a study on the Indian paper wasp, *Ropalidia marginata* to see whether winner and loser effects exist. We found both winner and loser effects in *R. marginata* and to the same degree. Behavioural repertoire accompanying these effects is significantly different for winners and losers, however, there was no change between subsequent contests for either winners or losers indicating that current behavioural repertoires accompanying these effects must have been stabilised to be at the optimum level. To our knowledge, this is the first such study reported in a eusocial species and represents an unexplored field of study in the context of eusocial species, and yields further insights concerning the determinants of behavioural dominance and how dominance hierarchies are built in social animals.

C25.4 Enforced help in a cooperative breeder

Markus Zoetl, University Of Cambridge
Tanja Schreier, Michael Taborsky

Investment in alloparental brood care in cooperatively breeding species might be enforced by punishing lazy helpers. However, recent reviews have stressed the lack of evidence for this mechanism in cooperative breeders and have argued that punishment is rare, if occurring at all in such groups. We investigated experimentally whether alloparental brood care provided by subordinates is contingent on social interactions

with dominant breeders in the cooperatively breeding cichlid *Neolamprologus pulcher*. We enhanced the need for brood care by temporarily preventing all individuals from caring for the brood. Subsequently, we either disabled or enabled physical contact between breeders and helpers, while leaving all group members in visual contact with each other. Only when physical interaction between helpers and breeders was enabled, helpers raised their effort in energetically costly brood care behaviour. Our results suggest that dominants coerce subordinates to provide costly help which would not be provided voluntarily, and that coercion is implemented by the aggressive behaviour of breeders.

C25.5 Habitat structure affects cooperative breeding in a fish

Joachim Frommen, Ethologische Station Hasli, University Of Bern
Frank Groenewoud, Hirokazu Tanaka, Michael Taborsky

In cooperative breeders, dominant individuals may tolerate helpers because they contribute to territory maintenance and defense. The need for such help can vary greatly, depending on ecological conditions. Thus, biotic and abiotic environmental conditions should strongly affect social structure. The cooperatively breeding cichlid *Neolamprologus pulcher* is distributed across a wide range of habitats in Lake Tanganyika. Accordingly, the demand of help in territory maintenance and defense should be expected to vary between populations. Here, we studied six populations of *N. pulcher* from locations differing in their substrate complexity and quality. The composition of social groups differed significantly between these populations. Group size and structure were related to habitat type, with habitats demanding more help comprising larger groups. Our results comply with the “pay to stay” hypothesis, which postulates that subordinate individuals must pay by cooperative behavior to evade evictions by dominant group members. This is corroborated by laboratory results showing that breeders more readily accept helpers if the demand for help is high.

C25.6 Ultimate and proximate causes of social competence in cooperative breeders

Barbara Taborsky, University Of Bern
Stefan Fischer, Alexander Kotrschal, Nadia Aubin-Horth

‘Social competence’ is the ability of individuals to optimise social behaviour depending on social information. It is particularly important in highly social animals. *Neolamprologus pulcher* is a cooperatively breeding cichlid living in highly variable social groups containing 3-40 members, both related and unrelated, juvenile and adult, female and male. Almost all activities in this species, including feeding, territory maintenance and defence, and rearing offspring, involve social interactions. In addition, social competence turned out to be very variable among individuals, and the species is experimentally well accessible. All this renders *N. pulcher* ideally suited to study the ultimate and proximate mechanisms underlying social competence. Here we asked: (i) Is social competence a general trait important in different contexts? (ii) Does it affect an individual’s fitness? (iii) Is it relevant in the natural environment? And (iv) what causes the variation between individuals? Our results show that (i) social competence affects performance across different social roles and contexts, (ii) high social competence allows more efficient and less dangerous conflict solutions, (iii) social competence varies with natural group size, and (iv) developmental effects causing individual trait variation are accompanied by differential programming of the hormonal stress axis and changes in relative brain size.

C26: Emotion & cognition

C26.1 Intraspecific variation in the response of the weeping lizard to conspecific distress calls

Antonieta Labra, Universidad De Chile
Michael Weymann, Claudio Reyes, Misque Hoare

The weeping lizard, *Liolaemus chiliensis*, is the only *Liolaemus* species for which there are reports of vocalizations, which is remarkable considering that the genus has more than 230 spp. These vocalizations, distress calls, mainly occur when individuals are subdued by a predator, and very rarely, when they are approached by a predator (i.e., without physical contact). For this species, it is known that vocalizations trigger in conspecifics immobility, followed by escape attempts. Considering that distress calls are remarkably similar across different vertebrate taxa, which facilitates eavesdropping, we tested if vocalizations of two separated populations (> 800 km) are similar, and if individuals of these populations react equally to heterotypic and homotypic calls. The northern population had a significantly more complex call (e.g., different frequency-modulated patterns and various non-linear phenomena) than the southern

population, and showed a higher response to homotypic calls. In contrast, the southern population has simple calls (e.g., without non-linear phenomena), and was equally reactive to the distress calls of both populations. Possibly, the complexity in signal production (vocalizations) is strongly associated to a finely tuned reception (hearing), which modulates the behavioral responses. Funds: FONDECYT 1120181.

C26.2 How fish appraise their environment: comparative study between different stimuli valences and personalities in European sea bass (*Dicentrarchus labrax*).

Sandie Millot, Ccmar

Marco Cerqueira, Maria-Filipa Castanheira, Catarina I.M. Martins

The large individual variation in behavioural responses to environmental challenges does not only depend on the situation to which the individual is exposed, but also on the cognitive evaluation that the individual makes of the situation. The goal of this study was to understand how sea bass appraised their environment by assessing the behavioural profiles of fish exposed to positive (social partners) and negative (net chasing) stimuli and how fish personality (reactive or proactive) influenced this appraisal. Ninety individuals were initially screened for coping styles using a restraining and an open field tests. Afterwards each individual was tested in a conditioned place preference tank (association of one side of the tank with either positive or negative stimulus). The swimming behaviour of each individual was recorded by video camera and analysed with the Lolitrack 2.0 software. Overall this study highlights the ability of fish to subjectively appraise stimuli with different valences, a characteristic that seem to have been evolutionary conserved throughout vertebrates. In addition, this study suggests for the first time a link between appraisal of both positive and negative stimuli and fish personality.

C26.3 Oxytocin induces an “optimistic” cognitive bias in dogs (*Canis familiaris*) both in social and non-social situations

Anna Kis, Research Centre For Natural Sciences, Institute Of Cognitive Neuroscience And Ps
Marta Gacsi, Jozsef Topil

Optimism refers to the extent to which one holds favourable expectations about the future, and is

influenced by current mood. The cognitive bias task has been used in case of several animal species to test how they judge ambiguous stimuli. Here we aim to test if oxytocin – a neurohormone that has been implicated in positive emotions – influences judgement bias in dogs.

Subjects first learned that a bowl contained a piece of food at the positive and was empty at the negative side of a room. Four groups of dogs (N=16 in each) were tested receiving oxytocin/placebo nasal spray, and participating in a social/non-social version of the cognitive bias task during which the bowl was placed at the negative, positive and ambivalent (in between positive and negative) locations. The latency to approach the bowl at each location was recorded and an “optimism” score (%) was calculated.

Subjects that received oxytocin pretreatment showed an optimistic cognitive bias compared to the placebo-treated groups in both conditions, although the effect was less pronounced in the non-social situation. Thus we conclude that oxytocin influences dogs’ judgement bias about ambivalent stimuli both in social and to a lesser extent in non-social situations.

C26.4 To measure what we intend to measure - animal models and human mental disorders

Erika Roman, Uppsala University
Bengt Meyerson

Relevant animal models to investigate the neurobiological basis for human mental disorders are a challenge. The problem is that the animal model should embrace behaviors that expresses and represents the particular human mental state that is the aim of the investigation. Anthropocentrism is a validity problem in this context, that is, to measure what we intend to measure.

To this end, an ethoexperimental test has been designed; the multivariate concentric square field (MCSF) test. It is unprejudiced and allows the animal to chose between a variety of environments including opportunity for exploration, risk assessment, risk taking, shelter seeking, incentive approach or avoidance in one and the same test session. The guiding principle for the MCSF test is the free choice of different environmental settings and items that provide the opportunity to detect essential features of the animal’s mentality. In this way a behavioral profile is generated.

Multivariate data analysis methods are used and a rank order procedure, “trend analysis”, is introduced. The trend analysis is based on individual

behavior strategies within the same or similar functional context, emanating from the same mental state. The applicability of the multivariate approach will be exemplified by a neuropharmacological investigation in rats.

C26.5 Impact of visual stimuli on emotional reactivity in European starling *Sturnus vulgaris*.

Laurine Belin, Umr 6552

Christine Aubry, Emmanuel de Margerie, Laurence Henry, Martine Hausberger

It is generally admitted that birds are particularly sensitive to some biologically relevant visual stimuli. Thus, “eyes” or “raptor” 2D pictures are predominant in studies aiming to test repellent signals. But the question is how such representations are really perceived by birds and whether they all elicit the same type of potential avoidance. In this study, we tested the hypothesis that reactions to supposed “repellent” visual stimuli may depend on context and type of stimulus. Captive wild caught European starlings were exposed to a variety of repellent visual stimuli presented on a LCD monitor: human, eyes, snake, raptor, as well as neutral stimuli. Starlings expressed approaches and avoidances as well as gazes towards the screen. Their behavioural profiles revealed that they classified these stimuli into two categories, one grouping humans and eyes representations, the other raptors, snakes and neutral images. The approach of the images by birds reveals that the “universal” supposed effect of some predator like stimuli may be questioned in non appropriate contexts such as cages. The classification of the stimuli by the birds shows nevertheless that they do perceive the 2D images but it is more the internal representation of the stimulus that may be involved. The effect of experience has been further tested by using hand raised starlings. The significance of these results both in terms of cognitive abilities of birds and experimental set ups will be discussed.

C26.6 The influence of coping style on generalisation in red junglefowl chicks

Alexandra Balogh, Linköping University

Josefina Zidar, Anna Favati, Hanne Lövlie, Olof Leimar

Stimulus generalisation, from a learnt to a novel stimulus, is a central psychological property that has been studied for decades. There is, however, little knowledge about individual variation in the tendency to generalise and the possible relation to animal personality. We trained red junglefowl chicks

to respond to two rewarded colours. A novel, intermediate colour was then presented in two subsequent generalisation tests. We found a strong initial preference for the novel intermediate colour. Further, the individual chicks differed in the strength of the initial preference for the novel colour, and this strength correlated significantly with their individual coping styles. The coping style was determined in a separate two-choice experiment, with a reversal of rewards. The flexibility (latency of response) at reversal was used as an indicator of the coping style, with short/long latency indicating reactive/proactive style. We found that chicks with a reactive coping style showed a stronger initial preference for the novel colour in the generalisation test. To our knowledge, this is the first evidence that coping styles are related to stimulus generalisation.

C27: Male-male competition

C27.1 Operational sex ratio affects male mating competition in a fish with dynamic sex roles

Karen De Jong, University Of Tuebingen

Trond Amundsen, Elisabet Forsgren

The operational sex ratio (OSR; the sex ratio of ready-to-mate individuals) was proposed to predict the strength of mating competition in 1976. This hypothesis has received correlational support from field studies, but controlled experiments have not produced conclusive results. We have previously argued that this may be due to differences in behavioural measurements between field and laboratory studies. To date, most laboratory experiments measure frequencies of competitive behaviours. However, frequencies will be affected by the number of encounters with mates and competitors, as well as the strength of competition. The propensity to compete at each encounter should more directly reflect a behavioural response. To test this idea we adopted a novel experimental design that allowed us to record both frequencies and propensities of competitive behaviours. Moreover, we manipulated the OSR without changing the adult sex ratio by varying the proportion of ready-to-mate females. As predicted, male propensity to court was higher in the male-biased OSR, while courtship frequency was not affected by OSR. Male-male interaction was more frequent in the male-biased OSR, even though male density was kept constant. Our results provide the first conclusive experimental evidence that the OSR as such affects competitive mating behavior as predicted by OSR-theory.

C27.2 Enforced monogamy affects the reproductive success and sexual ornamentation but not the sperm quality of male guppies

Gunilla Rosenqvist, Ntnu

Tonje Aronsen, Frode Fossay, Christophe Pélabon, Clelia Gasparini, Camilla Kalvatn Egset, Geir Rudolfsen

Relaxing sexual selection by enforcing monogamy could affect traits involved in both pre- and post-copulatory sexual selection. In this study, we compared the sperm quality, sperm number and sexual ornamentation (orange colouration) of male guppies (*Poecilia reticulata*) from replicated populations maintained under either a polygamous mating regime or under enforced monogamy for 12 generations. We also used artificial insemination to measure the reproductive success of one male from each mating regimes in direct competition. We found no differences in sperm numbers or motility between males from the two mating regimes, however males from the polygamous mating regime had significantly higher reproductive success and more orange coloration than monogamous males. Our results indicate that relaxed sexual selection can have negative effects on male fitness. We suggest that the most likely explanation for our results is the accumulation of deleterious mutations in the absence of sexual selection. We believe that our findings are particularly important in the context of relaxed sexual selection under captive breeding.

C27.3 Dominance is not always an honest signal of male quality

Mari Pölkki, University Of Turku

Raine Kortet, Ann Hedrick, Markus J. Rantala

Females prefer dominant males as mating partners in numerous species. Male dominance rank is considered as an honest signal of male quality because only healthy males in good condition are thought to be able to win fights with other males. Here, we tested whether activation of the immune system influences the success of males in male-male competition and mating in the field cricket, *Gryllus integer*. We activated the immune system of males with a nylon monofilament (to mimic a parasitoid larva) and arranged fights between male pairs to assess male dominance and associated mating success. Activation of the immune system with nylon monofilament substantially enhanced the fighting success of males during male-male competition but had no effect on mating success. However, sham-manipulation (a wound only) did not have any effect on fighting success although

females mated more often with dominant males. Our study suggests that when male crickets meet an apparent survival threat they may behave more dominantly, probably due to terminal investment. Male success during male-male competition is not always an honest signal of males' quality, but females may be able to detect this dishonesty.

C27.4 Variance in male lifetime reproductive success and opportunity of selection in a sexually promiscuous anthropoid primate

Constance Dubuc, New York University

Angie Ruiz-Lambides, Anja Widdig

In mammals, variance in lifetime reproductive success (LRS) is predicted to be greater for males than females because they are less limited by gamete production and parental investment. While a handful of species characterized by a high degree of polygyny support this prediction, less is known for sexual promiscuous species. Here, we used 20 years of genetic data to investigate whether male LRS is skewed in rhesus macaques (*Macaca mulatta*), an anthropoid characterized by a high level of sexual promiscuity. We calculated LRS for 211 males and 275 females of the Cayo Santiago population reaching sexual maturity and either died of natural causes or reached senescence using 3199 potential offspring surviving their first year of life. We first compared the strength of reproductive skew between males and females (B index), and then assessed the standardized variance of male LRS, a good estimate of the opportunity for selection (I). LRS was more skew in males than in females, but showed a low standardized variance ($I=1.3$) suggesting a relatively low opportunity for selection. Together, these results further support that variance is more pronounced in males, but that the strength of the phenomenon is lower in species facing low degree of polygyny.

C27.5 Resource value differentially affects fighting success between reproductive and non-reproductive seasons.

Zakea Sultana, Wakayama University

Inter-male competition for resources is usually studied during species' reproductive seasons because fighting is common and conspicuous. But how this competition compares to that during the non-reproductive season is rarely investigated. Here, we compared competition for burrows between the reproductive and non-reproductive seasons in a mud crab. We conducted two natural and three experimental observations. Under natural

conditions, we observed fights between residents and intruders in (1) reproductive and (2) non-reproductive seasons, and found similar results in both seasons. Two factors, body size difference and residency, contributed equally to fight outcomes. In experiment (3) during reproductive season we created an intruder by capturing a resident male and placing him in the burrow of another resident to induce a fight. (4) We repeated this but first placed a female in the burrow before introducing the intruder. Findings for both experiments were similar to those for natural fights. (5) During the non-reproductive season, we repeated the third experiment and found a different result: fight outcome was determined by the difference in body size, not residency. This is the first study to show that differing subjective value of a resource between the reproductive and non-reproductive seasons affects the fight outcomes.

C27.6 Demographic related changes in structure of male seal dominance rank hierarchy: “top” ranking males are lost from a declining colony.

Sean Twiss, Durham University

Amy Bishop, Emily Perrin, Anna Woodhead, Patrick Pomeroy

Grey seals are polygynous, colonial, annual breeders. Males compete to maintain positions among female aggregations to secure copulations. Male dominance hierarchy structure is highly conserved, exhibiting the same ogee (reversed) curve form across colonies differing in habitat, female distribution and sex ratios. Typically, relatively few individuals comprise a group of clearly dominant top ranking males, a few are clearly subordinate, whilst a larger group of mid-ranking males have very similar dominance scores. At Scotland’s North Rona colony, male-male aggressive interactions have been recorded over 24 years, encompassing multiple generations of males and a period of marked population decline (by over 60%). A disproportionately high reduction in the number of males ashore has led to an overall increase in mean female:male ratio. Detailed examination of dominance hierarchies over this period revealed a change in the form of the hierarchy, with an increase in linearity and loss of the group of ‘top ranking’ males. Examination of individual dominance ranks over successive years indicates that this effect is not due to individuals losing status, but due to top ranking males failing to return to the colony. This study highlights how long-term behavioural studies of known individuals can uncover hidden processes in population dynamics.

C28: Social insects

C28.1 Bees use social information as an indicator of safety in dangerous environments

Erika H. Dawson, Qmul

Lars Chittka

Avoiding predation is one of the most important challenges that an animal faces. Several anti-predation behaviours can be employed yet simply using the presence of conspecifics can be a good signal of safety in an environment full of predators. Here we show for the first time that the bumblebee, a pollinator at risk from multiple predators, uses social information as an indication of safety in an otherwise dangerous environment. Bumblebees (*Bombus terrestris*) were trained to differentiate between dangerous (i.e. a type of flower that harboured mechanical models of crab spiders, a sit-and-wait floral predator that attacks pollinators) and safe flowers. When test subjects were presented solely with the spider-infested flower species, there was a significant preference to only land on flowers occupied by other feeding conspecifics. Yet when safe flowers were available, subjects ignored this social information, demonstrating that the attention to social cues is confined to dangerous situations. Interestingly, we found that bees only used this social anti-predation tactic after having had previous foraging experience with conspecifics suggesting it is a learnt strategy. Our findings demonstrate a previously unknown social interaction in pollinators which may have important implications for counteracting the indirect effects of predators on plant fitness.

C28.2 Can bees see at a glance?

Vivek Nityananda, Queen Mary University Of London

Peter Skorupski, Lars Chittka

Humans and monkeys can categorize scenes extremely rapidly, making visual decisions about scenes presented even for only 20 ms. Is this capacity to represent and process scenes in a sensory snapshot a consequence of the bigger brain size and computational power of primates? Other animals, such as insects, have far smaller brains and relatively poor visuo-spatial resolution and potentially limited processing power available for parallel processing. One might, therefore, expect them to be incapable of such rapid decisions and to have to actively scan the scene instead. No studies have, however, investigated whether non-primates have the capability to ‘see at a glance’ or not. We

asked if bumblebees could learn to detect and discriminate between visual patterns which were presented for durations of 100 ms or less. We find that bumblebees can detect the presence of stimuli and discriminate between certain stimuli even when they are presented as briefly as 20 ms. This is the first demonstration of a non-primate being capable of rapid visual feature extraction, indicating that insects might be able to capture key features of the world around them 'at a glance'.

C28.3 Career choice in red wood ants

Ivan Iakovlev, Institute Of Systematics And Ecology Of Animals, Siberian Branch Of RAS
Zhanna Reznikova, Natalya Atsarkina

In a developmental study we examined how personality traits affect professional specialisation in red wood ants *Formica aquilonia*. Ants were put through a battery of tests individually at different ages. All tests simulated natural situations such as encounters with enemies and predators, searching for food, avoiding obstacles, and learning the way home in a maze. It turned out that job choice in red wood ants progresses through their ontogeny and is closely connected with the combination of psychophysiological characteristics of individuals, such as the intensity and number of aggressive reactions, the ability to learn how to avoid danger or to solve searching problems. We have demonstrated that career choice in red wood ants is based on behavioural syndromes rather than on age polyethism. A few individuals that enjoy explicit combinations of behavioural peculiarities serve as models for the rest of the ants which, in turn, possess only intermediate characteristics. The most distinctive feature of scouts is their high exploratory activity; they also form spatial memory faster and keep the information longer and more precisely than members of other professions. This is the first experimental evidence that ants' personal traits affect their career preferences at the early stage of their ontogeny.

C28.4 Logical use of landmarks in foraging ants

Yukio Gunji, Koibe Universtiy
Tomoko Sakiyama

Although it is known that foraging ants use visual cues, researchers claim that ants do not have a cognitive map and they just trace a sequence from a scaffold to another. However, ants have to identify a landmark indicating multiple cues till the sequence from a nest to feeder are established. We here

propose a landmark use model based on the dynamical interface between two kinds of logic. Landmarks and route between landmarks are represented by node and edge in a directed network, and is transformed to a partially ordered set (POS). It is assumed that an ant walks in a POS and identifies a landmark in terms of both the property of landmark (L1) and the set of accessible landmarks from the very landmark (L2). In another talk (TS_YPG) we show that ants use logical operation for L1 and L2. In our model, two kinds of logical operations entail a logical conflict which has to be dynamically removed. We finally show that POS in our model evolves to a particular structure by dynamical removal of the logical conflict and that the structure can be found in real ants, *Camponotus japonicas*.

C28.5 Biochemical crowdsourcing through oral fluid-exchange in ant colonies

Adria LeBoeuf, University Of Lausanne
Richard Benton, Laurent Keller

Communication is essential in high-functioning social groups, from social insects to humans. How do ants bring about colony-wide change without language or top-down control? While ants are traditionally thought to communicate mostly through pheromones, we are testing whether trophallaxis – a method of mouth-to-mouth liquid transfer – may also be an important pathway for communication enabling a form of chemical crowdsourcing. Given the power of trophallaxis to rapidly distribute liquids throughout the colony, trophallaxis provides an excellent means of information transfer, especially for compounds unstable outside the body. Socially exchanged fluids, e.g. seminal fluids, often carry ancillary information that alters behavior. To date, the contents of trophallaxis fluids have not been thoroughly analyzed and thus the precise function(s) of this striking behavior remain unknown.

Using nano-liquid chromatography tandem mass spectrometry and gas chromatography mass spectrometry, we have biochemically analysed the protein and small-molecule-hormone components passed between individual ants during trophallaxis. In addition to the anticipated insect gut proteins, we have also found proteins potentially involved in the hormonal regulation of social insect behavioral maturation – the age-related transition from nurse to forager. Proteins passed between nestmates vary depending on the social caste of the donor and have high sequence similarity to well-known insect hormonal regulators, suggesting that by passing behavior-altering hormones and their regulatory

molecules to one another, nestmates might influence one another's behavioral maturation. These biochemical studies are being paired with a highly quantitative, barcode-based ant tracking system to measure the behavioral causes and effects of trophallaxis and the long-term behavioral effects of candidate proteins.

C28.6 Exploration, exploitation and dodging the costs of central-place foraging: insights from radio-tagged ants

Elva Robinson, University Of York

Foraging animals face an exploration-exploitation trade-off when allocating their time and energy. Social species, such as ants, can benefit from having many individuals. Collectively, a colony's foragers can explore many sites simultaneously and can also exploit food sources efficiently by means of rapid recruitment. Some ant species use a dispersed nesting strategy in which a colony is spread across multiple nests. A recent model predicts that compared to living in a single central nest, this dispersed-nesting strategy should increase a colony's exploration success. However, the model predicts that this could come at a cost, because dispersing foragers across many nests makes recruitment, and therefore exploitation, less effective. The invasive and dispersed-nesting Pharaoh's ant (*Monomorium pharaonis*) was used to test these hypotheses, with RFID technology enabling tracking of individual workers. Colonies housed in single or multiple nests were tested to determine how exploration and exploitation behaviour are influenced by the colony's nesting structure and whether colonies can avoid the costs of having a dispersed foraging body by recruiting ants from several nests at once. The results shed light on how the behaviour of these ants contributes to their success as a globally invasive pest.

C29: Personality 2

C29.1 Personality development in pet dogs from puppyhood to adulthood - a longitudinal study

Stefanie Riemer, University Of Vienna, Veterinary University Of Vienna, University Of Lincoln
Corsin Mueller, Ludwig Huber, Zsofia Viranyi, Friederike Range

A recent meta-analysis found moderate temporal consistency of personality in domestic dogs (Fratkin et al. 2013, PLOSOne). However, prior studies have focused mainly on certain outcomes (e.g. guide dog success) or single traits (e.g. reactivity), and there is

a lack of studies on when personality stabilises in dogs and which traits are more amenable to change. Therefore, to investigate individual and group level trajectories of personality development, 72 Border collies were assessed repeatedly between the ages of six weeks and two years. At six weeks, the puppies were tested in a personality test. When the dogs were around six, twelve, and at least 18 months old, their owners filled in dog personality questionnaires. Over fifty dogs furthermore participated in a personality test as adults. While the results of the six-week test were poor predictors of future behaviour, the owners' assessments of behaviour traits at six months were highly correlated with their later assessments. At the group level some changes occurred as the dogs matured, such as an increase in intraspecific aggression; nevertheless, the rank order of individuals remained stable for the majority of traits. The study provides new insights into patterns of personality development in dogs.

C29.2 Personality research in wild-type zebra finches (*Taeniopygia guttata*) - establishing selection lines for behavioural traits

Yvonne Wuerz, Bielefeld University
Oliver Krueger

Stable individual differences in behaviour, termed personality in human psychology research, are increasingly also studied in animals. We have developed a standardized test battery comprising five behavioural traits to establish consistent individual differences in behaviour ('animal personalities' or 'behavioural syndromes') to study their genetic and environmental causes as well as the covariation with fitness in a captive population of wild-type zebra finches (*Taeniopygia guttata*). We measured general activity in the home cage, boldness towards a novel object, exploration in a novel environment, fearfulness in a tonic immobility test and aggression towards a mirror. All traits have been found to be considerably repeatable. We established selection lines for three of the measured traits - fearfulness, exploration, and aggression - and will report on trait heritabilities and fitness differences between the divergently selected lines.

C29.3 Integrating the study of cooperation and personality: towards a comprehensive behavioural type

Valentina Balzarini, University Of Bern
Michael Taborsky, Joachim G. Frommen

The study of animal personality has traditionally focused on a limited selection of behavioural traits, including activity, aggression, exploration and boldness. However, these four categories of behaviour may not comprehensively represent an individual's 'personality'. In highly social animals, for instance, the propensity to interact with and help others can constitute an important part of consistent interindividual variation. Here we asked whether in the cooperatively breeding cichlid *Neolamprologus pulcher*, helping behaviour relates systematically to other behavioural traits. Specifically, we included cooperative behaviours like territory maintenance and defense in the analysis of the animals' behavioural types. Helping propensity, reaching from "primarily altruistic" to "dead selfish", may represent a different behavioural axis than the bold-shy continuum. We show that in *N. pulcher*, individual helpfulness relates consistently to other personality traits such as exploration tendency and aggression. This is consistent with the social niche hypothesis and hints on the importance of considering behavioural consistency and correlation beyond the traditional behavioural categories hitherto considered in personality research.

C29.4 Personality may be expressed differently in social and non-social contexts.

Christina Lehmkuhl Noer, University Of Copenhagen
Esther Kjar Needham, Sophie Wiese, Torben Dabelsteen

Individuals of the same species may vary consistently across time and context in suites of behavioural traits and in this way express different personalities. For instance, approach behaviours may express different levels of boldness/shyness. We investigated to which extent such behaviours were consistent in 47 farmed wild type American mink across four different contexts, two non-social (novel object tests \pm a loud noise) and two social (mirror test and live mink test). NO's and mirror were placed in the back end of the test subject's cage, the live mink in a small cage next to the back end of the cage. All behavioural variables were analysed using PCA. The results showed consistency in the inter-individual variation across the two non-social contexts, forming a non-social bold-shy dimension, and consistency across the two social contexts, forming a social bold-shy dimension. The lack of consistency in approach behaviour across non-social and social contexts may be driven by differences in the motivational systems involved in survival and reproduction, respectively. It could be argued that we have identified different aspects of

personality. However, the rationality of requiring consistency in behaviours across all contexts to define personality may also be questioned if contexts differ too much.

C29.5 Personality in a wild insect

David Fisher, University Of Exeter
Tom Tregenza, Rolando Rodriguez-Munoz

The study of animal "personality" is becoming more widespread as appreciation grows that many individuals are limited in phenotypic space. Current studies typically involve captive vertebrates and invertebrates in laboratory conditions, with a limited but growing number using free-living vertebrates. However, there is a gap in our knowledge regarding the potential expression of personality in wild invertebrates. Additionally, studies in the wild of long-lived vertebrates tend to focus on a short portion of their lives or points at distant intervals. We intensively monitored a population of wild field crickets (*Gryllus campestris*) during pre-adulthood and over their entire adult lives, regularly re-capturing free-living individually identified crickets and testing them for three distinct personality traits; boldness, activity level and exploratory behaviour. I will present and discuss the results from the first field season, revealing the extent of personality in the wild crickets and the repeatability, stability and relatedness of the different traits in relation to ontogeny and age. I will also explore the potential for further research using this study system, such as linking personality to fitness, and comparing data from our laboratory based measures with observations of behaviour in the wild made by our extensive network of video cameras.

C30: Development

C30.1 Players gonna play: juvenile rough-and-tumble play enhances adult male sexual performance in American mink

Jamie Ahloy Dallaire, University Of Guelph
Georgia J. Mason

What is play for? Rough-and-tumble play (R&T) is hypothesized to prepare males for adult sexual behaviour. However, existing support from deprivation studies confounds play partner absence with social isolation. We tested this hypothesis using experimental manipulations more specific to R&T, using large populations of fur-farmed mink. In initial observations of 60 males, juveniles' R&T frequency positively predicted copulation number and

duration in their first breeding season 6 months later. Using 2609 juveniles, we then tested nine modifications to housing or social groupings, identifying three that significantly increased R&T compared to standard mixed-sex, same-strain pair-housing (extra-large cages; male-male pair-housing; mixed-strain pair-housing). These three treatments also increased adult anogenital distance (corrected for body mass) above controls at least in one sex, suggesting increased masculinisation. One group (mixed-strain-housed males; $n = 16$) was followed to the breeding season. They initiated copulations faster and copulated for longer than controls ($n = 15$), with individual R&T again predicting copulation duration. Thus, experimentally promoting R&T enhanced male sexual performance, supporting this hypothesis about the function of play. Furthermore, effects were possibly mediated via increased masculinisation. Next, we plan to investigate all three high-R&T treatments' effects on testosterone levels, as well as sexual performance, in both sexes.

C30.2 Behavioural and molecular responses to a social challenge in a cooperative breeder reared in different social environments

Cecilia Wikstrom, University Of Bern
Stefan Fischer, Nadia Aubin-Horth, Barbara Taborsky

Social competence, the ability to optimize the social behaviour based on social information, can increase the Darwinian fitness of animals. This ability is known to be shaped by early social experience, but the molecular mechanisms driving this developmental variation are largely unexplored. We tested how juveniles of the cooperatively breeding cichlid *Neolamprologus pulcher* reared in different social environments cope with a social challenge, and how brain gene expression relates to rearing environment and social behaviour. Juveniles were reared for two months either with or without a breeder pair and a helper. Subsequently, juveniles of both rearing conditions were either exposed to an asymmetric contest over a resource, or to a control treatment without social interactions. Directly afterwards fish of challenge and control treatments were sacrificed for brain gene expression (GE). We compared (i) the expression of social behaviour between fish reared with or without older conspecifics and (ii) the expression of 10 brain genes between fish of different rearing backgrounds and fish exposed to challenge or control treatment. These analysed genes code for hormones and receptors known to be important determinants of social behaviour. GE was measured

in the hypothalamus and telencephalon, two key brain areas important for social behaviour.

C30.3 Social Background Matters - Development of Social Behavior and Social Integration in Male Zebra Finches (*Taeniopygia guttata*)

Tim Ruploh, Bielefeld University
Hans-Joachim Bischof, Nikolaus von Engelhardt

Social experience during development can have a strong impact on developmental trajectories and modify morphology, physiology and behavior. Recently, we have shown that the expression of males' courtship and aggressive behaviour in a highly social avian species, the zebra finch (*Taeniopygia guttata*), can be influenced by the adolescent social environment. We here investigated whether differences in social experience during adolescence also impact on an individual's social integration and if courtship and aggressive behaviour can predict the social integration performance. Zebra finches were kept in pairs (male-female or male-male) or larger mixed-sex groups (3 males and 3 females) during adolescence and were exposed to a group of unknown conspecifics during adulthood. Male social integration, courtship and aggressive behaviour were quantified directly after the introduction to the group and 48 hours later. Group-reared males were better socially integrated in both observation periods indicating that a greater amount of social stimulation during adolescence enhances sociality during adulthood. However, male courtship and aggressiveness could not predict the individuals' integration into the group. We discuss alternative explanations for the difference in social integration and how to test these in future research.

C30.4 Responses to Predator Chemical Signals are Modulated by Early Olfactory Experience in the House Mouse

Vera Voznessenskaya, Institute Of Ecology & Evolution
Tatiana Malanina, Artem Klinov

Chemosensory detection may be an important aspect of predator avoidance strategy. We showed that exposures of mice *Mus musculus* to urine from feral cats *Felis catus* under semi-natural conditions significantly affected survivorship of offspring. In the current study we examined the influence of the Felidae family pheromone L-felinine on the reproduction of mice and how the response to predator odours could be modulated by early

olfactory experience. Olfactory thresholds to cat urine and L-felinine were measured with automated olfactometer (Knosys, USA). Number of newborn pups and sex ratio was recorded. Corticosterone metabolites were monitored non-invasively. Percent of animals with block of pregnancy was significantly higher ($n=26$, $P<0.001$) in adult mice exposed to L-felinine. Exposure of adult mice to L-felinine also affected sex ratio ($n=26$, $p<0.001$) in favour of males. The observed effects could be explained in part by long lasting elevation of corticosterone under L-felinine exposures ($n=13$, $p<0.001$). Exposures of mice to cat odours (urine, felinine and derivatives) during critical period for odour sensitization (14-28 days after birth) lowered the olfactory thresholds by two-three fold which is adaptive for the predator detection. At the same time corticosterone response stayed unchanged indicating the innate nature of the response.

C30.5 Is risk-taking the privilege of youth? A behavioural study in wild mice, *Mus spicilegus*.

Marie Lafaille, LEEC
Christophe Faron

In nature, mammals are often confronted with potentially risky situations but their behavioural responses to these situations generally differ according to age. Pre-adults are more prone to take risks, whereas aged individuals are often described as anxious. These risky behaviours may be adaptive notably in pre-adults in helping to successfully disperse. In the mound-building mice, *Mus spicilegus*, two different age cohorts are concerned by dispersal and consequently by risk-taking behaviours (2 and 6 month-old individuals). In this study, the exploratory and risk-taking behaviours of these two age cohorts were compared through three different tests (open-field, elevated plus maze and novel object exploration test). Behavioural differences found between age groups and sexes are discussed in the context of dispersal.

Furthermore, because these mice do not live more than ten months in nature, the anxiety-like behaviors of extra-naturally aged individuals (12 and 24 month-old) were also evaluated in order to estimate if one year-old mice already present signs of ageing. Surprisingly, these two age groups have opposite profiles with an unexpected high level of exploratory and risk-taking behaviours in the oldest. These results are discussed in the context of a hypothetic survival of 12 month-old mice to winter climatic conditions.

C30.6 Behavioural plasticity: handle with care.

Hilton F Japyassú, Federal University Of Bahia (Brazil)
Pedro L B Rocha, Andre Mendonça

Behavioural plasticity (BP), the ability of an organism to express different performances in different contexts, is a major component of fitness in heterogeneous landscapes. Enhancement of heterogeneity in anthropic fragmented landscapes is potentially selecting for plasticity, increasing the importance of BP for contemporaneous evolution. Although BP is sometimes difficult to measure, there are various handy indexes of stereotypy (SI) which could be used to assess BP, since the literature takes as a premise the existence of a negative plasticity/stereotypy relationship. We formally test this premise, checking for the existence of a negative correlation between three available SIs and a corresponding measure of BP. Foraging responses of seven spider species to two distinct prey types were used as raw data for MANCOVA analyses. Our results do not indicate negative correlations between BP and SIs; indeed, the opposite relationship appears. Based on these unexpected results, we discuss the conceptual relation between plasticity and stereotypy, put forward a framework of analysis that can accommodate the conflict between theoretical and empirical research, and propose a new index for estimating BP. We also relate this new framework with emerging concepts in the area of behavioural syndromes, such as behavioural stability and temperament.

C31: Conservation

C31.1 Informing the links between behaviour and vital rates in a capital breeding mysticete to measure the effects of whalewatching activities

Fredrik Christiansen, University Of Aberdeen
Marianne H Rasmussen, David Lusseau

Human disturbances of wildlife, such as tourism, can alter the activities of targeted individuals. Repeated behavioural disruptions can have long-term consequences on individual's vital rates. To manage these sub-lethal impacts, we need to understand how short-term behavioural changes can be linked to individual's vital rates. We compared minke whale *Balaenoptera acutorostrata* behaviour on a feeding ground in the presence and absence of whalewatching boats in Iceland, using individual focal follows. Activity states were inferred from movement metric data and transitions between states were estimated using Markov chains. Activity budgets were then estimated using Monte Carlo

simulations. Spatially explicit capture-recapture models were used to estimate the seasonal exposure of individual whales to whalewatching boats, so that the seasonal effect of whalewatching activities on the activity budget of minke whales could be estimated. This in turn was linked to female body condition (FBC) using published bioenergetic data. Finally, changes in the FBC were linked to foetal growth, and hence reproduction. Our findings suggest that although the immediate bioenergetic costs of whalewatching interactions were relatively high, the cumulative time spent with whalewatching boats throughout the feeding season was very low, resulting in a non-significant effect on FBC, and consequently foetal growth.

C31.2 Sex in murky waters: anthropogenic disturbance of reproductive behaviours in the pipefish model system

Josefin Sundin, Uppsala University
Gunilla Rosenqvist, Tonje Aronsen, Anders Berglund

Animal behaviours are affected by human induced environmental change, which in turn may alter species interactions, population dynamics and evolutionary processes. In marine ecosystems, overfishing, eutrophication and ocean acidification is currently changing the environment at an unnatural speed. We use pipefish as our study organism, which is a family of specialized marine fish practicing male pregnancy. Through a series of controlled laboratory experiments we show that anthropogenic disturbance alter several aspects of reproduction, including courtship behaviours, mate choice, mating propensity and reproductive success. We show that the way in which the environmental stressors alter reproductive behaviours may vary both between and within the sexes, populations and species. Further, different environmental stressors, such as turbidity, hypoxia and altered pH levels, elicited different responses, sometimes in opposite directions. Thus our studies emphasises the complex way in which environmental change may alter reproductive behaviours. Given the increase in human disturbance on ecosystems, answering these questions is not only important to better understand how environmental fluctuations affect evolutionary processes, but also for conservation biology and studies on the resilience of organisms to anthropogenic induced environmental change.

C31.3 A model of optimal diving for bottlenose dolphins under human disturbance

John Symons, University Of Aberdeen

David Lusseau

Short-term behavioral responses to human disturbance are well documented in cetaceans, including responses similar to those observed under natural predation risk. However, to understand potential long-term consequences of human disturbance at the population level, we need to first link these short-term responses to bioenergetics. A model of optimal diving for three functions of predation risk (decreasing instantaneous risk (DIR), increasing instantaneous risk (IIR), and no predation risk) was developed for a population of bottlenose dolphins (*Tursiops truncatus*) in Doubtful Sound, New Zealand. Individual focal follows were conducted and the inter-breath interval during foraging activity were recorded. Using mixed effects models, we found that males significantly increased bottom times and performed fewer bottom dives when boats were present, matching predictions of our model for DIR. In contrast, females significantly decreased bottom times and increased the frequency of bottom dives, matching predictions from the model for IIR. Therefore, our results suggest differences in perception of risk between sexes. The estimated decrease in net-energy gain over the course of a foraging bout for both sexes (with females being more impacted) can affect bioenergetics, and ultimately long-term vital rates and is therefore of particular concern as the population meets the IUCN criteria for critically-endangered.

C31.4 Improving conservation management of New Zealand's rarest kiwi (*Apteryx rowi*): Effects of early rearing experience and optimal release group size.

Rachael Abbott, Victoria University Of Wellington.
Ben Bell, Nicky Nelson

Early rearing experience can have significant impacts on the behaviour of animals reared in non-natural situations for conservation management. Rowi are critically endangered flightless ratites which form monogamous, highly territorial pairs with extended periods of parent-offspring association. Restocking of the sole remaining rowi population involves rearing chicks on predator-free islands isolated from adult conspecifics. To reflect adult social organisation, releases traditionally took place in pairs or small groups. We hypothesised that as a result of behavioural mechanisms induced by pre-release experience, individuals in larger groups would have a higher survival rate than those in small release groups. We tested this experimentally by manipulating release group size over 3 years.

Modelling revealed that of all variables tested, group size was the only factor with significant influence on post release survival ($n=67$, $p=0.036$). Survival of individuals in small groups was significantly lower than that of individuals released in large groups. We suggest that social attraction and increased conspecific tolerance resulting from an individual's rearing environment are the reason for this. Our findings have informed conservation management leading to changes in release protocols, and triggered further research into behavioural plasticity and long term effects of rearing conditions in conservation management.

C31.5 Behavioural insights into the conservation of long-distance migratory birds in a rapidly changing world

Rob Thomas, Cardiff University
Renata Medeiros, Adam Seward, James Vafidis,
Jeremy Smith

The behaviour of individuals often underlies the responses of animal populations to environmental change. Therefore, behavioural studies can provide key insights into the impacts of climate change on animal populations. I present a series of case-studies, of the behavioural mechanisms underlying the responses of long-distance migratory birds to climate-driven ecological change, in contrasting ecosystems: (i) Strategic buffering of energy reserves against starvation during migration, in European Storm Petrels (*Hydrobates pelagicus*), in response to climate-driven changes across a marine ecosystem. (ii) Effects of climate-driven ecological change, on the breeding behaviour, migratory fuelling strategies, and overwinter behaviours, of three species of migratory songbirds which differ in their breeding /wintering habitat, diet and migration strategies. These songbirds are: Northern Wheatears (*Oenanthe oenanthe*) breeding in upland grasslands, Pied Flycatchers (*Ficedula hypoleuca*) breeding in deciduous woodlands, and Reed Warblers (*Acrocephalus scirpaceus*) breeding in reed-beds. These case-studies identify a range of behavioural mechanisms by which climate change is already affecting migratory populations, and highlight the dual role of phenotypic (including behavioural) flexibility and micro-evolutionary change in facilitating adaptation to rapidly changing conditions on a global scale. Understanding these mechanisms also identifies priorities for conserving long-distance migratory birds in the face of current and future climate change.

C31.6 Competition for nest sites causes global variation in bumblebee declines

Andrew Higginson, University Of Bristol

Pollination is vital for ecosystem functioning, but pollinator populations worldwide are declining. Among bumblebees there is strong but unexplained variation between species in the extent of declines. Bumblebee queens compete for nest sites, which may be limited in degraded environments. I used an evolutionary model to predict the outcome of competition between queens that differ in size and emergence time. The model shows that a reduction in nest-site abundance would have greater negative impacts on late-emerging species, especially those that have larger queens, due to their more stringent nest-site criteria rather than a lack of empty nest sites or an increased frequency of fighting. In contrast, early-emerging species with large queens are predicted to decline only slightly. These predictions are supported by data on the declines of 43 bumblebee species worldwide. Increasing the density of nest sites is likely to reverse the loss of these important pollinators. The model predicts that gradually declining nest site availability will lead to an accelerating decrease in populations due to the escalating effects of competition, implying that revised conservation policies are urgently required to conserve pollinator populations.

C32: Cooperation

C32.1 Sequential joining promotes cooperative groups with self-interested participants

David Wheatcroft, Uppsala University

Understanding why individuals perform behaviours that benefit others, but entail costs to themselves remains a difficult problem in behavioral ecology, because individuals should do best by letting others act alone. Such behaviours are usually framed in terms of "dilemmas" in which each individual makes their decision to participate without knowledge of what the others will do. However, individuals in natural systems may vary in how they benefit, meaning that some individuals may profit even from performing the behaviour alone, and groups often form sequentially, meaning that subsequent joiners can use knowledge of others' decisions when making their own. Using avian anti-predator groups called mobs as a model system, I conducted experiments on mob formation in three diverse communities in the Indian Himalayas during the last 5 years. I found that individuals are likely to mob predators alone when in close proximity, but that they can also be incentivized to join more distant

mobs as long as a sufficient number of other birds are already mobbing. My results suggest that game-theoretic dilemmas can be resolved in natural systems through self-interested, but sequential decisions.

C32.2 How to Maintain Cooperation: Behavioural mechanisms limiting cheating behaviour in the cleaner wrasse *Labroides bicolor*.

Max Gray, University Of Cambridge
Andrea Manica, Redouan Bshary

Cooperation fundamentally requires both parties involved to derive a benefit from the relationship. When cheating occurs one party incurs a cost and if an individual is cheated too frequently there will be no net benefit to the relationship. Therefore cheating above a certain threshold will destabilise a cooperative system, possibly to the point where cooperation may no longer occur at all. *Labroides bicolor* is an obligate cleaner feeding exclusively off other fish. By removing ectoparasites (“cleaning”) from many other species of reef fish the cleaner benefits by nourishment and decreased predation risk. However, *Labroides bicolor* also cheats by consuming client mucus or healthy tissue, to the cost of their so-called clients. *Labroides bicolor* cheats significantly more frequently than other congeneric cleaners that are involved in cleaning mutualisms with very similar reef communities. So how does this species remain in a functional mutualism at a higher cheating frequency than its closely related species? I present evidence that in a minority of cases the mutualism has in fact destabilised. Also using data from manipulative aquarium experiments supported by non-invasive field observations, I discuss several key behavioural mechanisms that limit cheating in interactions with the majority of client species.

C32.3 Behavioral responses to inequity in reward distribution and working effort in corvids

Claudia Wascher, University Of Valladolid
Thomas Bugnyar

Sensitivity to inequity is considered to be a crucial cognitive tool in the evolution of human cooperation. The ability has recently been shown also in primates and dogs, raising the question of an evolutionary basis of inequity aversion. We present first evidence that two bird species are sensitive to other individuals’ efforts and payoffs. In a token exchange task we tested both, behavioral responses to inequity in the quality of reward (preferred

versus non-preferred food) and to the absence of reward in the presence of a rewarded partner, in 5 pairs of corvids (6 crows, 4 ravens). Birds decreased their exchange performance when the experimental partner received the reward as a gift, which indicates that they are sensitive to other individual’s working effort. They also decreased their exchange performance in the inequity compared with the equity condition. Notably, corvids refused to take the reward after a successful exchange more often in the inequity compared with the other conditions. Our findings indicate that awareness to other individual efforts and payoffs may evolve independently of phylogeny in systems with a given degree of social complexity.

C32.4 Stress and cooperative levels in a cleaner fish mutualism

Marta Soares, ISPA-Instituto Universitario
Sonia Cardoso, Alexandra Grutter, Rui Oliveira,
Redouan Bshary

Both human and other animals alike need to be able to shift their behavioural output in order to optimize their decision-making process, along with a dynamic and sometimes stressful social environment. Here we tested a hypothesis that cooperative behavioural flexibility is mediated by stress-mediated mechanisms, in a cleaning mutualism involving the cleaner fish *Labroides dimidiatus*. When interacting with other fish, cleaner fish are faced with the decision to cooperate by removing other fish ectoparasites or to cheat by removing their mucus instead; and are known to use a highly diverse behaviour repertoire to persuade their clientele to visit, to increase the duration of inspection and to promote their return in the near future. We found that stressed cleaners responded to their visiting clientele by providing more tactile stimulation however, they were also cheating clients more often. On the contrary, the blocking of the glucocorticoids receptors led to an increase of cleaning inspection duration. Our results demonstrate that the role of stress and stress responses are key for producing changes on individuals’ levels of cooperation. This might be the primary hormonal mechanism affecting vertebrate interspecific cooperation through which cognitive social flexibility develops and further adjustments to ecological and social factors arise.

C32.5 Lifetime patterns of cooperation and competition; tests for role specialisations in the banded mongoose.

Jennifer Sanderson, University Of Exeter
Sarah Hodge, Andrew Young, Mike Cant

Individual differences in cooperative investment can be consistent and persist after life-history variation has been controlled for. This suggests that plasticity of cooperative behaviours may be limited, and individuals may be constrained to different behavioural roles within a society. We examine consistent individual differences and cross-context correlations of both cooperative and non-cooperative behaviours to test for behavioural roles within a wild population of banded mongooses (*Mungos mungo*). We find evidence for consistent individual differences in both cooperative and competitive behaviours. Positive correlation of individual differences across cooperative contexts suggests that individuals are not specialised to different cooperative activities, rather they may be specialised as helpful and selfish individuals. However, individual differences are not correlated between the contexts of cooperative offspring care and non-cooperative mating behaviours, suggesting that individuals do not show lifetime specialisations to roles as carers and breeders. Evidence for lifetime consistency of individual differences is suggestive of lifetime behavioural trajectories; our results suggest that banded mongooses develop along trajectories of high or low helper effort. This suggests that variation in helper effort may be attributable to early-life environment and advocates further study into early-life effects to determine the factors that lead to different behavioural trajectories within animal societies.

C32.6 Ecology of cooperation and the cost of memory

Zoltan Barta, University Of Debrecen
Michael Taborsky, Jacint Takalyi

Cognitive capabilities play an important role in reciprocal altruism. Nevertheless, it is rarely investigated how cost of these capabilities interplays with the evolution of cooperation. With an individual-based evolutionary simulation, we investigate how the cost of memory influences the evolution of direct reciprocity in groups of non-relatives.

The modelled individuals have reserves and memory. Maintaining memory has a reserve cost. Individuals spend the day foraging solitarily and gather on a common place in the evening. Here those individuals who have high reserves can share food with others. Sharing depends on the strategy

of the individual (ALLD, ALLC and TFT) and, in the case of TFT, on information of the partner's previous behaviour: whether it has shared or not in the past. Strategy and memory size are controlled by genes. When memory size is fixed for each individual direct reciprocity easily evolves under aggregated food and if maintaining high level of resources is costly.

Allowing memory size to freely evolve hampers the evolution of cooperation. Under this scenario direct reciprocity only appeared if memory cost was almost zero. When individuals can choose a partner based on its memory size cooperation quickly evolves even for rather large cost of memory.

C33: Bird song

C33.1 New Zealand bellbirds: parallel song learning abilities of male and female juveniles.

Dianne Brunton, Massey University
Barbara Evans, Michelle Roper

The endemic NZ Bellbird (*Anthornis melanura*) is an ideal model for testing cultural evolution of song. Bellbirds are honeyeaters that have a natural range that includes most offshore islands and the majority of NZ's forests. Most significantly both sexes sing prolifically and defend resources using song. Song learning is a key factor in the evolution of dialects and there is a critical relationship between timing of song learning, dispersal and the formation of geographic dialects. While it is undisputed that many species have sex differences in song usage, vocal learning abilities of female songbirds are effectively unknown. In this study we quantify and compare the vocalizations of 1) male and female juvenile bellbirds of comparable ages, and 2) same sex songs of adults and juveniles. Songs were recorded in February 2013 at Lady Alice Island, an island off the coast of north-eastern NZ. Juvenile bellbirds of both sexes ranged in age from 2-8 weeks post fledging. Song development and complexity was similar for both male and female juveniles and sex differences in song types were apparent for all ages. Both sexes had a plastic song phase and song crystallisation occurred within 8 weeks post-fledging. Studies following individual chicks are underway.

C33.2 Do you hear what I hear? Early-life stress in European starlings (*Sturnus vulgaris*) affects auditory learning in females, but not males

Tara Farrell, Western University
Amanda Morgan, Scott MacDougall-Shackleton

Adverse early developmental conditions negatively affect song learning and song quality in songbirds. Most research on developmental stress and birdsong focuses on males. Females are understudied in part because they do not produce song in a manner like males. However, song has evolved through signaler-receiver networks and the effect stress has on the ability to receive auditory signals is equally important, especially for females who use song as an indicator of mate quality. We subjected juvenile European starlings (*Sturnus vulgaris*) to either an *ad libitum* or unpredictable food-supply from 35-115 days of age. In an operant conditioning task, starlings' abilities to perceive differences in absolute frequency and relative frequency were assessed. We found that females reared in control conditions acquired both discriminations faster than females raised in our unpredictable conditions. There was no difference between treatment groups for males. Currently, birds are being assessed on a colour association task to determine if female deficits were general or specific to auditory discrimination. Our results indicate that developmental stressors have sex-specific effects on cognition, perception, and song development.

C33.3 A Daily Oscillation in the Fundamental Frequency of Song

William Wood, Cnrs

Roseberry Thomas, David Perkel

Complex motor skills are more difficult to perform at certain points in the day (for example, shortly after waking), but the daily trajectory of motor-skill error is more difficult to predict. By undertaking a quantitative analysis of the fundamental frequency (FF; ~"pitch") of thousands of zebra finch syllables per animal per day we find zebra finch song follows a previously undescribed stereotyped daily oscillation. The FF of harmonic syllables rises across the morning, reaching a peak near mid-day, and then falls again in the late afternoon until sleep. This oscillation, although somewhat variable, is consistent across days and across animals. This oscillation does not require serotonin, as animals with serotonergic lesions maintained daily oscillations in FF. We hypothesize that this oscillation is driven by underlying physiological factors, possibly including body temperature, which could be shared with other taxa. Song production in zebra finches is a model system for studying complex learned behavior because of the ease of gathering comprehensive behavioral data and the tractability of the underlying neural circuitry. The

daily oscillation that we describe promises to reveal new insights into how time of day may influence the ability to accomplish a variety of complex learned motor skills.

C33.4 How a songbird with a continuous singing style modulates its song when territorially challenged

Nicole Geberzahn, Cnrs

Thierry Aubin

Birdsong serves to attract females and to deter territorial rivals. Male songbirds vary aspects of their song when engaged in territorial interactions. Such variation may be indicative of certain traits of the signaler such as fighting strength, condition or aggressive motivation and may be used by receivers in decisions on whether to retreat or to escalate a fight. This has been studied intensively on species that sing discontinuously, in which songs are alternating with silent pauses. We studied contextual variation in the song of skylarks (*Alauda arvensis*) a songbird with a large vocal repertoire and a continuous and versatile singing style. We exposed subjects to playbacks of conspecific song and recorded their vocal responses. Males sang differently when singing spontaneously with no other conspecific around than when they were territorially challenged. In this last case, males increased the sound density of their song: they increased the proportion of sound within song. They seem to do so by singing different elements of their repertoire when singing reactively. Furthermore they increased the song consistency: they reproduced more faithfully the spectral properties of syllables when singing reactively. Our findings suggest that skylarks use sound density and consistency to indicate their competitive potential.

C33.5 Birds trained iteratively with their own developing song produce normal song as adults

Olga Feher, University Of Edinburgh

Kenta Suzuki, Kazuo Okanoya, Ofer Tchernichovski

We raised zebra finch brother pairs in two different experimental conditions: one in each pair grew up in complete acoustic and social isolation and the other, housed individually in a sound isolation box, was trained with its own song. The trained birds pecked on a key which resulted in the playback of one of the bird's own songs randomly selected from a library of 20 recent songs. The song library was updated every 20 minutes to expose the bird to his most recent songs. This is practically an iterated

learning experiment in a single individual, where that individual learns from his own behavioural output which gets regularly updated throughout development. We observed that songs of birds trained with their own songs, in contrast to their isolate brothers' songs, developed more or less normally and became wildtype-like without any external song model. Both song rhythm and phonetic song structure appeared wildtype-like in the songs of self-trained birds. We believe that the externalised self-feedback was sufficient to jumpstart imitation mechanisms that result in wildtype song even in the absence of an external song model.

C33.6 Environmental and genetic control of brain and song structure in the zebra finch

Stefan Leitner, Max Planck Institute For Ornithology
Katherine L. Buchanan, Andrew T. D. Bennett, Clive K. Catchpole, Roswitha Brighton, Joseph L. Woodgate

Birdsong is regarded as a classic example of a learned trait with cultural inheritance. However, there is presumed to be some degree of inherited control on the mechanisms underlying song structure. We quantify the relative genetic and environmental contributions to song structure and brain development in the zebra finch, and examine the role of genotype-by-environment (G*E) interactions in neural development. We partially cross-fostered nestlings and raised them under control conditions or mild nutritional restriction and, in adulthood, measured the volumes of key brain nuclei in the song control system and quantified song structure. Neuroanatomy and song both showed low levels of heritability and are unlikely to be under selection as indicators of genetic quality. HVC was almost entirely under environmental control, suggesting that song has the potential to act as an honest signal of phenotypic quality. G*E interaction was important for brain development and may provide a mechanism by which additive genetic variation is maintained, which in turn may promote sexual selection through female choice. Our study demonstrates the fundamental importance of environmental conditions for vocal learning and neural development in songbirds and suggests that selection acts on the genes determining vocal learning, rather than directly on the underlying neuroanatomy.

C34: Avian cognition & neuroscience

C34.1 Three-Strikes and You're Out: A Multidimensional Refutation of the Bischof-Kohler Hypothesis

Lucy Cheke, University Of Cambridge
Nicola Clayton

The Bischof-Köhler hypothesis (Suddendorf & Corballis, 1997) states that episodic foresight, the ability to travel in the mind's eye to a future scenario, is necessary to be able to disengage from current feelings to cater for future needs and desires. Furthermore, the hypothesis states that this ability is unique to humans and that animals are "stuck in time" and can only act for the fulfilment of current needs. Here we shall present a three-pronged investigation into these predictions. First, the hypothesis claims that planning for future desires involves episodic foresight. This is investigated by assessing the extent to which performance on tests assessing this ability is related to performance on other episodic cognition tasks in adults. It is also assessed whether this ability develops at the same time as other episodic cognition in children. Finally, the claim that this ability is unique to humans is assessed using evidence from food caching corvids. It is concluded that the claims of the Bischof-Köhler hypothesis cannot be supported by the empirical evidence, and the utility of the hypothesis for the field is discussed.

C34.2 Possible relation between migratory behavior and new neuronal recruitment in the adult avian brain

Anat Barnea, The Open University Of Israel
Yoram Yom-Tov, Shay Barkan

Correlations between learning and neurogenesis in the adult brain suggest that brain plasticity is an adaptation to environmental changes. We compared new neuronal recruitment in related bird species: migrant (*Acrocephalus scirpaceus*) and resident (*A. Stentoreus*), in three seasons. We hypothesized that resident birds are exposed to fewer environmental stimuli than migrants that experience significant spatial changes twice a year, and hence predicted a higher new neuronal recruitment in brains of migrating birds. Wild birds were caught, treated with a cell birth-date marker and kept in captivity for five weeks. Then, labeled neurons were counted in three brain regions which are known to process spatial information. More new neurons were found in migrant than in resident birds, in all brain regions and seasons. We suggest that the more new neurons in migrants enable enhanced navigational

abilities. Additionally, a seasonal pattern was found in both species, with less new neurons in spring than in summer and autumn. The seasonal trend could be explained by the fact that during the breeding season (spring) the birds stay close to their nests, while after breeding they expand their home range and recruit more new neurons in order to memorize new areas.

C34.3 Necessity or capacity? Physiological state predicts problem solving performance in house sparrows

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Ádám Z. Lendvai, Csongor I. Vágási, Laura Patras,
Peter L. Pap, Erna Vincze, Sándor Papp, Bálint
Preisznér, Gábor Seress, András Líker

Innovative behaviors such as exploiting novel food sources can grant significant fitness benefits for animals, yet little is known about the mechanisms driving such phenomena, and the role of physiology is virtually unexplored in wild species. To test the effects of physiological condition on problem solving success, we studied the behavior of wild-caught house sparrows in four novel tasks of food acquisition, one of which was presented to the birds in repeated trials; and we investigated the relationships of individual performance with relevant physiological traits. We found that performance was individually consistent across the four tasks. Birds with lower integrated levels of corticosterone, the main avian stress hormone, solved the most difficult task faster and were more efficient learners in the repeated task than birds with higher corticosterone levels. Birds with higher concentration of total glutathione, a key antioxidant, solved two relatively easy tasks faster, whereas birds with more coccidian parasites tended to solve the difficult task more quickly. Our results indicate that various aspects of physiological state influence problem-solving performance in a context-dependent manner, and that the capacity for problem solving, such as cognitive skillfulness, is more likely to drive individual innovation success than necessity due to poor condition.

C34.4 Variation in innovation performance in birds: A measure of cognitive flexibility?

Andrea Griffin, University Of Newcastle
Francoise Lermite, Madeleine Patience, Marjorie Perea, David Guez

Innovation is increasingly recognised as a key source of phenotypical plasticity, evolutionary change and

adaptation to environmental change. In both primates and birds, cross-taxon variation in innovation rate, a field-based count of novel foraging behaviours, is positively correlated with cross-taxon variation in relative brain size, a finding that underlies the idea that innovation rate is a measure of cognition. Using the highly invasive Indian myna, *Acridotheres tristis*, we attempted to validate innovation as a measure of cognitive flexibility *within* species. To do so, we explored the relationship between inter-individual variation in innovative ability and inter-individual variation in performance on an alternative measure of cognitive flexibility, namely a serial discrimination cue reversal learning task. We hypothesised that if innovative ability is a measure of cognitive flexibility within species, then faster innovators should be faster reversers. Contrary to expectations, results revealed that although faster innovators learned an initial discrimination faster, they were significantly slower to reverse on each of four successive cue-reversals, suggesting that innovators may be faster learners, but may also be more fixed in their behavioural patterns. These findings shed doubt on whether innovative ability can be used as a measure of cognition at the within-species level. Broader implications for our understanding of intra- and inter-species variation in innovation will be discussed.

C34.5 Scared but not stiff: Neophobia drives feeding innovation in urban magpies

Toni Vernelli, University Of Exeter
Charlotte Piggot, Stephen Lea, Natalie Hempel de Ibarra

The cleaning behaviour has been used as a classic example of mutualism, with benefits to cleaners and clients. Although much has been studied on the behavioural aspects of these mutualistic interactions, little is known about physiological processes that underlie these interactions. The neurotransmitter serotonin or 5-hydroxytryptamine (5-HT) is involved in the regulation of vertebrate social behaviour while its activity is usually related with social status and aggressive behaviour. Here we tested if the serotonergic system is responsible for the modulation of cooperative behaviour, in the best studied cleaning mutualism, between the Indo-Pacific bluestreak cleaner wrasse *Labroides dimidiatus* and their visiting clientele. We've found that exogenous administration of 5-HT agonist 8-Hydroxy-2-(dipropylamino)tetralin (8-OH-DPAT) and selective serotonin reuptake inhibitor (SSRI) fluoxetine caused a substantial increase of cleaners' motivation to inspect clients without affecting their

intraspecific interactions, which suggests a particular effect of 5-HT on interspecific behaviour but not of an overall effect on social behaviour. Additionally we've discovered that 5-HT antagonists WAY-100635 and p-chlorophenylalanine lead to a substantial decrease of cleaning inspections. To our knowledge, our study is the first to link the effects of neurotransmitter action (serotonin) to cooperative behaviour, beyond the usual focus of its influence on conspecific social behaviour.

C34.6 Nest building materials: birds pick the right stuff

Ida Bailey, University Of St Andrews
Kate Morgan, Marion Bertin, Sue Healy

Although there is considerable evidence that birds select where to build their nests through experience it is assumed that birds' choice of nesting materials is predominantly innate. Here we tested that assumption by asking zebra finches whether building, reproductive success, nestling or post-dispersal experiences with materials with different physical attributes affected males' subsequent choice of nesting material. The birds learned to avoid poorer materials and preferred better building materials in proportion to the amount of building experience they had of those materials. Breeding success and parentage were not important. Zebra finches are, then, capable of learning to choose nest material based on its physical suitability for a task, much as other species learn to select objects with which to make tools. This makes nest building an excellent model for understanding the evolution of the cognitive abilities, especially those associated with the choice and use of materials, for whatever purpose, based on their physical properties.

C35: Inter-specific communication

C35.1 The ecology and evolution of eyespots in lepidopteran caterpillars

Thomas Hossie, Ottawa-Carleton Institute Of Biology
Thomas Sherratt

Many lepidopteran caterpillars appear to be protected from predation by insect-eating birds because they possess "eyespot" - a pair of conspicuous markings on the body generally thought to resemble the eyes of a predator. This explanation dates back at least to Henry Walter Bates over 150 years ago, and remains a widely cited explanation for these markings today. Yet, the phenomenon has received little attention from evolutionary biologists and our current

understanding of eyespot function comes largely from indirect evidence and anecdote. Using artificial caterpillars we provide empirical support for a protective effect of eyespots against insect-eating birds, as well as examine how additional traits such as body colour and defensive posture affect their protective value. This research has revealed interactive effects between eyespots and body colour, and additive (but not synergistic) effects of eyespots and apparent "head" shape. To complement this we have conducted phylogenetically controlled analyses of eyespot evolution in the Sphingidae to test hypotheses that explain why eyespots have arisen in some lineages but not others. Collectively, this work provides some of the first empirical support for the protective value of eyespots in caterpillars and helps us understand the conditions under which it is likely to evolve.

C35.2 Facultative Expression of Crypsis Induced by Non-Predatory Heterospecifics

Kit Magellan, Universitat De Girona

Behavioural traits may form effective camouflage strategies either alone or through enhancing morphological crypsis. Movement between microhabitats can facilitate choice of appropriate background to maximise crypsis. However, movement may increase the risk of detection by predators so an alternative behavioural strategy is to reduce movement. An additional factor that has received little attention is the presence of non-predatory heterospecifics who may induce facultative expression of behavioural crypsis through indirect effects on predator-prey relationships. Using a recently discovered, highly cryptic fish I found that this prey species preferred to remain motionless when in plain sight and this behaviour increased in the presence of predators thus enhancing their morphological crypsis. However, *G. 'nebula'* differentiated between predatory and non-predatory heterospecifics, the latter inducing increased movement even when predators were present. The presence of non-predatory heterospecifics thus to some extent ameliorates the effects of predators. This facultative expression of crypsis may be facilitated by provision of information regarding predators, promotion of movement through disturbance or a capacity for heterospecifics to be used as camouflage to enable essential movement. This study highlights the need to consider prey, predator and other heterospecific species together as part of an ecological network to enhance the effectiveness of conservation.

C35.3 Role of structural blue and pigmentary orange coloration in aposematic signalling of the highly variable Australian bug *Tectocoris diophthalmus*

Pavel Stys, Charles University In Prague
Alice Exnerova, Dana Jezova, Scott Fabricant

While red or yellow and black are seen as 'typical' aposematic colours, iridescent blue-green, which is not uncommon in insects, may provide another type of warning signal for predators. We tested this hypothesis using Australian Harlequin Bugs (*Tectocoris diophthalmus*), which displays pigmentary orange and/or iridescent structural coloration. We tested the bugs against wild-caught and hand-reared European Great Tits (*Parus major*). Using dried bugs with mealworms hidden inside, we first tested innate preference between highly-iridescent and non-iridescent (orange) bugs. We then trained birds to discriminate between unpalatable (high-iridescent or non-iridescent; quinine-soaked mealworms) and palatable bugs (black-painted; water-soaked mealworms). In a generalisation test, we tested birds against all three, plus novel phenotypes (orange with black markings, iridescent with black markings). Birds showed an initial bias against high-iridescent bugs, stronger for wild-caught birds. Both colour phenotypes were equally efficient cues in inducing avoidance. In generalisation tests, wild-caught birds showed highest aversion against high-iridescent and novel orange-black bugs, and treated iridescent-black similarly to black. Hand-reared birds avoided high-iridescent bugs most, but they also discriminated between iridescent-black and black. Birds experienced with local red-and-black aposematic bugs may generalise to iridescent-and-orange bugs, while naive birds may associate unpalatability with iridescence. Funded by CSF-grant P505/11/1459.

C35.4 The origins of disguise: masquerade evolved from superficial resemblance to cryptic ancestors

Hannah Rowland, University Of Cambridge
John Skelhorn, Graeme Ruxton

Masquerading organisms visually resemble inanimate objects such as stones, sticks or bird-droppings. These species gain protection from predation because following detection by a predator they are not identified as prey, and predators find it more difficult to detect masquerading prey, and are less motivated to search for them if the local density of unrewarding models is high. Despite the support

for the function and evolutionary dynamics of masquerade, the conditions under which it initially evolved are untested. Here we show that masquerading species evolved from cryptic ancestors. We manipulated wild predators' (blue tit, *Cyanistes caeruleus*) experience of a putative model and examined their subsequent foraging behaviour on artificial prey that were either cryptic, imperfect masqueraders that shared pattern elements with cryptic prey but had a superficial resemblance to the model, or perfect masqueraders. Both perfect and imperfect masqueraders benefited from misclassification when predators had experience of the model, but imperfect masqueraders suffered increased predation when predators had no experience of the model. Mutations that lead to superficial resemblance resulted in reduced crypsis, but misidentification of prey by predators outweighed this cost, but only when predators had prior experience of the model.

C35.5 Masquerade versus crypsis: adaptive change in defensive strategy during the ontogeny of butterfly larvae.

Reika Sakurai, Rikkyo University
Eri Yoshikawa, Toshitaka Suzuki

Animals have evolved a variety of defensive colour patterns that reduce the risk of predation. For example, body colour of some animals matches their background (crypsis), while other animals resemble inedible objects (masquerade). The larvae of *Papilio* butterflies show an interesting pattern of morphological change during their development: the earlier instars masquerade as bird droppings, while the later instars match their colouration with the leaf colour of their host plants. We conducted a field experiment to test whether this change in the defensive strategy is adaptive. Four types of pastry caterpillar differing in both their colour (dropping and leaf) and size (small and large) were produced and placed on the leaves of the host plants, and their survival rate was examined. At smaller size, the masquerading prey as bird droppings suffered lower probabilities of being attacked by birds than cryptic prey, while the cryptic prey had lower predation at larger size. Our results suggest that masquerading prey has a greater survival value than cryptic prey only when their body size is similar to their model objects (e.g. bird droppings). This study provides the first experimental demonstration that the ontogenetic change in the defensive coloration in butterfly caterpillars is adaptive.

C35.6 How patterns enhance the confusion effect

Innes Cuthill, University Of Bristol

Scott Watkins, Roland Baddeley, Nick Scott-Samuel

Despite the recent surge in research on camouflage, there has been little on camouflage for moving animals, or for animals that live in groups. In these situations, whilst movement breaks even the most cryptic pattern, coloration can serve a purpose beyond concealment: any pattern that disturbs either visual pursuit or recognition should be favoured. One plausible mechanism for such interference is the “confusion effect”, whereby the grouping of similar-looking animals impedes the visual isolation and tracking of prey. Here we empirically investigate how the confusion effect interacts with pattern type, using animations of computer generated zebra fish (*Danio rerio*) shoals, and presenting them to human ‘predators’ searching for a smaller target fish within the shoal. Across four experiments, our results indicate that higher contrast, striped patterns are more effective than lower contrast stripes, or no pattern, and that stripe orientation may interfere with different mechanisms – vertical stripes impeding target tracking and horizontal stripes boosting mutual crypsis – both of which would act to lower predation.

C36: Hormones & behaviour

C36.1 Solving a paradox: context-dependent effects of maternal testosterone in the Rock Pigeon (*Columba livia*)

Bin-Yan Hsu, Behavioural Biology, University Of Groningen

Martina Mueller, Cor Dijkstra, Christoph Gahr, Ton Groothuis

In many animal species mothers differentially bestow their eggs with hormones. The increasing pattern of yolk testosterone (T) concentrations over the avian laying sequence is interpreted as mitigating effects of hatching asynchrony by boosting the later hatching chicks. However, why would avian mother first produce hatching asynchrony, classically regarded as an adaptation, and then compensate its effect by maternal T? We hypothesized that maternal T is only beneficial for the chick under good food conditions, when mothers aim to raise the full brood, but detrimental under poor food conditions when brood culling is needed. We studied this in the rock pigeon, in which first eggs contain much lower T concentrations than last and second eggs. We created clutches of two first eggs, one injected with T to the level of the

second egg (T chicks), and one injected with vehicle (C chicks). Pairs were then housed under either good or poor food conditions. Only in the good condition T chicks grew faster than C chicks. Only in the poor condition, T chicks had a much higher early mortality than C chicks. These results solve the above paradox, and may explain contradictory results of *in ovo* T injections in the literature.

C36.2 Interaction effects of dietary unsaturated fatty acids and cortisol concentrations on cognitive abilities in domestic guinea pigs (*Cavia aperea f. porcellus*)

Matthias Nemeth, University Of Vienna, Department Of Behavioural Biology

Eva Millesi, Karl-Heinz Wagner, Bernard Wallner

The dietary intake of unsaturated fatty acids (UFAs) can improve learning abilities and memory retention, while prolonged physiological stress and elevated levels of glucocorticoids negatively affect cognitive functions. However, UFAs modulate the hypothalamic-pituitary-adrenal (HPA) axis, resulting in reduced glucocorticoid concentrations. In this study, interaction effects of dietary UFAs (n-3, n-6, and n-9 fatty acids) and physiological stress response on cognitive abilities were investigated in guinea pigs. Influences on spatial learning and memory were determined in a radial maze. The test paradigm consisted of a three-day learning phase and a test for memory retention, performed after social confrontations of UFA-supplemented and control animals. Daily saliva cortisol concentrations were analysed using enzyme immunoassays. The radial maze task revealed positive effects of dietary UFAs on learning abilities, but no cortisol-related effects were detected. Cortisol concentrations throughout subsequent social confrontations were in general elevated compared to the learning phase, but remained lower in UFA-supplemented animals compared to control animals. However, this long-term stress negatively affected memory abilities during the retention test in control animals, while no such effects were detected in UFA-supplemented animals. These findings suggest a diminishing effect of dietary UFAs on physiological stress reactions and the related negative consequences for memory retention.

C36.3 Hormonal control of nocturnal migration

Leonida Fusani, University Of Ferrara

Francesca Coccon, Alfonso Rojas, Wolfgang Goymann

Migration is a complex behaviour that involves a number of physiological adaptations. Most Passerine birds migrate at night despite their diurnal pattern of activity outside the migration periods. The switch from a diurnal to a nocturnal pattern of activity occurs several times during a migratory season, when birds interrupt temporarily their journey to rest and refuel at stopover sites. Early studies from our groups suggested that melatonin, the “hormone of darkness”, regulates this behavioural transitions. In particular, melatonin levels at night were reduced in birds showing migratory restlessness, indicating that a decrease of circulating melatonin could facilitate the diurnal-to-nocturnal switch. When this hypothesis was tested during spring migration by treating wild birds with melatonin to induce a stopover, we found no effects of the treatment on migratory behaviour. However, when we repeated the experiment during autumnal migration, we found strong, significant effects. Here we will present the results of this recent work and discuss why the migratory programme is more sensitive to melatonin in autumn compared to spring migration.

C36.4 Hormonal effects on the vocal communication and anti-predator behaviour of cooperative breeding meerkats (*Suricata suricatta*)

Ines Braga Goncalves, University Of Zurich
Marta Manser

Animal vocalisations are characterised by individual differences in production rate and acoustic structure. This variation can partly be explained by the social and environmental contexts that individuals experience and by their internal state. Thus, they can provide information concerning the producer’s age, size, rank, sex and endocrine status. Individual differences in androgens and glucocorticoids have been repeatedly associated with competitive ability, social rank, vigilance behaviour and reproductive success, and with variation in calling behaviour. Meerkats are cooperative breeding mammals that have a highly developed vocal communication system, which they use to coordinate their spatial organisation, social interactions and anti-predator behaviour. Thus, meerkats are an ideal study system in which to explore links between behaviour, vocalisations and hormones in animal societies. Experimental elevation of glucocorticoids significantly increased close calling rate in males but not in females. This may potentially reflect a greater role of subordinate males in the maintenance of group cohesion, where close calls seem to play a major role, in periods of

greater predation risk. Overall, our results show how androgens and glucocorticoids can affect vocal communication and behaviour in meerkats with potentially significant consequences to group cohesion and coordination of anti-predator behaviour.

C36.5 Both maternal and endogenously-produced testosterone increases siblicidal aggression in black-legged kittiwake chicks (*Rissa tridactyla*)

Martina Muller, University Of Groningen
Yvonne Roelofs, Kjell Einar Erikstad, Borge Moe, Ton G. G. Groothuis

Animals routinely produce more young than they can afford to rear. Siblings therefore face a life and death struggle of competing with each other to obtain enough food to survive. In siblicidal birds, first-hatching chicks assume a dominant social position in the nest due to their size advantage and when threatened with starvation fatally attack subdominant later-hatching young. Avian mothers provision consecutively-laid eggs with differing concentrations of testosterone in patterns that have been suggested to enhance or counteract the abilities of early-hatching young to kill their younger siblings. But until now, the effect of maternal testosterone on siblicidal aggression has never been tested. In an experiment with siblicidal black-legged kittiwakes (*Rissa tridactyla*), we found that exposure to elevated testosterone in eggs increased sibling aggression. On the other hand, sibling aggression might also be facilitated by endogenously-produced testosterone, as has been frequently suggested but not yet tested. We experimentally elevated testosterone in the circulation of kittiwake chicks and showed for the first time that testosterone-treated chicks were more aggressive toward their sibling than were control chicks. Our findings show that testosterone influences sibling aggression both via long-term organizing actions during prenatal development, and also via short-term activation during the postnatal period.

C36.6 Examining a pathway for hormone-mediated maternal effects: Yolk testosterone affects behaviour, androgen receptor expression and testosterone production in the domestic chick

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Kristina A. Pfannkuche, Bernd J. Riedstra, Christophe Gahr, Ilse Weites, Christiaan Wolf, Manfred Gahr

Maternal testosterone in avian eggs can induce both short- and long-term changes in physiology and

behaviour of the offspring, including androgen-sensitive traits. However, how the effects of maternal hormones are mediated remains unknown. We studied the possibilities that maternal androgens affect behaviour by affecting endogenous androgen production and /or androgen receptor (AR) densities in the brain influencing the sensitivity to androgens. Testosterone within the physiological range or vehicle only was injected into the egg yolk of unincubated chicken eggs and behaviour, comb size, AR mRNA expression in different brain nuclei as well as plasma testosterone levels were measured in two week old chicks that had hatched from these eggs. Testosterone treatment feminized chick behaviour and tended to reduce adult comb size and down regulated chick AR mRNA expression as well as plasma testosterone levels. The same effect on AR expression was also found in embryos just before hatching, although plasma T levels during embryonic development were not affected by the treatment. We are currently studying the possibility that the suppression of AR expression is caused by DNA silencing.

C37: Primate social behaviour

C37.1 Competition over personal resources favors cooperation in human groups

Jessica Barker, University Of Arizona
Pat Barclay, Kern Reeve

Members of social groups across taxa face a trade-off between selfishly producing personal resources and cooperatively producing shared group resources. While many group resources (such as cooperatively hunted big game) are shared equitably, many personal resources (such as food hunted individually) are monopolizable. In such cases, an individual may benefit by investing effort in taking others' personal resources, and in defending one's own resources against others. We use a game theoretic model to predict that when such competition over personal resources is possible, individuals will invest more in cooperative production of a shared group resource, and will also obtain higher payoffs from doing so. We test and find support for these predictions in two laboratory economic games with humans, comparing people's investment decisions in games with and without the options to compete over personal resources or invest in a group resource. Our results help explain why people cooperatively contribute to group resources, suggest how a tragedy of the commons may be avoided, and highlight unifying features in

the evolution of cooperation and competition in human and non-human societies.

C37.2 Transitivity in male social bonds - friends of friends are friends in dispersing male macaques

Oliver Schalk, University Of Gottingen
Julia Ostner

Establishing social cliques is a heritable feature of human social behavior suggested to carry adaptive benefits. Increased cliquishness has been shown theoretically to facilitate the evolution of cooperation in social networks which may generate these benefits. Although the strength of an individual's social bonds has been shown to increase fitness in birds and mammals including primates few studies investigated the effects of strong social ties beyond the dyadic level. For comparison with human friendships it is especially promising to investigate transitivity of social bonds in the dispersing sex where close genetic relatedness is rare. Here present analyses on almost 6000 hours of focal animal data of wild Assamese macaques (*Macaca assamensis*) where post-dispersal males form strong social bonds with other males that increase their reproductive success. We classified dyadic frequencies and duration of grooming and close spatial association above the average across all dyads as strong bonds. In each of six years of observation with changing group composition and changing social bonds we found that the vast majority of strong social bonds were transitive. We excluded the possibility this resulted from proximity effects. Our results suggest that the formation of social cliques within larger networks evolved early in our evolutionary history.

C37.3 Dominance, but not kinship, influences social interactions in females of a tolerant macaque species, *Macaca nigra*.

Julie Duboscq, German Primate Center
Dyah Perwitasari-Farajallah, Bernard Thierry, Antje Engelhardt

Dominance and kinship are important factors of macaque social organization. Females form linear matrilineal hierarchies, preferentially interacting amongst kin. Hierarchical and nepotistic constraints differ between macaque species and follow a gradient from despotism to tolerance: female social interactions are expected to be less constrained by dominance and kinship in tolerant species than in more despotic species. However, this question has scarcely been investigated in tolerant species. We

investigated the influence of dominance and kinship on female social interactions in wild tolerant crested macaques, *Macaca nigra*. We examined relationships between dominance, kinship and a variety of social interactions. Regardless of their degree of genetic relatedness, females close in rank exchanged more grooming, approached each other more often, and had more symmetrical positive interactions. Closely related females only had more consistent exchange of grooming across time, regardless of rank difference. Thus, crested macaques followed the predictions for tolerant macaques in that kinship had little effect on social interactions, but contrasted theory in that dominance rank biased social interactions. Further investigations will be necessary, for example on female-female competition and reciprocal altruism, to understand better variations in social interactions in macaque societies.

C37.4 Social structure of a semi-free ranging group of mandrills (*Mandrillus sphinx*): which role for central individuals?

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Cedric Sueur, Delphine Verrier, Jean-Louis Deneubourg, Odile Petit

Most studies initially considered mandrill groups to be an aggregation of one-male-multifemale units, with males occupying central positions in a structure similar to those observed in baboon species. However, a recent study hypothesized that mandrills form stable groups with few permanent males, and suggested that females occupy more central positions than males within these groups. In this study, we used social network analysis to investigate the identity and the role of central individuals in a semi-free ranging group of mandrills. The betweenness and the eigenvector centrality for each individual were correlated to kinship, age and dominance. Our results showed that the cumulative distribution of betweenness followed a power function. This property showed that some group members, mostly females, occupied a high central position. Moreover, we found that these central females were also high-ranking individuals. Finally, a resilience analysis showed that the simulated removal of individuals displaying the highest betweenness values splits the network into small subgroups and increases the average number of isolated subgroups. Critically, this study confirms that females appear to occupy more central positions than males in mandrill groups. These

females also seem to be crucial for group cohesion and probably play a pivotal role in this species.

C37.5 Orangutans are not motivated to benefit others in a choice paradigm.

Yena Kim, Primate Research Institute, Kyoto University
Jae Chun Choe, Hyuntak Park, Masaki Tomonaga

Humans are unique in the way of voluntary helping to each other even though it sometimes demands substantial costs. However, there has also been growing evidence for prosociality among non-human primates, especially chimpanzees and capuchins, living in complex societies. Prosociality has often been described as a major factor which facilitates group living. However, there has never been explored whether the solitary primates, such as orangutans, share those propensities. Here, we tested 4 orangutans, 2 males and 2 females, using an apparatus which allowed them to make either a prosocial (both an actor and a recipient get rewards) or a selfish choice (only an actor gets a reward). Two orangutans (one male and one female) played an actor's role, and all individuals participated as a recipient. When the subjects were tested without a recipient to confirm if they understood the task, they chose a double rewarding option significantly more than expected by chance (87.3%) to get the rewards from the both sides. However, when they were paired, they did not show any significant prosocial bias toward the recipients (51.3%). Our results suggest that the orangutans may not be as sensitive to others' welfare as other primates living in complex social environments.

C37.6 Nobody watching? Responses of chimpanzees to cues of conspecific observation

Daniel Nettle, Newcastle University
Katherine Cronin, Melissa Bateson

Recent evidence has shown that humans are remarkably sensitive to artificial cues of conspecific observation when making decisions with potential social consequences. Whether similar effects are found in other great apes has not yet been investigated. We report data from two experiments in which individual chimpanzees took items of food from an array either in the presence of an image of a large conspecific face, or a scrambled control image. In Experiment 1 we used three versions of the face image varying in size and the amount of the face displayed. In Experiment 2 we used a fourth variant of the image with more prominent coloured

eyes displayed closer to the focal chimpanzee. The chimpanzees did not look at the face images significantly more than at the control images in either experiment. Although there were trends for some individuals in each experiment to be slower to take high-value food items in the face conditions, these were not consistent or robust. We suggest that the extreme human sensitivity to cues of potential conspecific observation may not be shared with chimpanzees.

P1 Intra- and inter-generational discounting in the climate game

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Jennifer Jacquet, Christoph Hauert, Jochem Marotzke, Manfred Milinski

In social dilemmas self-interest is in conflict with group targets. Although defectors gain most when the target is reached, everybody suffers individually in case of failure. Avoiding dangerous climate change is an even more challenging dilemma by its additional intergenerational nature: immediate benefits may be preferred and future returns especially when benefiting future generations thus 'discounted'. We investigated both intra- and intergenerational discounting in a collective-risk experiment related to the climate change game. Each of six students of 32 groups received an operating fund and a fixed monetary endowment. In course of 10 rounds players could invest to collect a threshold amount or when missing the threshold, to risk losing their endowment with a high probability. The rewards of defection (what is left in operating fund) were immediate, while the rewards of cooperation (the endowment) were 1) delayed by one day, 2) delayed by seven weeks, or 3) delayed by several decades. The third indicates a diluted intergenerational benefit implemented by planting oak trees if the group reached the target. The further away in time the benefits of cooperation would occur, the fewer groups collected the target sum. Discounting of future returns depicts a severe problem for climate change abatement.

P2 Effects of wind turbine noise on song and response behaviour in chaffinches (*Fringilla coelebs*)

Mieke C. Zwart, Newcastle University

Jonathon C. Dunn, Philip J.K. McGowan, Mark J. Whittingham

The number and distribution of wind farms has increased considerably over the last 20-30 years. Their impact on wildlife is not fully understood, but it is clear that some species avoid wind turbines, potentially due to wind turbine noise. While urban noise has been linked to vocal adjustments and variation in reproductive success and population distribution in birds, the effect of wind turbine noise has not yet been studied. We investigated whether the territorial response of male chaffinches to a singing rival male is affected by wind turbine noise. Three different soundtracks (chaffinch song, wind turbine noise and chaffinch song with wind turbine noise) were played to a population of chaffinches in

a coniferous wood. In the absence of wind turbine noise, chaffinches responded more aggressively to the intruder than with wind turbine noise. Our results suggest that reproductive success might be affected by wind farms due to disruption of auditory signals.

P3 Behavioural syndromes and extinction risk in forest rodents from Bahia, Brazil

Juliana Malange, USP

Patricia Izar, Pedro Rocha, Hilton Japyassu

Ecological studies revealed that species are not randomly distributed in altered landscapes. Instead, these distribution patterns are associated to the level of specialization to habitat resources. Behavioral syndromes engender ecological trade-offs and thus have important consequences to adaptability. We analyzed how personality and the plasticity level associated to this trait are coupled and correlated to differential vulnerability to disturbance. We studied four forest rodent species, vulnerable (V: *Akodon cursor*, *Necromys lasiurus*) and not vulnerable (NV: *Euryoryzomys russatus*, *Hylaeamys laticeps*). The behavioral syndrome was estimated on the basis of tree behavioral tests in laboratory: open field, aversive open field and hole board field test. Synthetic variables representing one distinct personality domain for each test (activity, exploration and neophilia) were obtained through a Principal Component Analysis. These domains was significantly correlated, suggesting a behavioural syndrome. NV species are more active, neophilic and explore more the arena than V species. This result suggests that current, anthropic selective pressures, are favoring bolder individuals and indicates that differential vulnerability to extinction is associated to general activity patterns. Moreover, behavioral stability indexes (following Assendorf 1999) also indicates that resilience is provided by traits variability occurring either at the populational (syndrome) or at the individual (plasticity) level.

P4 Is there inbreeding within an isolated semi-captive population of Japanese macaques (*Macaca fuscata*)?

Claudia Radler, University Of Graz

Cornelia Franz-Schaidler, Elfriede Kalcher-Sommersguter, Kristina Sefc

Japanese macaques (*Macaca fuscata*) are seasonal breeders and live in groups containing several female matriline and unrelated males which are the dispersing sex. We investigated the distribution

of paternity in a large semi-captive group of Japanese macaques ($N=140$ individuals) which originates from a founder population of 40 individuals imported to the Affenberg Landskron, Austria, in 1996. No transfer of individuals occurred since then. This leads to the assumption that there is a high risk of inbreeding, followed by the question if there are any countermeasures to lower possible disadvantageous effects of this risk. Paternity could be resolved in 44 individuals out of a total of 92 descendants and showed that reproduction among closely related individuals was as frequent as expected by chance (permutation test, n.s.). However, analysis of behavioural data collected during the breeding season showed that particularly females avoid sexually motivated contact with closely related males ($\rho = -0.692$, $p = 0.004$, $n = 15$) but not vice versa ($\rho = -0.202$, n.s. $n = 18$). This may represent a behavioural mechanism to avoid inbreeding among closely related mating partners on the part of the females which appears to be not perfectly efficient, however.

P5 The effect a seal exclusion device has on catches in a pontoon trap for salmonids

Linda Calamnius, Harmångers Maskin & Marin
Mikael Lundin

A current conflict in the Bothnian sea is between fisheries and seals. The increasing population of grey seals (*Halichoerus grypus*), has led to an increase of raided fish and damaged gear. To reduce damages a seal exclusion device (SED), was mounted in the entrance to a pontoon trap. Two hypotheses were tested; (1) that the SED would not only keep raiding seals out of the trap, but that it would simultaneously deter larger fish from entering the trap, (2) that it would extinguish the behaviour of raiding seals. The findings of this study showed that there were no significant differences in size of caught salmon (*Salmo salar*) between the experimental trap and the control. Interesting to note is that the largest salmon caught, was caught in the experimental trap. However, it did show differences in size of caught trout (*Salmo trutta*), with significantly larger fish in the control trap, indicating differences in behaviour between the two species. The number of seal visits in both traps was very low, with a frequency of 0,01 visits per filmed hour in the experimental trap and 0,02 in the control. This suggests that the predation most likely occurs in other parts of the trap.

P6 Are native raccoon dogs (*Nyctereutes procyonoides*) affected by invasive raccoons (*Procyon lotor*)?

Yayoi Kaneko, Tokyo University Of Agriculture And Technology

Eiji Kanda

Raccoons quickly increased in wild at Japan, after a cartoon film was in boom in 1970's and introduced to pet industry resulting irresponsible abandonment. To observe interspecies relationship between the raccoon and similar body sized raccoon dogs, we examined 1) home range size and spacing pattern, 2) habitat selection, 3) activity time, in a suburb of Tokyo, by radio-tracking in three data sets: 1) before raccoon invasion (BRI period, 1990~1991, raccoon dogs, two males and two females), 2) after raccoon invasion (ARI period, 2008~2010, raccoon dogs, two males and two females; raccoons, four males and two females). Home range size of raccoon dogs in BRI period was 49.6ha in average ($n=4$, MCP) but it shrank to 21.1ha ($n=4$) in ARI period. The raccoon home range size was 415.3ha in male ($n=4$) and three times larger than females (151.0ha). The two breeding female raccoons occupied and exclusively used forest-agriculture boundary habitat where raccoon dogs preferred in BRI period. A raccoon dog pair spaced and bred in a neighboring isolated green area, but in the end was eliminated by local people due to maize damage problem. This indicates apparent competition occurred between the two species.

P7 Deer, biodiversity management and ecotourism in the Hebrides: conflict or mutual benefit?

Hagen O'Neill, University Of Durham

Sean Twiss, Philip Stephens, Alastair Ward

One challenge in managing red deer populations is maintaining a balance in resource production whilst minimising the negative impacts on land-use needs. A new management scheme is planned for an island estate in the Inner Hebrides, aiming to promote biodiversity on the island whilst moving significantly away from 'traditional' land use. The island features breeding habitat for rare Lepidoptera, and this new management scheme aims to promote these habitats through controlled grazing pressures, whilst avoiding the negative impacts of deer overabundance. However, it is anticipated that changing the landscape will correlate with an increase in tourist activity. Utilizing red deer as a primary grazing species, it is imperative to understand the impacts that increasing levels of tourism may have on the behaviour and grazing

intensity. Key behaviours will be mapped both spatially and temporally in response to tourism-disturbance. Furthermore, the efficacy of red deer over traditional sheep breeds in promoting breeding habitat will be explored through exclusion plots. The following research questions will be addressed: 1. Can red deer act as an appropriate grazing species to promote habitat beneficial for rare Lepidoptera? 2. How will varying levels of tourist activity influence red deer behaviour and habitat use throughout the island?

P8 Vicuña (*Vicugna v. mensalis*) herds modify their behaviour after being captured and sheared: implications on conservation and management

Omar Siguas, Uab

Edgar Quispe, Wilmer Arrana, Marcos Espinoza, José Contreras, Jorge Cassinello, Jordi Bartolomé

We present here evidence of a modification in foraging and guarding rates in vicuña herds subject to a traditional shearing management in Central Andes, Perú. The study was conducted from March to December 2011. We recorded behaviour of a vicuña population made up of ca. 300 individuals, living in semi-captive conditions and captured once a year for shearing. We registered foraging and guarding rates of adult males and females as well as calves, and distinguished three periods: before being captured, after being captured for marking and after being captured for shearing. Guarding behaviour is predominantly made by males, it is negatively related to group size, and varies according to the habitat and management period, decreasing significantly after shearing. Foraging behaviour rate is higher in females than in males and lambs, and significantly increases for all individuals after capture and shearing, it is positively related to group size. We hypothesize that after shearing vicuñas are prone to increase their daily foraging rate due to energy demands; this affecting their guarding rate and in turn their vulnerability to predators.

P9 *Bombus terrestris* as an entomovector for suppressing *Botrytis cinerea* in open field strawberry

Marika Mänd, Estonian University Of Life Sciences
Reet Karise

Strawberry *Fragaria x ananassa* is a fruit crop grown worldwide but diseases such as grey mold (*Botrytis cinerea*) frequently limit the yield. Most of *Botrytis* infection on fruits originates from the flowering

period. Use of foraging bees as disseminators of biocontrol agents to flowers is known as entomovector-technology. The aim of this study was to investigate to what extent bumblebees *Bombus terrestris* collect strawberry pollen and suppress *Botrytis* in open fields. Most of studies have been conducted under greenhouse conditions. To each bumblebee hive a special dispenser was attached containing the biofungicide Prestop-Mix (*Gliocladium catenulatum*). Two treatments were established: bee-delivered Prestop-Mix treatment and control. All berries were counted. Pollen from homing foragers were gathered and determined. Our study showed that the pollen gathered by bumblebees contained 25-40% of strawberry pollen and that 1/3 of the bees visited mostly strawberry during one foraging trip. There was negative correlation between proportion of strawberry pollen in the corbiculas and weight of pollen pellets. As strawberry flowers provide mostly pollen, it is likely that bees switch to plant species with more nectar. The rate of strawberry infection by *Botrytis* decreased from 18% on untreated control plots to 6% on bumble-bee-visited-plots.

P10 Do parasites affect behaviour? An experiment with greenfinches and coccidians

Tuul Sepp, University Of Tartu

Peeter Hõrak, Marju Männiste, Richard Meitern

Ecoimmunological studies often stress the necessity to measure associations between immune function and other important functions of an organism in natural infection models. Greenfinch coccidiosis seems to be an ideal model for answering ecoimmunological questions, since wild birds are chronically infected with these intestinal parasites and the infection intensities are easy to manipulate. We asked how suppression of natural chronic infection and experimental re-infection of wild-caught captive greenfinches affect different measures of behaviour. Additionally, we studied the correlations between behaviour and disease resistance/disease tolerance. Although we predicted that higher infection would cause a drop in overall activity, our study design allowed to distinguish between different components of activity (hopping, flapping). Additionally, we measured the latency to feed in the presence of a predator image. We also investigated how corticosterone content of feathers grown during the experiment might be associated with changes in behaviour and infection intensity.

P11 Behavioural changes in hosts and parasite in a newly established host parasite interaction on the Galapagos Islands

Arno Cimadom, University Of Vienna

Sabine Tebbich, Birgit Fessl, Rebecca Hood-Novotny

The parasitic fly *Philornis downsi*, is an obligate parasite of bird nestlings. In its larval stage it lives in birds' nests and sucks blood from the nestlings. This recently introduced parasite has a dramatic impact on the unique bird community of Galápagos.

Observational as well as experimental studies did show that especially the Darwin's finches suffer a high brood loss due to *Philornis* parasitism and this contributes to the dramatic decline of several species. Our data suggest that behavioural changes have evolved in both the host and the parasite in this recently established host parasite interaction. The parasite has changed its oviposition behaviour: while previously it probably laid its eggs only in nests where chicks had already hatched, its larvae are now found in incubating nests. At least one host species seems to react by abandoning the parasitized nests during the incubating stage and several host species have shown a new form of tool use. They take leaves of an endemic plant species with repellent properties and rub them into their feathers.

P12 Behavioural variations in different environmental contexts: adaptation or plasticity?

Claire Dufour, Institut Des Sciences De L'Evolution

De Montpellier, Université De Montpellier

Neville Pillay, Guila Ganem

Behavioural variation across environments can result from adaptive diversification, although uncoupling plasticity from genetic adaptation remains a challenge. We studied variation in social behaviour in the African striped mouse (genus *Rhabdomys*). The genus comprises 6 mitochondrial clades which radiated 4.3 mya ago across several biomes, characterised by distinct climate and vegetation. *Rhabdomys* taxa vary in their sociality, being group-living in arid areas and solitary in moist grasslands. To test the role of plasticity versus adaptation in social behaviour variation in the genus, we compared this trait in its two most genetically distant taxa, *R. bechuanae* and *R. dilectus*, which occur in different environments in allopatry and sympatry. We investigated whether macro and microhabitat selection (e.g. climate, vegetation type, cover) and geography (allopatry versus sympatry) predict variation in social behaviour (e.g. group size, recognition) in the two

taxa. Group-living behaviour was investigated by staging behavioural interactions and radio-tracking mice in different conditions. We determined home range overlap, nest sharing, group size and behavioural interactions between familiar and unfamiliar mice of the two taxa. Our results suggest that habitat is an important factor shaping behavioural variation in both taxa and raise questions about the mechanisms of their coexistence in sympatry.

P13 Behavioural plasticity in response to environmental manipulation among zebrafish populations

Anuradha Bhat, IISER Kolkata

Emilia P. Martins

Plastic responses can have adaptive significance to organisms occurring in unpredictable environments. Zebrafish (*Danio rerio*) occur in a wide range of habitats and environments that fluctuate frequently across seasons. We measured three behavioural traits (aggression, latency to feed, and shoaling distance) among 2 wild and 1 laboratory bred zebrafish populations in four environments differing in water flow and vegetation regimes. We found that the degree of plasticity varied with the behaviour tested (context) and among populations. In general, vegetation increased aggression and water flow decreased latency to feed after a disturbance, but the patterns were population dependent. For example, while wild zebrafish fed more readily in vegetated and/ flowing habitats, lab reared fish showed little variation in foraging across different environmental conditions. Zebrafish from all the three populations were more aggressive when tested in vegetated conditions. In contrast, while all the populations differed in shoaling distance, within populations, they showed little variation in shoaling distance across environmental conditions. These results suggest that behavioural flexibility is both population and context dependent and likely influenced by genetic+environmental mechanisms in zebrafish.

P14 Evolution of parasite ecology in the North African blackbird *Turdus merula mauritanicus*.

Djemadi Imed, Laboratory Ecology Of Terrestrial And Aquatic Systems

Belabed Adnene, Bouslama Zihad

A strong interspecific competition can be observed during situations of transient dynamics of interaction, and rarely between species in stable

phase of coexistence. The biological invasions are the second cause of biodiversity loss; the competition has received less attention mainly because of the importance that was given to invasive species themselves. Our study focuses on the competition between an invasive species "the Eurasian Collared Dove *Streptopelia decaocto*" and a native species "the North-African Blackbird *Turdus merula mauritanicus*" which are the most abundant species in our study sites; and which have similar nesting sites, mostly on common Cypress (*Cupressus sempervirens*).

Bonter (2010) predicted that the abundance of ecologically similar species would be inversely proportional to the abundance of the Eurasian Collared Dove. Data analysis of studies conducted between 2006 and 2011 has shown a trend of elevated nests from the ground for the Dove and the opposite trend for the Blackbird. Indeed, the average height of nests above ground decreased for the Blackbird of 7.8 \pm 3.62 m in 2006 to 3.62 \pm 0.95 m in 2011, while the Eurasian Collared Dove recorded the heights of the order of 5.727 \pm 1.378 m in 2010 and 6.487 \pm 2.372 m in 2011.

This readjustment of nests describes an adaptive strategy of both species mark their territory; one of them has chosen to nest at an important height (the Eurasian Collared Dove) and the other lowered the average height of their nests a half, between 2006 and 2011.

P15 Migrants in winter: song, territoriality, and individual success in trans-Saharan migratory birds

Marjorie Sorensen, University Of Cambridge

Trans-Saharan migratory birds spend over 60% of the annual cycle thousands of kilometers away from their European breeding grounds; however, little is known about their winter ecology. In particular, many Palearctic-breeding species sing vigorously in Africa, but the function of this behaviour is entirely unknown. Do migrants use song in territorial defence and does song reflect individual quality as on the breeding grounds? I investigated these questions in Great Reed Warblers (*Acrocephalus arundinaceus*) overwintering in Zambia, using physiological indices of body condition, and radio telemetry to determine space-use patterns. I asked whether the incidence of song was related to movement strategies and whether each of these was related to body condition. I found that individuals held overlapping home ranges rather than defended territories, which suggests winter singing does not serve in territorial defence, and that only 45% of males sang. Singing males were in better condition and left earlier for spring migration

than their non-singing counterparts. I will also report on results from comparisons of summer and winter song complexity and the role of testosterone in winter singing. A better understanding of the winter ecology of Palearctic-African migrants may have implications for the conservation of declining long distance migratory songbirds.

P16 Prenatal social conditions influence sex-specific growth and postnatal behaviour in domesticated guinea pigs

Nikolaus von Engelhardt, University Of Bielefeld
Gabriele Kowalski, Anja Günther

Prenatal social conditions affect litter size, sex ratios, growth and behaviour in many species. Crowding or social instability often result in reduced growth and more anxiety-like behaviour in offspring. Typically understood as a detrimental consequence of prenatal stress, a more recent interpretation is that such effects represent adaptations to the social environment. Should this be true, we would expect low and high social densities to exert opposite effects. We studied this by housing female guinea pigs individually or in groups during pregnancy. Litter size and birth mass were similar, but individual housing reduced growth of daughters and increased growth of sons. Also, offspring of individually housed females were slower to react and less active when subjected to stressful situations. A week later, they ran back to their mothers faster when separated and were less likely to approach an unfamiliar object. In one of two experimental batches, offspring sex-ratio was strongly male-biased. Reduction of female growth and increased anxiety indicate potentially detrimental effects of prenatal social stress. However, the effects on growth and sex-ratio were contrary to those found in earlier studies on prenatal stress and social instability in guinea pigs, which suggests a potentially adaptive adjustment of development.

P17 Lifespan the predisposing factor for the evolution of sociality in birds

Emeline Mourocq, University Of Zurich
Michael Griesser

Family formation usually occurs when mature offspring forgo independent reproduction and dispersal, and remain with their parents. The factors promoting delayed dispersal and onset of independent reproduction remain still largely unknown. The family formation theory suggests that a delay in the onset of reproduction is a "best-of-

bad-job” strategy in response to dispersal constraint due to a shortage of breeding openings. However, this approach fails as an ultimate explanation for family formation across species. Life-history theory predicts that longevity favours a late maturity and consequently predispose for the evolution of family cohesion, but this hypothesis remains untested. A comparative analysis on 33 species was conducted to test the link between the onset of independent reproduction and lifetime reproductive breeding success. We found that lifespan is a key factor determining the onset of independent reproduction, and therefore as well for family formation. While medium and long-lived species showed a fitness benefits in a lifetime perspective from a delay onset of reproduction, these species do not necessarily live in families. These results suggest that ecological factors might play a subsequent role for the evolution of family formation. Overall, our findings give insights to explain the distribution of family-living across species in birds.

P18 Seasonally distinct life histories and the occurrence of a Pace-of-Life Syndrome in a medium sized rodent

Anja Guenther, Bielefeld University
Fritz Trillmich

Ecological conditions affect life history strategies between and within species. The pace-of-life syndrome (POLS) hypothesis suggests that individuals experiencing different ecological conditions should differ in suites of physiological and behavioural traits that have coevolved with their individual life histories. Additionally, studies regarding animal personalities provide evidence that personality should covary with physiological and life history traits. Thus, personality might be integrated in the POLS.

We tested predictions of the POLS using a medium-sized rodent (*Cavia aperea*). Cavies allocate available resources to growth and reproduction when born in spring, but delay reproduction until the next year and are thereby forced to maximize survival probability when born in autumn. In response to these predictable life-cycle differences, different personalities should be advantageous: spring-born animals should be risk-prone to succeed with immediate reproduction, while autumn-borns should be risk-averse to survive. By dynamically changing photoperiod we tested whether and how behavioural and physiological traits adjust to seasonality. We investigated seven behavioural traits and several physiological traits. Additionally, we checked for the occurrence of cross context correlations. We found distinct differences fitting

the POLS in most of the behavioural traits and in a few physiological traits. Also, we found a behavioural- physiological syndrome in cavies.

P19 Do Paternal Grandmothers Invest in Accordance with Paternal Resemblance of Grandchildren?

Lisa Leaver, University Of Exeter
Joanne Smith

If evolution has shaped grandmothers to invest in their grandchildren discriminatively in relation to probability of relatedness, paternal grandmothers should attend to cues of paternal resemblance in grandchildren and invest accordingly, whereas maternal grandmothers should not. We tested whether the relationship between grandmothers and grandchildren was correlated with parental and grandparental resemblance cues of those grandchildren in two separate studies. Two separate groups of adult grandchildren completed questionnaires that explored the relationship between self-reported resemblance and various measures of relationship quality, which we equated with investment. In Study 1, we asked about maternal and paternal resemblance and investment from grandmothers. Grandchildren who reported higher paternal (but not maternal) resemblance reported significantly better relationships with their paternal grandmothers. There was no effect of resemblance to either parent on relationship quality with maternal grandmothers. In Study 2, we asked about resemblance to grandmothers in addition to resemblance to both parents. Investment was higher from maternal grandmothers than paternal grandmothers. Although resemblance does predict investment, it was grandparental resemblance, rather than parental resemblance, that predicted investment, and this did not differ between maternal and paternal grandmothers. We conclude that resemblance to self influences grandmother investment, regardless of probability of paternity.

P20 Socioeconomic position, extrinsic mortality and health behaviour: Testing a behavioural ecological model

Gillian Pepper, Centre For Behaviour And Evolution, Newcastle University
Daniel Nettle

Background:

Socioeconomic gradients in health behaviour are pervasive and well documented. However, there is still no consensus on their causes. We previously

presented a behavioural ecological model which showed that extrinsic mortality risk limits the extent to which investment in health extends life expectancy or enhances fitness. If people of low socioeconomic position (SEP) are exposed to greater extrinsic mortality risk, this could lead them to adaptively disinvest in their future health, thereby creating socioeconomic gradients in health behaviour. We collected data to test this prediction.

Methodology:

We surveyed North American adults for measures of SEP, effort in looking after health and perceived extrinsic and intrinsic mortality risks. We used general linear models to examine the relationships between SEP, perceived mortality risks and effort in looking after health. We also tested whether the association between SEP and effort in looking after health was mediated by perceived extrinsic mortality risk.

Results:

SEP was associated with effort in looking after health, even with age, sex and income controlled. Lower SEP was associated with higher perceived extrinsic mortality but there was no relationship between SEP and perceived intrinsic mortality. Both perceived extrinsic mortality and perceived intrinsic mortality predicted effort in looking after health. However, perceived extrinsic mortality risk accounted for a substantial component of variation not accounted for by perceived intrinsic mortality risk. The converse was not true. The effect of SEP on effort in looking after health was completely mediated by perceived extrinsic mortality.

Conclusions and Implications:

Our findings support the predictions of our previously presented model. They also demonstrate that a meaningful portion of the SEP gradient in health behaviour might be explained by inequalities in exposure to extrinsic mortality risk.

P21 The role of salient eyes during nest defence in the wild jackdaw (*Corvus monedula*)

Gabrielle Davidson, University Of Cambridge
Nicky Clayton, Alex Thornton

Eyes or eye-like stimuli have frequently been shown to elicit vigilant responses in birds. This has been most heavily studied in a predator-prey context, but the role of eyes as signals in interactions between conspecifics is unexplored. Jackdaws (*Corvus monedula*) have pale blue irises which are conspicuous against their dark feathers, and are visible from outside the cavities where they nest. As jackdaws compete for nest sites, I hypothesise that their eyes may act as a warning signal to indicate that a nest is occupied and deter intrusions by

conspecifics. This hypothesis was tested by placing circular images the size of a jackdaw's head inside the entrance of the nest box where jackdaws were prospecting. I used four stimuli: a control (all black); all black with super-imposed jackdaw eyes; a jackdaw head with standard eyes, and a jackdaw head with photo-shopped dark rook eyes. Wild jackdaws responded fearfully to both images with standard pale jackdaw eyes, but showed no increase in vigilance to an image of a jackdaw head with rook eyes. This is the first study to demonstrate the potential salience of eyes as a signal to defend against conspecific competitors in a natural setting.

P22 Predictive value of behavioural tests on mate choice and on male reproductive success in the zebra finch (*Taeniopygia guttata*)

Fabio Miazzi, MPI For Chemical Ecology
Barbara A. Caspers, E. Tobias Krause

Evaluation of those male phenotypic traits that are honest signals of their quality is thought to drive female mate choice, to select suitable partners to sire the offspring. Due to their sexual dimorphism in plumage ornaments and singing ability, zebra finches have been extensively used as a model species for investigating the evaluation of visual and acoustic cues in mate choice, but there is still little agreement about their effective value and their relative importance. We used three single sensory modality behavioural tests, to assay the relative importance of visual, acoustic and olfactory cues in female mate choice in this species, and to evaluate their predictive value on female preference toward males both in a live test and during the breeding period, and finally on the males' reproductive success. We show that, even though we were able to obtain non-random choice in the behavioural tests, these, including the live test, were scarcely predictive of the female preference during the first days of the breeding period, which was the only measure that reliably predicted the males' reproductive success. We suggest that single behavioural tests should be used with more caution, because they can be not fully predictive of the offspring's sire. This talk will explore concepts of awareness and consciousness in the context of the various circumstances in which animals are deliberately killed. It will focus on what we can infer about consciousness from what we know about the neurophysiology of perception and also on what probable correlations exist between an animals' perceptive awareness, and the ways in which we attempt to measure this phenomenon.

P23 The evolution of social monogamy in mammals

Dieter Lukas, University Of Cambridge
Tim Clutton-Brock

Because of its prevalence in contemporary human societies, the evolution of social monogamy in non-human mammals has intrigued biologists for over a century. The two principal explanations are that social monogamy has developed where there is strong selection for some form of paternal care or that it has evolved where males cannot defend access to more than one female. During this presentation, we will present results derived using recently developed techniques of trait reconstruction for more than 2500 non-human mammalian species to identify evolutionary transitions to social monogamy and assess the characteristics of the species in which they occurred. We will use these findings to compare between the predictions of alternative explanations of the evolution of social monogamy.

P24 Late emergence and local deficiency of males resulted in low annual reproductive success in yellow ground squirrel females (*Spermophilus fulvus*).

Nina Vasilieva, A.N. Severtsov Institute Of Ecology And Evolution, Russian Academy Of Sciences
Andrey Tchabovsky

Various factors could restrict the time and energy available for individuals in different species and affect reproductive decisions. We studied variation in annual reproductive success among females in yellow ground squirrel (*Spermophilus fulvus*) in relation to age, body mass, previous reproduction, time of emergence and social environment at the day of spring emergence. We observed permanently marked squirrels ($N_{\text{females}}=160$) in the wild (Saratovskaya oblast', Russia) in 2004-2008. Age and body mass didn't affect female reproduction, except for the fact that the mean juvenile body mass was lower in yearlings than in adults. Previous reproduction had no influence on female survival, physical conditions or reproduction during the next year. The local density of females didn't affect the female reproduction. The only factor found to positively affect the probability to wean a litter was the density and the overall fraction of males: possibly, deficiency of males may prevent fertilization of some females. The quality of juveniles depended only on the date of the spring emergence: the later a female emerged, the lower was the body mass of her pups, and the fewer

offspring survived. Thus, time constraints had a strong effect on female reproduction in this long-hibernating species. (Supported by RFBR 12-04-31279).

P25 Do reproductive potentials attract? An analysis of personal ads in Estonian Internet dating site

Peeter Hõrak, Tartu University
Ulvi Piirisalu

In modern theories of human sexual selection there are two conflicting hypotheses. First, the "Reproductive potentials attract" which, according to parental investment theory, suggests that men search for signs of fertility in women but women seek for men with high socioeconomic status. Second hypothesis, the "Likes attract", states that people tend to choose mates similar to themselves over a variety of traits. We test these hypotheses in a data-set data retrieved from an Estonian online dating site built in 2007 specifically for the purpose of studying sexual selection in humans. In support of the "Reproductive potentials attract" hypothesis we found that women's demand for partner's income correlated most strongly with their own attractiveness and that men's income correlated most strongly with their demand on partner's attractiveness. On the other hand, income was the least sought trait for women and partner's attractiveness was not the most sought trait for men. In Support for the "Likes Attract" hypothesis, we found that users' self-perceived levels of most traits correlate most strongly with stated importance of the same traits in a sought partner. Thus neither of the hypotheses could be refuted and both were partially supported, which suggests that both hypotheses may require reformulation.

P26 Investment vs vulnerability tradeoff during brood transport in *Diacamma indicum*

Rajbir Kaur, IISER-Kolkata
Sumana Annagiri

Animals relocate their dwelling places for various reasons. During colony relocation, unlike any other animals, ants need to transport their brood in addition to the adults from their old nest to their new nest. As almost no information is available on the mechanism of brood transport, we conducted relocation experiment on ($n=12$) colonies with individually marked ant. We found absence of specialized ants that transport only brood and there was a complete overlap between transport of adult

and brood. An interesting tradeoff exists between vulnerability and investment among the different kinds of brood items. The larvae are more vulnerable and represent smaller investment of the colony while pupa due to their covering is less vulnerable but represents bigger investment of the colony. We examined the preference for different categories of brood by individual ants in choice experiments (n=203) during relocation. This provided us another platform to investigate the adaptation of this superorganism to handle the investment and vulnerability tradeoff.

P27 Testing the low-density hypothesis for reversed sex change in protogynous polygynous fishes: field experiments in the cleaner wrasse *Labroides dimidiatus*

Tetsuo Kuwamura, Chukyo University
Tatsuru Kadota, Shohei Suzuki

Protogynous (female to male) sex change is theoretically predicted when large males monopolize matings with females. In such polygynous species, however, the reversed sex change by the smaller one in a pair of widowed males has recently been confirmed by removing all females from the study area. In low-density populations of a polygynous species, most males can acquire only a single mate (i.e., facultative monogamy), and some of them may happen to become single due to mate loss. To simulate such a situation, we conducted female removal experiments to make a part of males widowed and the other males remain monogamous in a coral reef fish *Labroides dimidiatus*. The widowed males accepted an immigrant, whether it was a male or female, to form a new pair. When there were no immigrants, the widowed males moved to search a new mate. They formed a new pair with the nearest widowed individual, whether it was a male or female, and never joined a monogamous pair. It is suggested that the reversed sex change is one of the tactics of widowed males to acquire a new mate, reducing costs of movement and male-male competition, in the low-density situation of a polygynous species.

P28 Only Fools Blame Their Tools: Using Spatial Proximity Loggers to Construct Temporal Social Networks.

David Mlynski, University Of Bath
Darren Croft, Natasha Boyland, Richard James

In sexually size dimorphic birds where the fitness return from male and female offspring differs, female may advantage offspring of the more beneficial sex according to the sex allocation theory. Females may affect performance of sons and daughters by differential allocation of resources to the eggs depending on their sex or by placing male and female eggs early or late in laying sequence. Here, we analyzed egg size variability in relation to embryo sex and laying order in the Common Pochard (*Aythya ferina*). We found that egg volume decreased with laying order for both sexes, however there were differences between male and female eggs, respectively. Female eggs decreased in size significantly faster than male eggs in laying sequence. Laying order was also found to interact with embryo sex. Eggs bearing female embryo were laid earlier in laying sequence than eggs bearing male embryo. There was no relationship between offspring sex and egg size, however we found positive correlation between egg size and female body-mass. We suggest that enhancing daughters in laying order of eggs and slower decrease of egg size for male eggs may represent female's ability of sex specific adjustment of offspring.

P29 Sexual inhibition in *Servaea incana* jumping spiders: expression and mechanisms

Vivian Mendez, Macquarie University
Phillip Taylor

Sexual inhibition has been studied extensively in insects but this research area remains very poorly developed in spiders. Once mated, females of many jumping spider species become sexually unreceptive and aggressive towards males but the mechanisms responsible for this sexual inhibition are unknown. We assessed the mating frequency of 88 *Servaea incana* (Araneae: Salticidae) females from maturation until death. Virgin females were highly receptive but sexual inhibition was induced immediately after their first copulation; females became aggressive towards their first mate and almost always rejected courtship from subsequent males. Even after experimental removal of their first and second batches of eggs (simulating predation), females very rarely remated. Given low levels of female remating, virgin females are at an extreme premium for male reproductive fitness. Males will have an advantage if they are able to discriminate female reproductive status, and invest in pursuits of virgin females (high paternity value, and low rejection risk) over mated females. We discuss results for two sexual inhibition experiments in *S. incana* and propose mechanisms that might mediate sexual inhibition in this jumping spider. Data of

population dynamics and natural history provide context to the findings of sexual inhibition experiments.

P30 Testing the Immunity Handicap Hypothesis: Testosterone, aggressiveness and immunocompetence in male Campbell dwarf hamsters (*Phodopus campbelli*).

Anastasia Khrushchova, A.N. Severtsov Institute Of Ecology And Evolution
Rogovin Konstantin, Shekarova Olga, Vasilieva Nina

Immunity Handicap Hypothesis (Folstad and Karter, 1992) supposes that female choose the genetically healthy male partner, basing on expression of his sexual characters and display behaviour in spite of testosterone's affinity to suppress antibodies production by B-lymphocytes. Suppression of acquired immunity by androgens is considered to be a cost of expression of secondary sexual characters. It is supposed that the successive male honestly informs female about high quality of his innate health. Up to now there were few attempts to estimate relationships between acquired and innate immunity and the relation of both systems to testosterone, testosterone related characters and reproductive success of males.

Our attempts to confirm the negative relationships between testosterone level in blood, aggressiveness, expression of external sexual characters and specific immunity response to sheep red blood cells (SRBC) in male Campbell dwarf hamsters (*Phodopus campbelli*) give ambiguous results in different variants of testing (including experimental manipulation of testosterone level and testing of males selected for low- and high immune response to SRBC). We also did not find convincing support for correlation between characteristics of innate and acquired immunity, as well as between innate immunity, testosterone, and expression of secondary sexual characters, and male reproductive success. The research was supported by RFBR grant 10-04-00278a

P31 Behavioral and hormonal traits of lactation in domestic cat (*Felis catus*)

Galina Alekseeva, A.N. Severtsov Institute Of Ecology And Evolution
Sergey Naidenko

The period of the highest costs for female's organism is related to lactation, particularly in species with long-term parental care. The aim of this study was to describe an effect of maternal behavior

and hormonal activity on female condition during lactation. The study was conducted at the experimental station "Tchernogolovka". We used video-taping of maternal behavior, collected blood samples and weighed females during lactation. Intensity of maternal behavior decreased as the kittens grew (Friedman ANOVA (F): N=6, df=4, T=8.48-16.64, p<0.05): time that mother spent with the kittens was correlated with duration of nursing which correlated with duration of grooming (Spearman rank order correlations (S): N=6, R=0.9, p<0.05). Concentrations of cortisol, testosterone and progesterone increased over lactation period (Wilcoxon matched pairs test: N=6, Z=1.99, p<0.05). Duration of nursing correlated with testosterone and cortisol concentrations (S: N=6, R=0.9, p<0.05 and N=6, R=-0.9, p<0.05 respectively). Females body mass decreased during lactation (F: N=6, df=2, T=9.33, p<0.05). Mothers' body weight correlated with grooming duration (S: N=6, R=0.9, p<0.05 and N=6, R=-0.9, p<0.05 for 1-2 and 3-4 weeks of lactation respectively). Thus, female organism is subjected to high physiological stress during lactation that influences its health status. Supported by RFBR grants 12-04-32028, 13-04-01465.

P32 Long-term and acute shifts of parental behavior in the biparental convict cichlid (*Amatitlania nigrofasciata*): Involvement of isotocin

Kazutaka Shinozuka, University Of South Florida
College Of Medicine
Shigeru Watanabe

Convict cichlids exhibit functionally different parental behaviors: retrieving as protection, and fin-digging as provisioning. These behaviors are expected to be switched adaptively. The present study investigated long-term and acute shifts of parental behavior. As a result, a long-term shift from retrieving to fin-digging was observed in females with 4 days to 15 days old fry. Conversely, females showed an acute shift from fin-digging to retrieving, in response to experimental manipulation of intraperitoneal drug administration, which could be regarded as a threat stimulus. The acute shift was sustained for 30 to 60 min after saline administration, but not oxytocin antagonist administration. These results suggest that female convict cichlids adaptively modulate parental behavior both in long-term and acute situations, and the isotocinergic system is involved in the acute shift.

P33 How experimental design influences the measurement of mate choice: a test using the seed bug *Lygaeus equestris*

Liam Dougherty, University Of St Andrews
David Shuker

Mating preferences may be tested using either no-choice (one option) or choice (multiple options) tests, but explicit comparisons between these two experimental paradigms remain limited. Studies using both paradigms to test for mate preferences in the same species frequently find stronger preferences using a choice paradigm compared to a no-choice paradigm. We used a fully-factorial design to explicitly test the role of male and female choice paradigm on patterns of pre-copulatory sexual selection on morphology in the promiscuous seed bug *Lygaeus equestris*. We performed mating trials in which we varied the amount of choice presented to each sex using a 2 x 2 factorial design, giving four choice treatments: no-choice, male choice, female choice and mutual choice. Overall we found evidence for weak directional selection on large female size and stabilizing selection on smaller than average male size. However we found no significant effect of choice paradigm on the strength of mate choice by males or females. There was also no significant difference between paradigms in copulation duration or female fertility. This is the first study to our knowledge that has attempted to quantify the effect of choice treatment on mating preferences in a rigorous way.

P34 Female moths do it all: advertise, compete and choose

Ally Harari, The Volcani Center
Hadass Steinitz, Adi Sadeh

The concept of a male sex pheromone as a sexual trait that is used by females to evaluate males as mates is widely accepted. By contrast, the idea of a female sex pheromone as a secondary trait is fairly new and evidence is scarce. In order to serve as an honest signal, sex pheromones, as other secondary traits that advertise condition, should bear a significant cost. Female sex pheromone in moths, as opposed to male sex pheromone, is typically released in minute amounts. Nevertheless, accumulating evidence demonstrates an imposed cost on female produced pheromone. Male moths, at the other side of the sexual selection equation, are generally sperm limited and as such are expected to gain from choosing a mate. We will discuss the option of mutual mate choice and intrasexual competition among both males and

females in the context of monandrous and polyandrous females.

P35 Communal nursing in a free-living population of house mice (*Mus musculus domesticus*)

Nicola Harrison, University Of Zurich
Manuela Ferrari, Anna Lindholm, Barbara Konig

Communal nursing in house mice is a key example of cooperation where females pool litters in the same nest and indiscriminately nurse own and non-offspring. The direct fitness benefits associated with communal nursing shown in laboratory studies suggest it to be a selected component of female house mice reproductive behaviour. However, there is surprisingly little known about communal nursing in wild mice. Here we use data from a long-term study of free-living wild house mice to address some basic questions about communal nursing and its fitness consequences. We aim to quantify the frequency of communal nursing, define how many individuals contribute to a nest, whether females use the same reproductive strategy in consecutive litters and determine if communal nursing influences offspring survival. Therefore, this study aims to test whether fitness benefits of communal nursing found in the laboratory are comparable to the free-living wild population.

P36 Effects of relative density of alternative male morphs on male-male competition and female choice

Lukas Knut Hilke, University Of Bern
Michael Taborsky

Negative frequency dependence yields equilibrium frequencies of alternative morphs in a population. In the shell brooding Lake Tanganyika cichlid *Lamprologus callipterus*, giant bourgeois and dwarf parasitic males represent different Mendelian morphs pursuing alternative reproductive tactics. Dwarf males parasitize the reproductive effort of bourgeois nest owners by intruding into snail shells in which females are spawning. If they successfully enter a shell, dwarf males outcompete nest owners regarding the number of eggs they fertilize. The presence and relative number of parasitic dwarf males in a population should influence (1) competition between males of the same morph, (2) behavioural responses of males of the respective alternative morph, and (3) female choice. Using a semi-natural setting in very large tanks we examined experimentally whether and how the density of parasitic dwarf males influences these

three parameters. The behaviour of both types of males, their relative reproductive success, and female choice were determined. The results partly support predictions derived from hypotheses explaining the coexistence of alternative reproductive tactics within a population.

P37 Prevention to male-induced pregnancy block in domestic horse mares

Ludek Bartos, Institute Of Animal Science, Praha, Czech Republic
Jitka Bartosova, Jan Pluhacek

We found that bringing a pregnant mare mated out of home with a strange stallion into a vicinity of a male who was not the father of her foetus increased probability of pregnancy disruption. Repeated sexual activity either by a home stallion or dominant gelding was observed shortly after the mare came from out-of-home mating. Pregnancy disruption was 7 times more likely event when the mare had no male company in her enclosure while home stallions or geldings were present in an adjacent enclosure. This seems to be a new phenomenon where a mare manipulates the male's paternity assessment by promiscuous mating (Behav. Ecol. Sociobiol. 65, 1567-1572). If she has no chance to do that she activates her pregnancy block. We extended the investigation and completed the results showing that mares mated out of home and brought home to environment with no male in vicinity has prevented any pregnancy block. This further confirms suggestion of the previous study. Thus the common practice, of transporting the mare for mating and then bringing her back to an environment with males, stallions or geldings, which did not sire the foetus, is the main cause of high percentages of pregnancy disruption in domestic horses.

P38 Plane geometry of the mammary complex and its role in neonatal piglets suckling behaviour

Janko Skok, University Of Maribor, Faculty Of Agriculture And Life Sciences
Katarina Praper, Dejan Åkorjanc

In the present research suckling behaviour of neonatal piglets in relation to mammary gland surface area and its activity was studied. Three sows with their litters (27 piglets) were included in this preliminary analysis. Throughout the lactation period there were on average 27 observations of suckling order per litter. Plane geometry of the mammary complex was investigated on the basis of

distances between neighbouring teats, which were measured continuously during lactation. Results revealed that the number of active glands at the end of lactation corresponded to the number of piglets in litter. Indeed, active glands which have larger surface area depended on using intensity – mammary gland has retained full activity when it was exploited in at least 58% of sucklings. However, results suggested that heavier piglets, whose gland stimulations is presuming more intensive, tend to occupied glands with larger surface area already at the very beginning of lactation, whereas suckling stability was not correlated significantly with surface area of mammary gland. According to results it is tempting to suggest that plane geometry of the mammary complex play an important role in suckling behaviour of neonatal piglets.

P39 Behaviour of the female during mating predicts reproductive outcome

Jitka Bartosova, Institute Of Animal Science Prague
Jana Dubcova, Miroslava Pokorna, Ludek Bartos, Martina Komarkova

Mating with preferred partner was suggested to increase the chance of successful reproduction in females. We investigated behaviour during sexual encounter (N=109) in domestic horses where the stallions were selected by the breeder and the mares experienced so called in-hand forced mating. This may further intensify unfavourable perception of the situation by the mare due to human assistance, physical immobilizing, almost no social interaction with the stallion, etc. We did not find any significant effect of female behaviour during mating on her reproductive outcome (i.e. giving birth a foal after mating) when behavioural variables were classified according to the levels of aggression (zero/low/high; P=0.9). Nevertheless, we detected particular behaviours that well predicted reproductive outcome, such as biting the bit, frequent ears movements, walking, headshaking or tendency to flight. More than 70 % of mares failed to reproduce when exhibiting one or more of listed behaviours usually described as conflict behaviours. In conclusion we found clear relationship between conflict behaviour of female during mating and her reproductive outcome. This suggests an active defence of the mare against reproducing with non-preferred sires. Supported by AWIN project (FP7-KBBE-2010-4).

P40 Helping Mama - daughters are ahead of sons to independence of maternal care in the Galapagos sea lion (*Zalophus wollebaeki*)

Paolo Piedrahita, University Of Bielefeld
Oliver Krüger, Kristine Meise, Fritz Trillmich

The lactation period is an important stage in mammals' development. In the Galapagos sea lion, a highly dimorphic species, male offspring is considered as the expensive sex in terms of energy demands. Male offspring are born bigger and maintain this sexual dimorphism along their life span. Nevertheless, it has been shown that maternal investment occurs in such a way that at the age of two years Galapagos sea lion juveniles showed similar survival probability in both sexes. In this context, theory may predict that regardless of age, bigger offspring may contribute quickly to their self-maintenance than poorly-nursed ones, thus diminishing maternal care pressure. To address this, we studied the foraging behaviour of Galapagos sea lion juveniles since birth throughout the age of two years (the weaning period). We found that irrespective of size, daughters showed more foraging efforts than sons during their first year of life. In several cases, this sex difference was maintained up to the age of two years. In the light of our results, we discuss that this behavioural differences between daughters and sons could be also reflected in the amount of energy allocated by mothers in the gestation of a new offspring.

P41 Genetic monogamy and extra-pair paternity in pair-living mammals

Maren Huck, University Of Derby
Eduardo Fernandez-Duque, Paul Babb, Theodore Schurr

The social organization of animals is often a poor indicator of their genetic mating system. True genetic monogamy has been reported for only three mammals. Male participation in infant care, the strength of the pair-bond, and the length of the breeding season have been associated with extra-group paternity rates in birds and mammals. We evaluated the relationship between these factors and the genetic mating system of pair-living mammals. We tested the prediction that male participation in infant care and the strength of the pair-bond would be negatively correlated with extra-pair paternity (EPP) rates, whereas the length of the breeding season would be positively correlated. We provide microsatellite evidence for genetic monogamy in a pair-living primate with bi-parental care, Azara's owl monkey (*Aotus azarae*).

The results were used together with published data of further 15 pair-living mammals in a phylogenetically-corrected generalized least square analysis relating male care, strength of the pair-bond, and length of breeding season to proportions of EPP in these species. The intensity of male care and the strength of the pair-bond, but not the length of the breeding season, were correlated with EPP rates in pair-living mammals, a finding similar to that found in socially monogamous birds.

P42 Parental effort in socially monogamous white-browed coucals (*Centropus superciliosus*) and classically polyandrous black coucals (*C. grillii*)

Wolfgang Goymann, MPI Fuer Ornithologie
Ingrid Schwabl, Christina Muck, Felister Urasa, Musa Makomba

The black coucal is the only altricial bird species with an obligate classical polyandrous mating system. In this mating system sex-roles are reversed resulting in female competition for territories and sole male parental care. It has been suggested that this unusual mating system is possible in black coucals, because – in contrast to closely related coucal species – this species relies on a temporally superabundant food resource, thus enabling females to quickly gather resources to lay a large number of eggs within a short period and at the same time allowing males to raise a brood without help from the female partner. We tested this idea by comparing the breeding phenology of black coucals with a close congener, the white-browed coucal. The white-browed coucal is socially monogamous and both parents provide parental care at approximately equal rates. We compared the parental effort between black and white-browed coucals and conducted an experiment during which we temporarily removed one partner to investigate whether the remaining partner is able to compensate and adjust its feeding rate accordingly. The results of this study and its implications for current ideas regarding the evolution of sex-role reversal in black coucals and birds in general will be presented at the meeting.

P43 Filial cannibalism in nesting fish: females prefer to spawn in nests with few eggs to many

Lotta Kvarnemo, Åbo Akademi University
Maria Norevik Andrén

In fish, egg-tending males often show full clutch cannibalism (eat the entire brood) if it is small. Because small females lay small clutches, any

female, but small females in particular, may be expected to prefer to spawn in nests that already contain many eggs to few, to ensure the combined brood is as large as possible. On the other hand, any female, but large females in particular, may prefer spawning in nests with few eggs, if high egg density or being the last to spawn affects egg survival negatively. To test these predictions experimentally, we let small or large sand goby females choose between two size-matched males, guarding a small and a large clutch, respectively. Both small and large females preferred to spawn in small-clutched nests, even though the combined broods did not exceed the brood size range at risk of full clutch cannibalism. This preference could not be explained by more courtship or parental effort by the preferred male, nor by reduced survival of densely laid eggs. However, others have found that sand goby eggs laid last in a nest are at increased risk of being cannibalized. Thus, our result might be explained by this effect.

P44 Experimental Mating Preferences Enhance Offspring Disease Resistance

Dustin Penn, Konrad Lorenz Institute Of Ethology
Kerstin Thonhauser, Michaela Thoß, Attila Hettyey,
Shirley Raveh

Mate choice may allow females to enhance offspring resistance to infectious diseases and we experimentally tested this hypothesis using F1 from wild-caught house mice (*Mus musculus musculus*): First, we tested females' attraction towards two males simultaneously presented in a partner preference assay ($n = 30$), and we then experimentally mated each female with either their preferred (P) or non-preferred (NP) male. Second, when the resulting offspring reached 15 weeks of age, 72 were experimentally challenged with *Salmonella enterica* (serovar Typhimurium, LT2). Third, we monitored infection dynamics (bacterial clearance) over three weeks, and we estimated individual heterozygosity at the major histocompatibility complex (MHC class II Eb, A β , and class I K loci) to determine whether these immune loci affected females' preferences or offspring disease resistance. We found that offspring from P males tended to have better bacterial clearance compared to those sired by NP males, though only among MHC homozygotes, and they had significantly higher fitness than those from NP males. Our results provide direct experimental evidence that female mating preferences can enhance the resistance of their offspring to infectious diseases.

P45 Male Courtship and Female Mate Choice in Tooth-billed Bowerbirds

Carmen Panayi, University Of Cambridge

Bowerbirds are a good species in which to study multiple sexual cues. The males rely on a suite of complex, multimodal behaviours to attract a mate. To investigate the relative importance of each aspect of courtship in the little studies tooth-billed bowerbird, I use a combination of observational and experimental methods. My aim here is to present the main questions addressed in my research, the initial findings from my first field seasons, and the direction of future research.

P46 Logical Foraging Based on Landmark Meaning in Ant *Camponotus japonicus*

Tomoko Sakiyama, Kobe University, Japan
Yukio-Pegio Gunji

Previous studies reported that ants seem to use a landmark as *taxon* which offers foragers only directional and unique information indicating the goal. Any landmarks are, however, might be used as a *locale* which offers positional information in the midst of the leaning process of landmarks, because they can have uncertain possible goals. It suggests that ants can utilize a landmark which indicates multiple goals, and that ants can have a cognitive map. To estimate whether an ant has a visual cue and manipulates multiple cues in a logical manner, we conducted an experiment in which each ant forager trained in Y-shaped maze with offering honeydew food and/or dead-end in upper branches. We set two logical training situations. 1: one of the upper routes of Y-maze was food located route and the other was dead-end. 2: both upper routes of Y-maze were food located routes or dead-ends. Given a pole as a landmark at the junction, an ant can lean that a landmark indicates "food AND dead-end" in the situation (1), and "food OR dead-end" in the situation (2). Our results show that ants can use visual cues and can manipulate logical expressions.

P47 Testing foraging models with honey bees: the reinforcement schedule approach.

Michel Sokolowski, Université De Picardie - Jules Verne
Alasdair Houston

Over the past decades, a lot of studies have been done about foraging behaviour. In this context, optimal foraging theory has been one of the most

influential approach. To test quantitative model predictions, researchers are faced to the problem of measuring behaviour, but also to the problem of how to control the environmental constraints concerning the resources. With honey bees, few studies have been able to test quantitative predictions satisfactorily. Recently, we developed an operant conditioning chamber for honey bees able to test reinforcement schedules. In the present study, we exposed honey bees to several fixed ratio schedules of reinforcement simulating the richness of the environment and we show how a quantitative model can predict most of the observed results. We suggest reinforcement schedules could be a useful tool in honey bee foraging research.

P48 Temperature And Food Availability Affect Risk Assessment In A Marine Fish

Govinda Lienart, James Cook University
Matthew D. Mitchell, Maud C.O. Ferrari, Mark I. McCormick

Temperature and food availability is known to affect the physiological condition of marine fishes, but how the interaction of these variables may influence predator-prey dynamics is still poorly understood. This study examined the interactive effects of food availability and temperature on the trade-offs between predator avoidance behaviour and foraging in juveniles of a tropical marine damselfish, *Pomacentrus chrysurus*. Predator avoidance behaviour was tested by exposing fish to chemical alarm cues obtained from skin extract of conspecifics. When detected, these cues elicit an antipredator response in fish, typically characterized by decreasing feeding attempts. Fish maintained under high food ration displayed distinct antipredator responses to chemical alarm cues, regardless of temperature. However, fish maintained in condition of low food ration and 3°C above ambient temperature did not display an antipredator response when exposed to chemical alarm cues, while those under ambient temperature did. These results suggest that individuals with lower physiological state due to limited food availability are more susceptible to increased temperature and may therefore take greater risks under predation threats to satisfy their energetic requirements.

P49 Psychological modulator of fish appraisal: how the predictability of appetitive and aversive stimuli

modifies the behavioural responses of Gilthead sea bream (*Sparus aurata*)

Marco Cerqueira, CCMAR - Portugal
Sandie Millot, Maria Castanheira, Rui Gonzalves, Rui Oliveira, Catarina Martins

Cognitive appraisal, i.e. the ability to subjectively interpret stimuli, has been described in several non-human animals. In fish, despite the recognition of complex cognitive abilities, very little is known about their ability to psychologically integrate environmental stimuli. This study aimed to understand how fish with different personalities appraised stimuli with different valences and whether predicting the onset of such stimuli modifies behaviour. Sea Bream, individually tagged, were initially screened for personality using a validated method (net restraining). Homogeneous groups (4 fish) of reactive and proactive individuals were used to test appetitive (food) and aversive (air exposure) stimuli on either a predictable (signalling the onset of a stimulus by a conditioned signal (light)) or unpredictable way (light dissociated from the stimulus). Behaviour was video recorded and analysed by Observer XT®. Fish subjected to predictable conditions show higher levels of anticipatory behaviour (swimming activity $p < 0.025$ and escape attempts $p < 0.035$), while individuals subjected to unpredictability exhibit higher frequency of freezing behaviour ($p < 0.001$). Fish personality did not influence the behavioural responses towards stimuli of different valence given in a predictable or unpredictable way. In conclusion, this study suggests that predictability is a psychological modulator of both appetitive and aversive events in fish.

P50 Oversupply of information reduces host exploitation efficiency of a plant pest insect

Barry Brogan, Newcastle University
Colin Tosh

Humans and other animals undertaking a task but supplied with an abundance of potentially distracting information often become task-inefficient or 'confused'. Here we apply principles of this 'confusion effect' to the behaviour of a major worldwide pest, the glasshouse whitefly, *Trialeurodes vaporariorum*. We analyse the whole organism settling behaviour and sub-epidermal stylet penetration behaviour of whiteflies on tomato while supplying them with volatiles from three alternative host plants. Whiteflies are largely unaffected by this treatment with the exception of sub-epidermal phloem seeking behaviour. Almost all control whiteflies supplied with clean air access the

tomato phloem within the 15h observation period but almost none of the volatile supplied flies access the phloem in the same period. We extract and present volatiles from two different sets of three alternative host plants and obtain a similar result, indicating that it is informational abundance per se and not the specific composition of volatile mixtures that is causing results. The use of host rather than non-host volatiles rules out deterrence effects. Results may partly explain the pest-protecting effects of mixed species cropping, a widely adopted practice in developing nations. The potential for results to be applied to the protection of crop plant monocultures is discussed.

P51 Recognition and discrimination of prey by great tits (*Parus major*)

Zuzana Karlíková, University Of South Bohemia, Faculty Of Science
Petr Vesele, Roman Fuchs

Ability of avian predators to discriminate equally looking prey with different chemical protection was tested. Great tits (*Parus major*) were confronted with similarly and non-warningly looking prey (carrying paper sticker with cockroach photo) which was both edible (cockroach – *Blaptica dubia*) and/or inedible (firebug – *Pyrrhocoris apterus*). Preys were presented simultaneously or alternately. During one session 14 presentation of prey (one or two items) were repeated to observe learning. After 7 days, there was a second session with other 14 presentations, to test memory. When the prey was presented simultaneously, during the first session only slow learning process was recorded in case of cockroaches. Anyway, during the second session most of tested birds managed to resolve edible and inedible prey. Contrary, in experiments with alternating prey; both prey species were gradually attacked by larger proportion of birds. Nevertheless, cockroaches were attacked more often than firebugs (during both sessions) and their edibility was discovered quite early during the learning process. At the beginning, the firebug provided some protection to the cockroach which disappeared during our experiment. The predator's experience with the cockroach weakened the protection of the firebug only in case of alternating presentations of cockroach and firebug.

P52 Evolution of risk sensitivity in sympatric three species of tits: insectivorous habit draws tolerance to risk

Ai Kawamori, The Graduate University For Advanced Studies
Toshiya Matsushima

Stochastic nature of food inevitably causes risk in the amount of gain, which most animals avoid. If animals depend on high-risk food, however, do they also show risk aversion? In this study, three closely related sympatric species of family *Paridae* were compared. Stable isotope analysis of wild birds revealed that Great and Marsh tits were more insectivorous, whereas Varied tits were more granivorous. We examined their choices between an un-risky food option (amount = 1, probability = 1) and a risky food option (amount = 3, probability = 1/3); notice that the expected amount was the same. Great tits showed risk proneness, whereas Varied tits showed risk aversion, and Marsh tits were intermediate between them. To reconstruct ancestral state of risk sensitivity using phylogenetic comparative methods, we simulated how large incompleteness of phylogeny (lack of close species' data and uncertainty of divergence time) shift the estimates. Furthermore, we compared preference to insects (mealworm) vs. seeds (sunflower), and found that the preference was correlated with the risk sensitivity at species level. The present results suggest that the insectivorous birds (Great tits) depend on high-risk food, thus are more tolerant to risk than the granivorous species (Varied tits).

P53 Anthropogenic noise alters shelter usage and foraging activity in fish

Kirsty E McLaughlin, Queens University Belfast
H P Kunc

Anthropogenic noise is becoming omnipresent, affecting species inhabiting aquatic and terrestrial environments. Noise has been found to affect a variety of aspects of fish biology such as hearing, stress levels, communication and avoidance behaviour. For example, fish have been shown to avoid areas closest to noise sources. However, we still have little understanding of how noise affects other fish behaviours, such as foraging and movement. Here, we examined the effect of anthropogenic noise on fish, focusing on sheltering behaviour, foraging activity and swimming behaviour. We found that exposure to noise increases sheltering behaviour, decreases foraging activity, but did not affect swimming behaviour. Fish that shelter more have less time available for essential activities such as mate attraction, territory defence or foraging. We reveal a causal link between time sheltering and foraging activity, demonstrating that increased sheltering led to a

reduction in foraging activity. This decrease in foraging behaviour may lead to a reduction in energy intake. To our knowledge this study shows, experimentally for the first time, how a noise-induced change in one behaviour can have a negative knock-on effect on other behaviours.

P54 Group-foraging and information transfer in European shags *Phalacrocorax aristotelis*: Implications for seabird conservation

Julian Evans, University Of Exeter
Sasha Dall, Stephen Votier

Despite many potential costs, colonial breeding is extremely common in many vertebrate species. In birds alone, colonial breeding has been shown to have evolved independently at least twenty times and it is estimated that at least 96% of sea bird species breed colonially. There have been many suggested hypotheses about the potential advantages of colonial breeding. One of these is that group living can improve foraging efficiency via deliberate or inadvertent sharing of foraging information. There are several similar theories on foraging information use within a colony, such as the information centre and recruitment centre hypotheses. While these theories have been examined via various theoretical and empirical studies for a quarter of a century, our insight into the relevance of information transfer in colonial animals is limited. Understanding how conspecific behaviour might affect foraging efficiency has clear fundamental implications, but may also have significant conservation relevance. This is especially the case for species reliant on patchy or ephemeral food sources. We assessed the value of foraging information in a colonially nesting seabird of conservation concern, the European Shag (*Phalacrocorax aristotelis*). We utilised a combination of GPS tracking and behavioural observation of several breeding colonies in the Isles of Scilly.

P55 Behavioural flexibility of the red ant *Myrmica rubra* in seed dispersal process (myrmecochory)

Audrey Bologna, Université Libre De Bruxelles
Claire Detrain

Myrmecochory is a mutualistic interaction: ants disperse seeds and plants provide a nutrient-rich appendage, the elaiosome. This process involves a diversity of partners as well as asymmetries in the cost-benefit balance drawn from this interaction. Indeed, one seed species can be dispersed by

multiple ant partners, and vice versa. Furthermore, asymmetries in the outcomes of the interaction can appear when seeds are buried alive in ant nests, or when elaiosome intake increases worker numbers in one case and decreases larva numbers in another (Marussich, 2006). The stability of each ant-plant relationship is therefore challenged by the relative benefits expected from this interaction.

We investigated the temporal stability of myrmecochory by offering, during 5 successive weeks, *Viola odorata* seeds to *Myrmica rubra* ant colonies. An important decrease in the harvesting process was noticed as soon as the second week. Likewise, a drastic reduction of elaiosome consumption appeared from the second week. Associative learning could be involved in this extinction process. Ants faced with a cost (e.g. elaiosome toxicity) could develop an adaptive strategy -expressed by a behavioural flexibility- to reduce it. The extinction phenomenon could have an impact on the strength of the links between partners in this mutualistic interaction.

P56 Prey depression by Bar-tailed Godwits foraging on lugworms

Sjoerd Duijns, Royal Netherlands Institute For Sea Research, NIOZ
Ineke Knot, Jan van Gils, Theunis Piersma

During the last decade the composition of the waterbird community in the Wadden Sea has changed drastically. Bivalve predators have declined, whereas waterbirds specializing on worms have increased, suggesting a response to changes in the benthic fauna. Although links between food and predator densities are now well established for some bivalve eaters, further work is in order for the links between worm-eating birds and polychaete worms. This requires data on bird densities and their food as well as the function that links them, i.e. the functional response. The type II functional response is commonly observed in the field but needs verification under controlled conditions to expand the range of food conditions and to avoid that the response curve represents site avoidance and attraction rather than food-abundance driven intake rates. We determined functional response relationships in female Bar-tailed Godwits (*Limosa lapponica*) feeding on lugworms (*Arenicola marina*), both in the field and under controlled captive conditions. The absence of a type II response curve in the field was explained by interference competition. Experimental probing increased lugworm depth, and increased depth of lugworms lowered the intake rates of Bar-tailed Godwits due to increased searching and not handling times.

P57 Are there hunters and gatherers in social spiders? Long-term behavioural consistency in *Stegodyphus sarasinorum*

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Divya Bellur, Hema Somanathan

Sociality in spiders is extremely rare. Social spiders co-operate in prey-capture, web maintenance, brood care and were thought to lack task differentiation. However, behavioural consistency in prey-capture was shown in the social spider *Stegodyphus sarasinorum* when sampled over a 3-day period. These spiders live upto a year, and the long-term dynamics of this consistency remains unknown. We examined a) the timespan and inter-individual variation of this behavioural consistency in a month-long experiment and b) for the first time, associations among individuals during prey capture using social network analysis. We find that while some spiders exhibit long-term behavioural consistency, others vary in their propensity to attack prey. Furthermore, we find that there are two strategies to participate in a hunt: 'subduers', who attack and subdue prey, and 'latecomers,' who do not participate in subduing prey and arrive later to feed on it. 'Subduers' were seen to form weak associations during prey capture. Within a colony some spiders display one strategy consistently, but most spiders alternate between the two. Our results suggest that behavioural consistency in prey capture could have colony-level consequences on foraging. We also discuss the advantages of using social-network analysis to investigate the dynamics of co-operation in social spiders.

P58 Selective caching and overwintering strategies in female Common hamsters

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Eva Millesi

Common hamsters accumulate body fat as internal and food stores as external energy reserves to survive the winter period in their hibernacula. Previous studies on a hamster population in Vienna revealed that adult females cached food throughout the active season and, as opposed to males, were rarely observed feeding outside their burrows. Due to reproductive effort, body fat accumulation in females is limited resulting in higher dependence on food stores and shorter hibernation periods compared to males. In this study we investigated

foraging behaviour in adult females to determine individual differences in the selection of food items carried into the burrow. We further distinguished between storable food items (i.e. seeds) and those that were inappropriate for long-term storing. In general, unstorable items were frequently but rather unselectively collected, whereas storable food was cached very selectively by spending 68-100% time above-ground collecting these certain plant parts. The behavioural patterns were supported by analyses of cheek pouch contents released in the live traps. According to differences in foraging behaviour, females showed a high individual variation in body fat proportions prior to winter and body temperature patterns during winter ranged from regular torpor bouts in some individuals to extended euthermic phases in others.

P59 Over-wintering strategies & foraging specialisation in Northern gannets (*Morus bassanus*)

Hannah Williams, University Of Exeter
Thomas Bodey, Ian Cleasby, Keith Hamer, Stephen Votier, Ewan Wakefield, Stuart Bearhop

Some seabird species interact with fishing vessels during foraging, but with their offshore foraging trips and wide-ranging migration we are unaware of the prevalence of this behaviour and its impact on individual success. We used stable isotope analysis (SIA) and light-level geolocators to examine the variation in the winter foraging strategies of Northern gannets (*Morus bassanus*) and the carry-over effects of these strategies on subsequent breeding success. Three samples were taken along the length of a winter grown feather from individuals from five UK breeding colonies for SIA. These samples provided longitudinal dietary information from which individual niche specialisation was quantified. Individuals from two breeding colonies migrated to four distinct wintering destinations and three foraging strategies have been identified in all colonies. Two of these strategies can be described as specialist and the third as generalist. SIA also identified offshore foraging at a higher trophic level than inshore foraging, suggesting that these individuals obtained their prey from fishing vessels. This work will assess the impact of fishing processes on individual success and how best to protect this migratory species at sea.

P60 Carbon dioxide levels inside the nest influence fungus relocation and excavation behaviour in leaf-cutting ants

Daniela Römer, Department Of Behavioural Physiology And Sociobiology, University Of Würzburg,
Martin Bollazzi, Flavio Roces

Leaf-cutting ants rear a symbiotic fungus that is the basis for colony's survival. To grow optimally, the fungus needs suitable environmental conditions, one of which is the CO₂ content of the air in the nest chambers, which varies across the soil profile. High concentrations are known to hinder fungal growth. Leaf-cutting ants should therefore avoid rearing fungus in places with high concentrations. We investigated whether ants relocate symbiotic fungus based on the CO₂ concentration of the nest environment. In the laboratory, workers of *Acromyrmex lundii* could relocate fungus into two humid chambers connected by a Y-shaped tube, which offered different CO₂ concentrations. It was evaluated whether workers avoid high concentrations (4% vs. 0.1% CO₂) and prefer concentrations as low as possible (1% vs. near atmospheric CO₂ values). A series with high concentrations (4%) in both chambers was performed as a control for side preferences. Additionally, the effect of increasing CO₂ concentrations on digging behavior was quantified. Ants avoided high concentrations yet actually preferred low to atmospheric values, likely because low CO₂ values are used as an 'inside-nest' cue. Elevated CO₂ levels also affected digging activity of workers, which are therefore expected to influence the spatial distribution of nest chambers.

P61 Impact of imidacloprid on the intake target of the bumblebee, *Bombus terrestris*

Sophie Derveau, Newcastle University
Geraldine Wright

Bees are chronically exposed to pesticide residues in stored food and in the countryside (crop, wild flowers, soil etc.). Sub-lethal imidacloprid doses have a strong impact on bumblebees (*Bombus terrestris*) foraging abilities. Different diets were used to test if bumblebees on a high protein diet are more likely to survive imidacloprid chronic exposure and need to eat more protein to survive. Bees were fed with a sucrose solution (0.5M) and casein solution to a range between 1:400 to 1:25 (protein to carbohydrate ratio). Bee's daily intakes were measured for 7 consecutive days. When there are exposed to imidacloprid, bumblebee's food intake

decreased. A shift was observed for cumulative consumptions with imidacloprid for each casein diet. However, when bees were fed with sub-lethal doses of imidacloprid, they were more likely to die sooner than in the control. Bumblebees' nutritional balance changes with imidacloprid exposition and changes their dietary regulation. Our results suggest that sub-lethal imidacloprid chronic exposure can affect bees' metabolism and as a consequence their foraging and feeding behavior.

P62 The nutritional optimum of the adult worker bumblebee (*Bombus terrestris*) depends on dietary source of essential amino acids

Daniel Stabler, Newcastle University
Pier Paoli, Susan Nicolson, Stephen Simpson,
Geraldine Wright

Dietary protein is the main source of essential amino acids required for growth, reproduction, and somatic maintenance for most animals. Adult workers in eusocial bee colonies, in contrast, often obtain free amino acids in floral nectar and may even exhibit limitations in their ability to digest protein. Here, using the Geometric Framework model for nutrition, we show that the nutritional intake optimum of adult worker bumblebees (*Bombus terrestris*) depends on whether bees consume solutions containing a protein (casein) or essential amino acids. When bees fed on casein solutions, their ability to balance their intake of carbohydrates and protein was limited to a range between 1:250 and 1:25 (protein-to-carbohydrate ratio). Outside of this range, they were unable to regulate both carbohydrates and proteins simultaneously. Bees fed solutions containing amino acids, however, were always able to balance their intake, but they were more likely to die sooner than those fed casein. Our data are the first to show that an animal's nutritional regulation depends on its source of essential dietary amino acids and imply that specific amino acids are involved in regulating protein intake.

P63 The use of ideas of Kolmogorov complexity for studying the variability of hunting behaviour and social learning in rodents

Sofia Panteleeva, Institute Of Systematics And Ecology Of Animals SB RAS
Zhanna Reznikova

The notion of Kolmogorov complexity is a useful tool for evaluating the variability of behavioural patterns (Ryabko et al., 2013). We investigated hunting

behaviour of laboratory reared mice *Mus musculus* (n=43; 85 stereotypical), rats *Rattus norvegicus* (n=30; 201), and gerbils *Meriones unguiculatus* (n=24; 315) towards cockroaches. Using the “alphabet” of 18 behavioural units common for all species, we expressed the hunting stereotypes as text files, reduced them to equal initial lengths, compressed them using a data compressor, and compared ratios of compression. The hunting stereotype in mice turned out to be most “laconic” and less “noisy” than in two other species. In gerbils the hunting stereotypes are least coherent. They killed victims only in 9.4% of cases, whereas in mice and rats the part of successful hunts was about 50%. In gerbils we compared ratios of compressions of stereotypes in young (30 days) “observers” before and after their visual contacts with hunting demonstrators, and revealed that social learning makes hunting stereotypes more laconic and coherent. We speculate that in social rodents completeness of the hunting stereotype is governed by “distributed social learning” as it has been shown for ants (Panteleeva, Reznikova, 2008).

P64 Using dung stable isotope analysis as a tool to assess dietary variation of African elephants: addressing sampling issues

Nicola Rodgers, Anglia Ruskin University
Dawn Hawkins, Guy Norton, Tamsin O'Connell

Stable isotope analyses have widespread applications throughout the natural sciences and are particularly useful when applied to dietary related questions. Different food and water types vary naturally in their isotopic composition and when consumed are incorporated into the bodily tissues and waste products of an animal. Therefore by analysing the isotopic values of tissues or waste we can indirectly assess dietary intake. When applying this technique to study the diet of elephants, dung is a useful material to analyse as it is easily accessible, non invasive and easy to export. Yet few people have considered some basic sampling questions; how much to sample, from where in a dung pile and from whom. These are crucial when samples are being collected from remote and sometimes dangerous field locations. We address these questions by assessing within and between individual variation of dung collected from captive elephants all fed on a similar diet. No variation was found within individual samples, indicating that researchers can sample from anywhere within a dung pile. Samples from the male of the group differed significantly from the 3 females, suggesting that it is important to know the individuals being sampled from.

P65 Intermittent Random Search Model with Misunderstanding Switch Pattern can show Levy-like Distribution

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Yukio Gunji

In intermittent random search in which slow motion to detect the target is discretely separated from the motion to migrate to another feeder, the high efficiency of Levy strategy (LS), i.e. time interval to switch these two phases is chosen from Levy distribution, is generally found. While it is reported that LS is consistent with searching behavior of real animals, some researchers claim that Levy-like distribution shown by animals is not necessarily produced by Levy process. We here propose an intermittent search model consisting of two phases which is not incorporated with Levy process. In this model, agent is basically correlated random walker (CRW), but memorizes its trajectory and counts the number of crossover in a trajectory. If the number exceeds a threshold, the agent resets the memory of trajectories and makes ballistic movement in the direction uncorrelated to the past. We also show that this model can balance a trade-off between macro search (exploration) and micro one (exploitation), which is shown by CRW. Finally we show that another intermittent model in which a long trail without crossover stochastically generated is regarded as a ballistic movement and entails reset of the memory, can show Levy-like distribution of the time interval.

P66 On the Importance and Interaction of Visual and Olfactory Signals in the Foraging Behaviour of the Honeybee

Verena Reinhardt, Johannes Gutenberg University Mainz
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Flowers display various colour and scent cues in order to attract honeybees. Our project presents the first systematic long-term exploration of how these cues are learned and remembered by bees, conducted as an ethological approach. For stimuli, we used colours which flowers frequently display to attract honeybees, and scents of flowers which bees typically pollinate. Free-flying worker bees were trained to a colour-scent compound stimulus and afterwards tested with conflicting stimuli, so that the previously rewarded colour was combined with a new scent, and the previously rewarded scent was combined

with a new colour. Choice rates were used to determine which factor was more important to bees. In contrast to previous reports, bees did not generally prefer scent over colour.

Moreover, this study explored whether a bee's preference of colour over scent (or vice versa) is reversible. Bees which initially preferred colour were afterwards trained on scent stimuli, and bees which initially preferred scent were trained on colour stimuli. All those bees were afterwards conflict-tested to check for changes in their preference.

The current study yielded some surprising insight into the strategies honeybees are using in pollination, and into the astounding behavioural plasticity their brains are capable of.

P67 Olfactory sensation can contribute to spiral search strategy in dispersing common shrews *Sorex araneus* L.

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Nikolay Shchipanov

Yearling common shrews were found different in their reaction on smell of conspecific in open field tests (Shchipanov et al., this volume). Here we report about "socially reactive" individuals only. Shrews were captured from wild and released after a trial at the area of capture. They were studied in multi-sectional maze. Four equal routs from the central chamber, ones lack of the path of a conspecific individual, ones with fresh (<5 minute old) tracks and ones with the elder tracks were suggested. The routs with 10-minutes tracks were selected significantly often and the routs with fresh tracks - significantly rare as compared to expected random selection. Taking into account that frequencies of occurring at some area of the home range make bell shaped normal distribution we argue that dispersing individual is undergoing 'centripetal' and 'centrifugal' stimulation resulted in selection of the position with optimal frequency of 10-minute tracks of a conspecific individual. This allows a shrew to find free home range nearest to the area of birth. Such a search corresponds to spiral search strategy.

P68 Who is willing to feed? The key-role of honeydew in ant- aphid mutualism

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Christophe Fischer, Georges Lognay, Lise Diez, Jacques Prieur, Francois Verheggen

Ants and aphids evolved mutualistic relationships: ants provide cleaning and protection in exchange of honeydew as energy source. We investigate how ants' behavior is shaped by the nutritive and informative content of honeydew. Concerning detection of aphids, volatile compounds of honeydew are attractive to the ants: they originate from microorganisms associated to honeydew and enable ants to distantly recognize their myrmecophilous partners. Concerning feeding behavior, dose-response curves reveal that honeydew sugars which are the most energetically beneficial to the ants 1°) are preferentially ingested and 2°) trigger the laying of an intense recruitment trail. Concerning recruitment behavior, the nutritive value of honeydew is not the only criterion used by ants to collectively mobilize nestmates to aphids. Indeed, information sharing between nestmates is also driven by the informative content of resources such as the presence of sugars (i.e. melezitose) that are specifically produced by the aphid mutualists. We discuss the relevance of honeydew nutrients and informational cues used by ants for recognizing their partners as well as for assessing of food value. This honeydew-driven behavior of ants is essential to understand how collective exploitation of aphid colonies proceeds and why mutualistic interactions between ants and aphids are maintained.

P69 The feeding behavior of the obligate but less specialized cleaning goby *Elacatinus figaro*

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Cleaner fish remove harmful ectoparasites from the body surface of other fish (usually called clients) and in turn receive food provisioning. Although it sounds equally beneficial to both intervenients, the true costs and benefits to cleaners and clients are variable. To assess the nature of the Brazilian goby *Elacatinus figaro* feeding behavior, cleaners and clients were collected at three locations along the Brazilian coast, in order to know in detail the cleaners diet and their clients ectoparasite loads. Ectoparasites were the most important item of this cleaning goby diet, but were less important than for other cleaner species (as the Caribbean gobies). Moreover, the importance of scales (a correlate of cheating) in their diet was also lower, which may imply a lower tendency on the part of *E. figaro* for cheating. Other alternative items were of great importance and revealed that *E. figaro* is a flexible cleaner. Ectoparasite load on the Brazilian clients was lower than in the Caribbean and in the Pacific, which may be the underlying cause for the cleaners

more alternative feeding aims. In conclusion, *E. figaro* seem to meet their energy demand through honest exploration of alternative food items, in contrast to other cleaner species.

P70 The cleaning behaviour of the Azorean facultative cleaners *Coris julis* and *Thalassoma pavo*

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Miguel Furtado, Ana Isabel Neto, Marta Soares

The cleaning mutualisms which involve species of small fish interaction with other fish, has mostly been studied for species living in tropical environments, and usually focus on obligatory cleaners. Indeed, the behaviour of facultative cleaner fish species that live in temperate waters are not well known, hence further work is still in need to fill this gap. We identified 10 sites in which our two facultative cleaner wrasse species, *Coris julis* and *Thalassoma pavo*, were actively inspecting other fish (aka at cleaning stations). Behavioural observations were performed through diving, between 2-5 m deep, at different sites in the coastal zone of São Miguel's island (Azores). For these observations, the behaviour of each cleaner and their clients were assessed during 30 min in each of the ten cleaning stations. We expect to obtain differences in the cleaning behaviour between the two cleaner species, along with differences arising from the visit of different species of clients, as well as potential links between inspection durations and client ectoparasite loads, tactile stimulation application and possible shifts in cleaner honesty according to client species. This will be the first thorough assessment and comparison of the importance of facultative cleaner fish behaviour living in temperate ecosystems.

P71 Potent social learning and conformity shape a wild primate's foraging decisions.

Erica van de Waal, University Of St Andrews
Christele Borgeaud, Andrew Whiten

Behavioural tradition has been an active topic in animal behavior since the renowned Japanese macaque studies of half a century ago, yet controlled field experiments to clearly identify social learning began only recently. We provisioned wild vervet monkeys with two bowls of maize corn died different colours, with one initially made strongly distasteful using bitter mountain aloe. Over four sessions, 109 monkeys in four groups learned to

take one colour and avoid the other. Four months later we offered both coloured foods untreated, just when a new cohort of infants was ready to take their first corn. Vertical social learning was demonstrated strikingly, with 27/27 infants taking only the coloured alternative eaten by their mothers. Just one infant ate the formerly distasteful coloured food, after its low ranking mother did. Ten males migrated from groups where one colour was favoured to a group where the opposite colour was eaten, and all but one conformed directly to the new group colour preference despite their countervailing prior personal experience. The one exception was a male who rapidly achieved high rank on immigration to his new group. These results demonstrate that potent social learning and conformity can shape behaviour in the wild.

P72 Changes in peck rate of food by domestic chicks (*Gallus gallus*) and the control of insect populations

John P Kent, Ballyrichard HS.

Flies, insects and midges are regarded as vectors in diseases such as schmallenberg in cattle and sheep and in T.B. in cattle. Vaccination may be a means to control these diseases. However, a focus on the ecology of food production with domestic animals could focus on the use of other species in the farm ecology that could act in the prevention of some diseases. Here I will focus on changes in behaviour of developing domestic fowl (*Gallus gallus*) that parallel changes at the physiological and ecological level, an understanding of which may help in developing an appreciation of these species role in the farm ecology.

Domestic chicks increase their peck rate at grain diet and insect prey till week 6 and then an unexpected decline in the peck rate is apparent. This parallels certain changes at the level of neuron development. It also parallels and compliments changes in the ecology, being hatched from spring and developing when the dietary needs are met by increases in the insect population which they help to control.

P73 Feeding Ecology Of Proboscis Monkeys (*Nasalis larvatus*) In Klias Peninsula, Sabah

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Diana Indim, Noor Azrin, Abd Rahman

Nasalis larvatus is one of the endemic species in Borneo and has received increasing attention in

recent years. In Sabah, this monkey has become an important flagship species for conservation, as well as an eco-tourist attraction. Captive breeding of the monkey may become necessary in the future. Therefore, it is important to study the feeding ecology in the wild to provide information on the feeding pattern to the responsible parties for them to supply this monkey with additional food supplement to ensure the success of captivity breeding programmes. In this study, the feeding ecology of the Proboscis monkey in a wild as well as the nutrient composition of the food taken by this monkey will be determined. Field sampling using scan sampling will be used to collect data on feeding behaviour and sample of food taken will be collected and identified. While, methods of the Association of Official Analytical Chemists (AOAC 1990) will be employed to assess the nutrient composition in monkeys' food preferences. The outcome of the study can provide information to the Wildlife Department on the plant preferences by the monkey in the wild, and the additional information to the zoo, as well as the proboscis monkey sanctuary management, on the nutrient composition of the food taken by proboscis monkey in the wild. Such information is useful to these parties for them to provide the monkey with other food supplement that suitable to this monkey to ensure their survival in the captivity.

P74 Can ants perceive affordance for food transport?

Kohei Sonoda, Shiga University
Mai Minoura, Yukio Gunji

In this study, we focused on food transport in the ant *Formica fusca*. We constructed square entrances by covering the ant's nests with bottomless boxes and gave the ants a large food item to import to the entrances. They adaptively imported it depending on the shape of the nest entrance. The results indicate that ants can perceive affordance for food transport.

P75 Short-term feeding behaviour of adult pine weevil (*Hylobius abietis*)

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Nordlander

The pine weevil (*Hylobius abietis*) is one of the most important forest pests in Europe. Yet little is known about its short-term feeding behaviour, which

describes patterns of food acquisition on a time scale of less than a day. These patterns are useful for understanding mechanisms of food intake limitations. We studied individual male and female pine weevils for 24 hours, each with both an intact and a girdled seedling of Norway spruce (*Picea abies*). Girdling is a commonly observed damage caused by the pine weevil on planted seedlings. The meal criterion (the shortest interval separating two feeding bouts) and meal properties such as feeding duration, meal size, and ingestion rate, were determined. The pine weevil makes on average about five meals per day with a duration of approximately 18 minutes each. Feeding and meal properties often differed between the sexes but not between the seedling treatments. In addition the effects of prandial correlations were assessed. The influence of the non-feeding interval before a meal on the duration of the following meal (pre-prandial) was stronger than the influence of the meal duration on the succeeding non-feeding interval (post-prandial). The observed results allow in-depth understanding of pine weevil feeding behaviour.

P76 Discrimination of pollen quality by a generalist pollinator, *Bombus terrestris*

Elizabeth Nicholls, University Of Exeter
Natalie Hempel de Ibarra

Considerable variation exists in the nutritional value of pollen produced by different flowers, and bees have been shown to display preferences for collecting from certain species over others. We tested bees' ability to assess the nutritional quality of pollen without digesting it, and their potential to associate floral features with this reward. Individual foragers were offered a choice between pure pollen and that which had been diluted with indigestible alpha-cellulose, or a choice between two samples which had been diluted to varying degrees. The sensory environment and foraging experience were tightly controlled. Whilst bees were expected to preferentially collect the most highly concentrated pollen samples, we found preferences varied and were influenced by both the degree of similarity between samples and the type of pollen experienced previously. Repeated exposure weakened preferences, with bees more readily collecting nutritionally poorer samples over time. Adding a coloured cue to facilitate discrimination prevented the weakening of preferences, providing samples differed sufficiently in terms of pollen content. Thus, fast learning of floral cues seems to preclude continuous reward evaluation, leading to pollen constancy, which may have played a significant role in the diversification of plant-

pollinator systems and the reward provisioning strategies employed by flowers.

P77 Parid foraging behaviours and techniques in an urban environment during the breeding season

Julia Mackenzie, Anglia Ruskin University
Nancy Harrison, Shelley Hinsley

Heterogeneous urban environments, such as parks and gardens, often have high plant species diversity and represent complex problems for foraging arboreal birds, with potential consequences for breeding success. In this study, we compared foraging behaviours of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*), two arboreal insectivores that are adapted to broadleaved deciduous woodland, during the breeding season in an urban heterogeneous habitat, the Cambridge University Botanic Garden. We aimed to assess the implications that habitat structure may have on their ability to forage successfully for nestling food. Both species differed in their behaviours with great tits using a wider range of foraging heights and different foraging locations and capture techniques than blue tits. Blue tits were observed 'hanging' from twigs more frequently, and, due to being lighter and more agile than great tits, appeared to be more effective at foraging in the wider variety of plants available in the heterogeneous vegetation of the garden. Although great tits attempted to modify their behaviour compared to studies on their woodland foraging, due to being constrained by their size and morphology, they appeared to lack the ability to forage as effectively as blue tits across the diverse plant species available.

P78 The function of leaf-caching behavior in leaf-cutter ant supply chains

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Leaf-cutter ants *Atta cephalotes* form supply chains to move leaf fragments from their foraging sites to the nest of the colony. The overall efficiency of this transportation system depends on its ability to dynamically integrate the supply rate of the cutter ants, the layout of colony's trail network and the processing rate of the workers remaining at the nest. In this study, we investigated the contribution of leaf-caches (way stations that can form near the production sites, along the trail, and near the nest) to the foraging efficiency of natural colonies. In particular, we assessed the improvement in leaf

uptake and transport when leaf caches were present near the leaf source (vs. dispersed leaves). We also measured the likelihood that leaves dropped along the trail (alone and at caches) were retrieved by foragers as a function of the distance to the nest (proxy for transportation effort), the size of the leaves, the size of the foragers, and the amount of local traffic. The results of our field study will be used to develop a model of the foraging behavior of leaf-cutter ants and will broaden our understanding of complex supply chains in biological systems.

P79 Coal tits prefer hoarding unpalatable food to eating it

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Camilla Blasi-Foglietti, Daniel O'Hagan, Daniel Wales, Donna Wintersgill, Sheren Yeung, Candy Rowe

Hoarding motivation and eating motivation are often linked in food-hoarding birds. For example, food deprivation increases both. In this study, we investigated whether unpalatable food that the birds are less likely to eat is also less likely to be hoarded. Coal tits (*Periparus ater*; hoarder) and great tits (*Parus major*; non-hoarder) were simultaneously presented with small pieces of peanut that had been soaked in 2% quinine solution, and pieces soaked in tap water. Both species spent more time eating the water-soaked pieces than the quinine-soaked pieces. When the pieces were small, this meant that quinine-soaked pieces were less likely than water-soaked ones to be completely eaten. Coal tits then hoarded these quinine-soaked pieces, whilst great tits dropped them after a brief taste. Our results suggest that although quinine acutely reduces the motivation to eat a particular food item, it does not reduce the motivation of food-hoarding birds to hoard that item. Since birds under negative energy budgets are less picky about eating toxic food items, this separation of hoarding and eating motivation is likely to be adaptive to coal tits, which often retrieve food under negative energy budgets.

P80 Nectar-plant flowering and consumption in the Clouded Apollo butterfly (*Parnassius mnemosyne*)

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Clouded Apollo butterflies spend much of their adult lifetime on feeding floral nectar. They might be

important pollinators of several plants on colline meadows. Their nectar plant usage is largely unknown. We aimed to (i) estimate the abundance of nectar plants and their consumption by Clouded Apollos and (ii) describe the dynamics of flowering and consumption for the most frequently used plant species throughout the 3–4-week flight period. Our study site was a 0.6 ha meadow in the Visegrádi-Mts, Hungary. Data were collected in 2009–2012, May. We listed flowering species and estimated their abundance and flowering rate along a random walk each 3 days. Nectar consumption of individually marked butterflies was recorded daily. Clouded Apollos fed on 36 of 66 insect-pollinated plant species. Cumulative consumption rate of the four most frequently used species was 72–89% in different years. Consumption rate varied between and within years and was not directly determined by nectar plant abundance: most of the preferred species were relatively rare, while some abundant plants were not consumed. Butterflies changed from an early-flowering disk flower *Fragaria viridis* to any of the three tube-like flowers *Ajuga genevensis*, *Silene viscaria* and *Dianthus giganteiformis*, as soon as any of them became abundant.

P81 Are sodium channels constraining the evolution of toxicity in *Phyllobates* poison-dart frogs?

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Adolfo Amézquita

Aposematic animals modify the behaviour of their potential predators by using conspicuous signals to advertise secondary defences. In poison frogs, aposematic signalling is correlated with dietary specialisation, higher aerobic scopes, and larger body size. The selective factors that evolutionarily shaped the aposematic syndrome have received much more attention than the intrinsic constraints to its evolution. In toxicity-based aposematism, the lack of resistance of an animal to its own toxins would constrain the evolution of such defenses, since . Hypertoxic frogs in the genus *Phyllobates* bear batrachotoxin (BTX), a potent alkaloid that causes irreversible neurophysiological damage on voltage-gated sodium channels. In an effort to understand the role of BTX resistance in the evolution of aposematism in *Phyllobates*, we built a phylogenetic hypothesis of the genus, mapped traits of the aposematic syndrome on the corresponding tree, and sequenced fragments of the muscular voltage-gated sodium channel involved in batrachotoxin binding. Several amino acid substitutions in sites involved in batrachotoxin

binding were found to coincide with the origin of BTX-based toxicity, but no evidence was found of a relationship between such mutations and strong variation in toxicity and other aposematic traits within the genus *Phyllobates*.

P82 Quantitative Tests of Countershading in Fish

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Innes Cuthill, Julian Partridge

There has been considerable debate over the benefit of the dorso-ventral colouring known as countershading. In terrestrial animals the primary theory is that the gradient will counteract the body's shadow caused by ambient light. In aquatic species, notably fish, countershading is the most common colour pattern, recorded in almost every taxon. However, there is little research on whether the dorso-ventral colour gradient of any marine animal matches the quantitative predictions for camouflage. So whether countershading fish aids crypsis in a world with two distinct backgrounds (seafloor vs. seabed), or creates a uniform colour which blends into the veiling light viewed horizontally, until now has remained plausible but untested.

Using life-size, anatomically accurate, uniformly coloured casts of a range of fish species, we took calibrated photographs underwater using natural light to quantify the pattern of illumination and shade. The image data were used to make quantitative predictions of optimal patterns of countershading under different conditions including depth of occurrence and body shape. We present data to highlight the pattern of deviation from predictions observed in real fish in relation to specific body shapes and depth (light) dependence.

P83 Parsing the roles of blue and orange warning signal components: innate avoidance, learning and generalization

Kimberly Pegram, Arizona State University
Ronald Rutowski

Warning colors deter predators from attacking unpalatable or toxic prey through innate avoidance or learning through sampling. Predators can also generalize a learned response to similar colors. Much of the research on warning colors has focused on long-wavelength colors (e.g. orange and red) and little is known about the role of short-wavelength coloration (e.g. blue) in warning signals, despite its presence in unpalatable animals in diverse taxa. Using Gambel's Quail chicks (*Callipepla gambelii*) as

predators, we tested if blue compared to orange and signals with both colors elicited innate avoidance from naïve predators and were as effectively learned and generalized. Blue did not elicit any innate avoidance, while orange and a combination of both colors were effective at deterring naïve predators. Predators learned to associate unpalatability with orange more quickly than with blue or blue and orange in adjacent patches. Predators exhibited asymmetrical generalization, in which birds were more likely to generalize from the color they learned as unpalatable (conditioned stimulus) to orange prey and prey displaying both colors than blue prey. We conclude from our experiment that orange is likely a more effective warning color, but blue can still be learned alone and when displayed adjacent to orange.

P84 Increased turbidity alters perception of risk in guppies

Helen Kimbell, University Of Hull

Human impacts in aquatic systems often result in increased turbidity either through algal blooms (caused by eutrophication), or sedimentation (caused by urbanisation, deforestation and increased rainfall). This degrades the visual environment, which in turn can influence the ecology and behaviour of aquatic organisms. Many fishes rely strongly on vision for a number of important behaviours including shoaling with conspecifics (an important anti-predatory behaviour) and detecting and responding appropriately to predators. We exposed shoals of guppies to increasing levels of turbidity and assessed the cohesiveness of the shoal, determined by averaging the distances between individual fish. We then exposed shoals to a simulated avian predation attempt and recorded escape manoeuvres and shoal cohesiveness immediately after the attack. At higher turbidity levels fish formed less cohesive shoals. Individuals within the shoal were also found to be less active in turbid water compared to clear. Turbidity also influenced how fish responded to an aerial predation attempt; no difference in shoal cohesion was detected, however individuals in clear water responded more strongly to predation attempts by swimming faster and further away. Fish in turbid water displayed reduced anti-predator responses, appearing to show a reduced perception of risk which could in turn affect predator-prey interactions.

P85 Countershaded camouflage patterns in simulated environments

P. George Lovell, University Of Abertay And University Of St Andrews
Olivier Pennachio, Graeme D. Ruxton, Innes C. Cuthill, Julie M. Harris

Animal camouflage cannot be studied without reference to both the environment in which the animal lives and to the animal from which it is trying to hide. In countershading, animals present a darker surface towards the sun (generally dorsal) and a lighter surface away from the sun (generally ventral). While reflectance varies across the body, radiance (combination of illumination, reflectance and location) appears uniform. There are at least two accounts of how countershading may work. First, through *background matching* (BM) different views of the animal are reliably associated with different backgrounds, so favouring different coloration (e.g. viewed from below, the light sky; from above, the dark ground). Second, through *obliterative shading* (OS), 3D cues to shape, from self-shadowing, are minimised. Here we use computer graphics to explore the differences between optimal background matching and obliterative shading in rendered scenes that allow precise control over illumination and viewing conditions. We find that variations in the light environment (sunny or overcast) influence patterns of shading; however the cost functions (background matching or self-shadow reduction) do not.

P86 Behavioural responses in foraging grey squirrels to auditory playbacks of competitors and predators.

Kimberley Jayne, University Of Exeter
Stephen Lea, Lisa Leaver

Studies of caching behaviour with corvids have revealed that in order to sequester food and reduce its theft, individuals appear to modify their hoarding behaviour if conspecifics are present and appear sensitive to what potential competitors can see. In addition, a few field studies have reported that some mammalian scatter hoarders show similar behaviour. For instance, grey squirrels have been found to adjust their caching behaviour in the visual presence of conspecifics and after being pilfered. Furthermore, foraging, caching and pilfering behaviour are also likely to be affected by the presence of nearby heterospecifics, including competitors and predators, but there is not as much research in this area. In our current study, we observed the behaviour of naturally foraging grey

squirrels in urban parkland across Devon, and manipulated the perceived presence of conspecifics, heterospecific competitors (corvids) and predators (raptors and canids) through auditory playbacks. Differences were found in the behavioural responses of grey squirrels during the different playback conditions, particularly vigilance and distance to safety, but the effects seemed to be short-lived. We discuss how during a season of high food competition, the changing demands of the environment may affect competition for resources, pilferage risk and predation risk.

P87 Geographically distant populations of Great Tits behave differently towards aposematic prey

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Variation in predator behaviour towards aposematic prey has been studied at interspecific and individual levels, but inter-population differences have been neglected. It could be expected that predator populations inhabiting environments with less diverse prey communities are more neophobic than those living in complex environments, and that different levels of neophobia interact with avoidance learning affecting behaviour towards aposematic prey. We compared the behaviour of wild-caught great tits (*Parus major*) from Bohemia (Czech Republic) and Central Finland towards aposematic red-and-black firebug (*Pyrrhocoris apterus*), non-aposematic brown-painted firebugs, novel objects and novel palatable non-aposematic prey (blue crickets). Finnish birds took more time to start exploring novel objects, and hesitated longer than Bohemian birds before resuming feeding in their vicinity. Latency to attack blue crickets did not differ between the two populations and was not correlated with the attitude towards novel objects. Tits from the Bohemian population mostly avoided aposematic firebugs and attacked brown-painted ones. Finnish birds were more likely to attack both firebug forms, and their individual attack latencies were correlated with latencies of attacking blue crickets. The rate of avoidance learning was not affected by firebug coloration, but Finnish birds killed more firebugs during avoidance learning. Funded by CSF-grant P505/11/1459.

P88 A rabbit's tail: Conspicuous rump patch causes predator confusion

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Prey animals display adaptive coloration which influences the predator-prey dynamic. Rhythmic tail-flashing occurs when a prey animal is fleeing with high speed from a predator, and its conspicuous white tail patch creates a blinking effect because of the fast rhythmic motion. This widespread phenomena (e.g. in ungulates, rabbits and hares) seems maladaptive because it provides a highly visible target for the predator. In terms of evolutionary function, there is no theory satisfactorily explaining on why rhythmic tail-flashing occurs during flight. We propose a new predator confusion explanation. Predators pay more attention to the 'blinking-tail' stimulus emerging from the rhythmic motion of the running prey than to the non-conspicuous rest of the prey's body. Predators lose vital time when the prey is making a sharp lateral turn and thereby the conspicuous signal of rhythmic tail-flashing suddenly disappears. We tested this hypothesis with 24 human 'predators' playing a computer game where they were asked to repeatedly 'follow' a fleeing 'rabbit' under two conditions: (1) with and (2) without a rhythmic flashing tail. We found that the presence of a flashing tail significantly reduced the number of correct decisions.

P89 Moving fast and deeper in the night: Anti-predatory behaviour of red deer hinds

Francisco Ceacero, Czech University Of Life Sciences
Enrique Paricio, Andrés J. Garcia, Tomás Landete-Castillejos, Laureano Gallego

In the Iberian Peninsula red deer is mainly active at dusk, keeping certain activity more during the night than during the day. Predation risk has been suggested as the principal factor determining this activity pattern. Along one year, a 4 locations camera trapping experiment was conducted in a fenced 900 ha protected area in Albacete (Spain). Red deer were attracted by multi-mineral supplementation settings. 5407 sets of 3 pictures each were analysed, 98.6% of the animals detected were red deer, and 1884 event of different length were identified. Single males and females, groups of males, group of females (with calves) and mixed groups were identified. Data was analysed using circular statistic (Oriana 4.0), showing that all grouping types showed the same mean peak of activity (around 22:25 solar time) except female groups, which showed it close to midnight ($P < 0.001$ in Watson's U^2 tests comparing distribution of the data for each group type). Rayleigh test confirmed not random distribution ($P < 0.001$ in all group types). Among groups, those composed only by females

spent also lower time around the feeders than males and mixed groups. All together support that activity patterns of Iberian red deer females with calves is related to anti-predatory strategies.

P90 Startle display in the European swallowtail butterfly as a secondary defence against attacks from great tits

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Stephan Eriksson, Sven Jakobsson, Christer Wiklund

Many animals reduce the risk of being attacked by a predator through crypsis, masquerade or, alternatively, by advertising unprofitability by means of aposematic signalling. Behavioural attributes in prey employed after discovery, however, signify the importance of also having an effective secondary defence if a predator uncovers, or is immune to, the prey's primary defence. In butterflies, as in most animals, secondary defence generally consists of escape flights. However, some butterfly species have evolved other means of secondary defence such as deimatic displays/startle displays. The European swallowtail, *Papilio machaon*, employs what appears to be a startle display by exposing its brightly coloured dorsal wing surface upon disturbance and, if the disturbance continues, by intermittently protracting and relaxing its wing muscles generating a jerky motion of the wings. This display appears directed towards predators but whether it is effective in intimidating predators so that they refrain from attacks has never been tested experimentally. In this study we staged encounters between a passerine predator, the great tit, *Parus major*, and live and dead swallowtail butterflies in a two-choice experiment. Results showed that the dead butterfly was virtually always attacked before the live butterfly, and that it took four times longer before a bird attacked the live butterfly. When the live butterfly was approached by a bird this generally elicited the butterfly's startle display, which usually caused the approaching bird to flee. We also performed a palatability test of the butterflies and results show that the great tits seemed to find them palatable. We conclude that the swallowtail's startle display of conspicuous coloration and jerky movements is an efficient secondary defence against small passerines.

P91 Lifespan development of attentiveness in domestic dogs

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Attention is pivotal to perception, cognition, working memory and executive control in all animals, and therefore its changes over their lifespan influence development and aging of all of these functions. Since domestic dogs live and work together with people, the attention they pay to humans and to their non-social environment strongly determines how dogs engage in interactions with humans and which roles they are suited for.

In this study we set out to investigate the lifespan development of attentiveness of pet dogs in naturalistic situations. We tested 145 dogs (0.5 - 14 years) with humans and with objects or food as attention attractors in order to assess their attentional capture, sustained and selective attention while controlling for their sensorimotor abilities. Our results indicate different developmental patterns when watching a human or a moving object, which may be explained by different life-long learning processes about such stimuli. During begging (alternating eye-contact with a human or looking for small food pieces on the floor), we found that dogs' selective attention and sensorimotor abilities peak at 3 - 6 years. This study is one of the first attempts assessing the age-related changes of attention in non-human animals across their lifespan.

P92 Ontogeny of stimulus enhancement in young corvids.

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Social learning is considered a cheap way of obtaining information about relevant features in the environment. However, information provided by others may not always be reliable, raising the questions if and when animals can come to tell apart reliable from unreliable demonstrations. We here tested this idea in young ravens (n=8), as they are renowned for using social information in various forms of object manipulation, including caching. We first investigated the predisposition of fledged ravens to show stimulus enhancement, subjecting individuals to a human experimenter touching specific objects once a week. As expected, birds readily showed a significant preference for handling those items that had just been touched. Next, we subjected birds to two types of (novel) human experimenters, one who provided reliable information about cached food by touching the object under which food was hidden, whereas the other one always touched the object under which no food was hidden. All ravens quickly succeeded in

the reliable condition but none of them reached significance in choosing against the non-reliable demonstrations in the course of 120 trials. We discuss whether ravens at this age cannot overcome the power of enhancement or cannot distinguish between reliable or non-reliable individuals.

P93 Sequence learning and traplining in hummingbirds

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T Andrew Hurly, Susan D Healy

Hummingbirds, like other pollinators, revisit flowers after they have refilled. To do so, birds may visit flowers in a spatial sequence or in a trapline. Although the ability of these birds to learn where, which and when flowers are rewarded is now well documented, it is not clear whether the birds forage in sequences. In a first experiment wild free-living rufous hummingbirds made more mistakes when visiting the intermediate flowers within the sequence than they did to the first and last flowers just as animals learning sequences in the laboratory do. In a second experiment, we trained birds to follow a spatial sequence of flowers according to a reliable temporal pattern. We will compare rates of learning spatial sequences relative to spatial sequences that have a temporal component. This latter is what traplining animals are expected to follow, although there are very few data on animals actually doing this in the wild.

P94 Effect Of Spinach Administration On Cognitive Behavior-Related Cholinergic Pathway In Rats

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Background: *Spinacia oleracea* Linn. (spinach) is a rich source of vitamins, especially folate, which is necessary for brain action. Operant conditioning technique is a type of learning in which the likelihood of a behavior is increased or decreased through rewards and/or punishments. This method deals with cognitive thought process. Discrimination between conditions occurs when a subject learns to respond to only one stimulus and inhibit the response to all other stimuli.

Objective: To determine whether spinach could improve cognitive impairment induced by scopolamine via operant conditioning system.

Material and Methods: 24 male Wistar rats were well trained the operant behavior in operant conditioning chambers. They were then randomly divided into four groups; 250, 500, 1000 mg/kg of spinach, and control. Rats were exposed to a 30-min session of the operant acquisition procedure after 30 minutes of scopolamine (an anticholinergic drug) injection. The operant behaviors of each rat were recorded under fixed ratio (FR) and variable ratio (VR) conditions.

Result: Spinach at 250 mg/kg significantly reversed the learning and memory impairment induced by scopolamine under both FR and VR conditions.

Conclusion: Spinach could promote the brain functions, especially learning and memory involved cholinergic pathway.

P95 Behavioural and physiological effects of finely-balanced decision-making

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It is likely that as decision-making becomes more complex or difficult, it is also more stressful. To explore how choice difficulty affects behaviour and physiology during decision-making, we used a titration methodology to design finely-balanced (and hence more difficult) decisions in chickens. During training, fifteen hens chose six (Q6) pieces of sweetcorn, rather than one (Q1) at least 90% of the time, *via* an unweighted push-door in a T-maze apparatus. This was defined as an unbalanced decision. During the titration phase a force was applied incrementally to the Q6 door, increasing preference for Q1. When each goal was chosen with approximately equal frequency, this was defined as a balanced decision. Each individual was then subjected to a further set of five balanced and unbalanced decisions in a pseudo-random order, during which some behavioural and physiological measures were taken during baseline and goal-viewing periods. The frequency of goal choice during balanced (Q1-36%, Q6-59%, no choice-5%) and unbalanced (Q1-11%, Q6-88%, no choice-1%) decisions, suggests we had obtained decisions of varying, quantifiable difficulty. Other behavioural and physiological measures were unaffected by decision category. However, Q1 choice outcome was associated with a higher heart-rate during the baseline period in unbalanced decision-making.

P96 NF-kappaB transcription factor is required for fear memory consolidation in fish

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Although it is generally accepted that memory consolidation requires regulation of gene expression, only a few transcription factors, including NF- κ B, have been clearly demonstrated to be involved in this process in mammals. However, there is no evidence of the participation of NF- κ B in memory consolidation processes in fish. Here, we demonstrate that inhibition of NF- κ B induced memory impairment in the cued fear conditioning paradigm in fish (*Leporinus macrocephalus*). Immediately after training (that consist of pairing an unconditioned and a conditioned stimuli, alarm substance and light, respectively) we infused intracerebroventricular κ B decoy, an inhibitor of NF- κ B consisting of an oligonucleotide that contains the consensus sequence. The retention test (exposure only to the conditioned stimulus) was performed 24h after training. When injected immediately after training, κ B decoy impaired memory consolidation since the animals don't display freeze behavior during test. In contrast, a one base mutated κ B decoy (control) had no effect and the animals displayed freezing behavior and a significant reduction in the locomotor behavioral endpoints analyzed with $p < 0.05$ (time duration, distance traveled and time spent in the top) during test. These results provide the first evidence that NF- κ B activation is necessary for memory formation in fish such as in mammals.

P97 Ecological relevance determines arginine vasotocin influence on cleanerfish learning abilities

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According to an ecological approach to cognition, a species ability to solve any task depends on its evolutionary history and on its specific ecological selective pressures. Proximate mechanisms are required to establish individual social competence, which optimizes social behaviour in relation to ecological significance. Here we show that arginine-vasotocin (AVT), a neuropeptide implicated in the regulation of social behaviour, is directly linked to the learning performance of the cleaner wrasse (*Labroides dimidiatus*). We tested the influence of this neuro-hormone upon these cleaners ability to solve two problems that varied in ecological relevance (an ecologically relevant task and an ecologically non-relevant task). Cleaners learned to

solve the first task more rapidly than the second one; however the influence of our tested neuropeptides differed considerably between problems. While blocking the effects of AVT increase these cleaners learning abilities, these effects would only stand for a task that reflects their specific learning rules under natural conditions. In the absence of ecological relevance, AVT was only responsible for a significant decrease of their learning aptitude. Our results show that neuropeptides (AVT and isotocin- IT) pathways should be directly implicated on the building of these animals' social cognitive competence and complex behavioural output and should also have a prominent role in the learning of key behavioural decision rules associated to their ecological context.

P98 Are distal and proximal visual cues equally important for spatial learning in tPA-deficient mice and their wild-type counterparts?

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Background: Evidences indicate that rodents use visual cues for spatial navigation, and that distal cues are more useful than proximal ones because of their more stable configuration. Glutamate is the main cerebral excitatory neurotransmitter and is largely involved in spatial memory processes. Interestingly, tissue-type Plasminogen Activator (tPA) is a neuromodulator of the glutamatergic neurotransmission also involved in spatial learning. Accordingly, the aims of this study were to investigate: i) The spatial abilities of wild-type mice (*Mus musculus*) with proximal and/or distal visual cues; ii) The possible role of tPA in spatial learning. **Methods:** We used a two-trial place recognition task with visual cues positioned inside of the maze (proximal) and/or on the walls of the testing room (distal).

Results: Wild-type mice are able to learn with both types of visual cues presented separately and an overshadowing of the proximal by the distal cues occurs when the two types of cues are available simultaneously. Interestingly, tPA-deficient mice are unable to solve these tasks by using distal cues.

Conclusions: The data show an overshadowing of visual cues during a spatial learning task and highlight an interesting phenotype in tPA-deficient mice, suggesting processing deficiencies in the entorhinal cortex where tPA is normally expressed.

P99 Behavior in unknown space and saliva testosterone levels in pigs

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Juraj Petrak

Aim of research was investigate relation between testosterone levels (TSL) and behavior in pigs in unknown space. We have tested 29 pigs (14 females and 15 males) with weight from 18.5 kg to 27.5 kg. Males were castrated during 2nd week after birth. Behavior in unknown space was tested in room for Open field test. Orientation reaction was evaluated by time spent standing, moving and lying near doors and in other part of room and by latency of defecation. Saliva samples for testosterone levels analyses were taken in calm state before testing and immediately after open field test. TSL were measured by ELISA method, commercial kit DiaMetra Testosterone saliva was used. Optical absorbance was measured by Microplate Reader Model DV 990BV4, UniEquip Deutschland. TSL varied from 78.91 pg/mL to 1131.06 pg/mL in calm state and from 93.12 pg/mL to 1589.36 pg/mL after test. We have not found correlation between TSL and time spent near door. We have found correlation between TSL and ratio of total duration of time spent near door or room ($r = 0,477$, $P = 0,009$). Mean duration of stop near door was higher in animals with higher TSL in stress ($r = 0,432$, $P = 0,019$).

P100 The appetitive effects of amino acids on learning in the honeybee (*Apis mellifera*.)

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Geraldine Wright

The honeybee gustatory system is comparatively simple and relatively little is known about what these insects are able to taste. Adult worker honeybees spend a large proportion of their time foraging for nutritional resources and amino acids are used both by themselves and colony members. Amino acids, the second most concentrated components of floral nectar, could provide a good source of protein to the honeybee diet. This study explored the gustatory sensitivity of honeybees to a number of amino acids using behavioural assays, with a future aim of linking gustatory receptors to their ligands in bees. We found that whilst honeybees are highly tuned to the detection of carbohydrates, this sensitivity was compromised following amino acid pre-feeding. Subjects demonstrated slower acquisition and reduced response probability in a learning paradigm toward a sucrose-only reward having received an amino acid solution 24hours earlier. Nutritional state was also found to influence gustatory sensitivity towards amino acids in honeybees. There is no clear split

between amino acid groups with learning responses differing between each amino acid solution, but it is clear that pre-feeding history and existing nutritional state has an effect on how bees respond to the presence of amino acids in reward solution.

P101 Scrub-jay re-caching cannot be attributed to stress.

James Thom, University Of Cambridge
Nicola Clayton

Western scrub-jays (*Aphelocoma californica*) live double lives, hoarding food for the future while raiding the stores of other birds. One tactic scrub-jays employ to protect their stores is "re-caching" - relocating caches out of sight of would-be thieves. A recent computational model replicates existing data without resorting to complex social cognition. The "Stress Model" asserts that re-caching is a manifestation of a general drive to cache, elicited by stress, rather than a desire to protect existing stores. Here, we present evidence strongly contradicting the central assumption of the model: that stress drives caching irrespective of social context. In Experiment (i) scrub-jays preferentially relocate items that they were watched hiding. In Experiment (ii) we find no evidence that stress increases caching. The Stress Model cannot account for scrub-jay re-caching in light of these findings.

P102 Testing cognitive capacities: Differences between individual and social group settings?

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Jutta Schneider

Testing animals in cognitive tasks individually limits distractions to the subjects during the task so that they can focus their full attention on the problem. However, such a test situation may only represent a maximal but not a realistic performance. Under natural conditions, particularly in group-living animals, individuals faced with a novel problem will have to cope with distractions from conspecifics and an often brief time frame for decision-making. To assess the validity of data gathered from parrots when tested in social groups, we compared the performance of two captive groups of orange-winged amazons (*Amazona amazonica*) that were tested singly or in groups on seven cognitive tasks. Despite the differences in testing environment parrots from both groups performed similarly on cognitive tasks. However, we found that the motivation to participate in the tasks was significantly higher for the subjects tested in their

social group. The latency until first touching the apparatus varied between few minutes for birds in a social context, and several days for singles. These findings suggest that, particularly in neophobic species, subject's missing willingness to participate in studies with individual settings may reflect personality traits such as boldness and fearfulness rather than the level of subjects' cognition.

P103 Development and automation of a test of 'executive function' in zebrafish

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Caroline Brennan

Zebrafish are a commonly used model organism in developmental biology. Recently, however, their utility as a model in behavioural neuroscience is beginning to be realised. Their progress in this regard is hampered only by a lack of validated behavioural assays. Deficits in executive function are found in a number of psychiatric disorders. Here, we describe the development of an assay of executive functioning in adult zebrafish (5-choice serial reaction time task), able to test aspects of impulse control and attention. We describe the process by which we validated the task using pharmacological manipulations, and subsequently designed and validated a fully automated version of the assay to test multiple fish simultaneously and with a greater degree of environmental control. We will also describe some initial findings relating to genetic contributions to fishes' performance in the assay, including the potential for heritability of performance characteristics.

P104 Stimulus- and subject-specific effects on the behavioural habituation/dishabituation test in Bengalese finches.

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To examine animal cognition for familiarity and novelty, discrimination tasks with behavioural reinforcement have been usually applied. Recent studies reported that spontaneous behaviours, such as vocalizations, could be available to detect a discriminative performance between familiarity and novelty in songbirds using a habituation/dishabituation method. However, those studies assigned only a few stimulus sets for all subjects, which might cause a problem of pseudoreplication. Therefore, we tried to expand

the method into more universal condition using a variety of stimulus sets. We used Bengalese finches and collected seven unfamiliar conspecific songs as a stimulus pool. A habituation song was randomly chosen from the pool for each subject and the bird was exposed to playback of the song repeatedly over 2 hours, then, the same habituation song and another novel song, which was randomly chosen from the stimulus pool as well, were presented respectively. We compared the number of call productions during playback of those two songs. Although the number was greater for the novel song than for the habituation song in some birds, the trend was not consistent when another stimulus set was used for those birds, suggesting the method may be not independent from stimulus- and subject-specific effects.

P105 Is the reaction on pointing an indication for the presence of a theory of mind?

Jeroen Van Rooijen

The idea that chimpanzees could react to pointing because they are closely related to man is anthropocentric. The idea that dogs react to pointing because they are since long domesticated by man is anthropocentric too. Dogs react to pointing because they have (like man, but unlike the chimpanzee) a cooperative foraging strategy. Further dog pointing gestures resemble human pointing gestures (unlike, for instance, bee pointing gestures).

The reaction to pointing is in dogs a species specific behaviour pattern (and, because this behaviour is found in all cultures, in man probably too). This behaviour is found throughout the animal kingdom (e.g. in ducks and sticklebacks). According to the principle of parsimony it is not always justified to assume that this behaviour is an indication of a theory of mind. Sometimes it is obvious that this behaviour can not be such an indication. For instance, naïve poultry chicks (without experience with food or finger) react with eating to a human finger pointing towards the food. Probably this finger is a model for the pointing beak of the mother hen. This reaction is the result of natural selection during the phylogeny, it cannot be an indication of a theory of mind.

P106 Jackdaws, crows, and stones - social learning in corvids.

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Ira Federspiel, Alice Auersperg, Alex Kacelnik, Auguste von Bayern

Social learning refers to learning resulting from the observation of the actions of other individuals. Among many social learning mechanisms, imitation is the most complex one and involves a precise copying of a complex, often multi-step, action performed by another individual. This process was so far observed only in a limited number of species, majority of which include primates. However, other large-brained, long-lived, social species, such as corvids, may also be a candidate employing imitative social learning in their daily lives. In a series of experiments we found that jackdaws (*Corvus monedula*) and New Caledonian crows (*Corvus moneduloides*) can learn how to solve a novel problem task by watching a conspecific performing a multi-step action. The action involved picking up a stone, carrying it to an apparatus, lifting it up, and releasing it into the mouth of a vertical tube, which would release a reward. One out of eight jackdaws, and two out of five New Caledonian crows succeeded. This result demonstrates that copying complex multi-step actions is not only limited to the primate lineage but may also be found in other distantly related species who share a similar socio-ecological way of living.

P107 Capuchin monkeys' response to intentional unfair offers in a two-choice ultimatum game.

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Evolution of cooperation is supported by inequity aversion. Recent evidence has demonstrated that humans are not the only species that respond negatively to disadvantageously unequalized outcomes. Here we investigated whether capuchin monkeys are sensitive to others' unfair intention, as well as the unfair result itself, in a two-choice ultimatum game. The proposer monkey offered one of two options of food reward and the responder monkey could either accept or reject the offered option. If the responder accepted it, both participants received the reward. On the other hand, if the responder rejected it, neither the proposer nor the responder obtained the reward. As a result, the responders tended to reject the unfair offer when there was a proposer more often than when there was none. Moreover, they rejected the unfair offer at the cost of the obtainable reward significantly more often when the proposer chose the option intentionally than when the proposer had no other option to choose. These results

suggest that capuchin monkeys may understand others' unfair intention. Sensitivity to intentional unfairness may be shared by at least one cooperative non-human primate species.

P108 Wild and domesticated zebrafish, *Danio rerio*, use different social learning strategies

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Individuals in some species learn information about food, predators, and potential mates indirectly from conspecifics, without taking unnecessary risks by learning directly for themselves ('social learning'). Social learning should be strategic rather than indiscriminate, and although it is often suggested that animals should show conformity ('copy the majority strategy'), there are surprisingly few tests of this idea. We tested whether timid, wild-derived zebrafish become bolder after socially interacting with bolder, domesticated fish (and vice versa) by manipulating their group composition. We found that wild zebrafish exposed to domesticated fish were bolder than controls, whereas domesticated fish exposed to the more timid, wild zebrafish did not differ in their boldness score compared to controls. The changes in the behaviour of wild fish persisted after the non-focal groups were removed; however, we found no evidence for conformity. Our findings indicate that zebrafish use social learning for assessing risk and adapt their social learning strategies to the costs of a perceived risk. Future studies should be able to utilize this model species to incorporate genetic and genomic tools to study the development and evolution of social learning.

P109 Exploratory behavior of the common shrew (*Sorex araneus L.*) in the open field

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Spontaneous behaviour of eleven yearling shrews captured from wild was recorded in the open field test for five minutes daily. The trials were conducted on the clean arena and on the arena previously used by a conspecific shrew. Horizontal locomotion, crouching in the corner, rearing against a wall and in the open space (unprotected) were distinguished as patterns for quantitative analyses. Freezing, grooming and marking behaviours were observed rarely. Locomotion was quantified with the VideoTrack system that drew the path, calculated its

length and velocity. Only some, “socially active” individuals changed their activity on the scent-marked surface, significantly reducing their path length, time spent in horizontal movement and the number of unprotected rearings. On the clean surface these “socially reactive” individuals took longer time from releasing till the first active movement, spent less time in horizontal movements, travelled shorter distance and with lower velocity, making less unprotected rearing. All shrews were released after experiments. Our results document behavioral diversity of reactions of the common shrews to social cues, in particular to scent markings of a territory. These differences may influence dispersal rate and territoriality of the yearling shrews.

P110 Information Seeking in the Rat

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William Roberts

Metacognition is awareness of what one does and does not know. Students given a choice between studying material they have learned well and material they have learned poorly prefer to study the less mastered material (Metcalfe, 2009). Recent studies suggest that primates also know about the state of their own knowledge and will seek unknown information to complete a task (Call & Carpenter, 2001; Hampton et al., 2004). We used a radial arm maze to look for metacognition-like behavior in rats. Each maze arm had a bulb mounted on it to serve as a signal light. Rats were trained to go to whichever arm was lit on a trial for reward. They then were trained to press a bar in the maze hub that led to immediate food reward and turned on a light in one randomly chosen arm of the maze. Once the rats learned to press the bar, the reward for bar pressing was discontinued. We report on the rats’ readiness to press the bar for information about the location of reward under conditions that varied the presence or absence information and amount of information to be gained.

P111 Gender effects on performance of domestic dogs (*Canis familiaris*) in a problem solving task.

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Heiko G. Rödel, Thierry Bedossa, Séverine Belkhir

Gender differences in cognitive processes are well known in various mammal species. Given the strong focus on gender effects in studies on e.g., spatial orientation, memorization, lateralization and problem solving abilities in humans and other

mammals, surprisingly little is known on such gender differences in dogs. We conducted such a study, focusing on a situation, where pet dogs had to open a box in order to obtain food reward. We studied 47 subjects (24 females, 23 males) and we compared their success in this task. Our findings show a clear gender effect on individuals’ ability to solve this problem. Males were significantly, by 45 % more successful than females in opening this box, measured across three trials. However, the latency to success did not differ between both sexes. In addition, the study was controlled for differences in training method, dog body mass and parameters of the owner. We propose that sex differences might be one of the major contributors to individual differences in pet dog performances during cognitive tasks, although its relative importance with respect to other factors, such as the dog’s temperamental traits or the presence of its owner might be explored in future studies.

P112 Dogs use physical cues about object presence to overcome associative learning effects: a study of search behaviour with transparent occluders

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Carlo De Lillo

When presented with a search task designed to contrast the effects of associative learning and object permanence, dogs are guided more by reward history than by cues provided by a human hiding bait (Ashton & Lillo, 2011). Here, we assessed dogs’ ability to use physical cues to overcome the effects of associative learning. Ten dogs repeatedly found occluded bait in one of two different locations before facing three reversal conditions which required searching transparent cups with: 1) a baited cup in the previously unrewarded location and an empty cup at the previously rewarded location; 2) a baited cup at a new location and an empty cup at the originally rewarded location; 3) a baited cup at the previously unrewarded location and an empty cup at a new location. Associative effects predict lower reversal performance in condition 1 that requires both the inhibition of previously rewarded responses and disinhibition of previously unrewarded ones. An equal performance emerged in all reversal conditions, suggesting that dogs override the effects of previous reward contingencies on the basis of the information provided by the detection of the bait in the transparent cups. This suggests that dogs benefit more from physical cues than human gestures, when adapting to change.

P113 Puzzle boxes for the kea's puzzle mind: exploration and mechanical problem solving in a mountain parrot.

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Michael Eigster, Mark O'Hara, Ludwig Huber

Playful object exploration, if assembled with some form of advanced sensorimotor intelligence and neophilia provides an excellent surrogate to produce environmental variation from which functional characteristics and novel solutions can be determined actively. Here we show that keas, New Zealand mountain parrots, possess such an assembly of traits. We will review a number of mechanical problems we offered to the keas in lab and field and we will focus on a task that is a variation of a trap table with a slanted platform where the birds were required to roll down a ball at the site with no trap in order to retrieve a reward. This task allowed us to distinguish between explorative and reward-directed behaviour when the birds targeted accurately on the peanut and when they did not. The results show that birds that used stick-tools in other contexts performed better, but most importantly the data show how the birds explored the novel traps and thereby improved in different conditions of the task contrary to the trap tube paradigm we tested earlier. This highlights the importance of considering exploration specifically in cognitive tasks in such explorative species.

P114 Large quantity discrimination in newborn guppies (*Poecilia reticulata*)

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Rudimentary numerical abilities have been reported in a wide range of animal species, including fish. Despite recent studies have shown that adult fish can spontaneously select the larger group of conspecifics, this ability seems to be limited at birth because newborn guppies are unable to discriminate among quantities of peers larger than 4. The present study aims to investigate whether newborn guppies can be trained to discriminate between large quantities. Subjects were required to discriminate between groups of dots with a 1:2 ratio. To dissociate the relative contribution of number and continuous quantities (i.e., area), fish were tested in three Experiments. In Experiment 1, number and continuous quantities were simultaneously available (7 vs. 14), in Experiment 2 only number was available (7 vs. 14) and in Experiment 3, the number was made irrelevant (10

vs.10; 1 vs. 1) but the ratio between cumulative area of each pair was 0.50. Subjects successfully solved the tasks in Experiment 1 and 2, providing the first evidence of large quantity discrimination in newborn fish. No discrimination was found in Experiment 3. A comparison with the onset of numerical abilities in the shoal-choice tests suggests that training procedure may enhance the salience of numerical information.

P115 Can Rats Travel Into the Past? Object Discrimination In the Context of What, Where and When

Katarzyna Piwko, University Of Warsaw

Episodic-like memory in rats, the integrated knowledge of what, where, and when, was recently interrogated by several studies. My aim was to validate the preference for the new (what-when) and the dislocated (what-where) objects in an eight-arm radial maze in ten consecutive phases. In this study, a group of ten male Wistar rats was presented with three types of objects. Animals received two training phases and a test phase. In the training phases each individual was presented with two copies of object - object A in phase 1 and object B in phase 2. In the test phase two arms remained empty for each rat, while the other contained two new objects (C), a dislocated and a non-dislocated copy of A and of B alike. Each set was individualised and random.

Data was analyzed using bootstrapped analysis of variance and NIR post hoc test. Results show that the new objects were more often explored than A objects (BCI: 0.124-0.940) and were explored for a longer time than A and B (BCI: 1.86158-7.25381 and 2.46398-7.49567, correspondingly). Difference between dislocated and non-dislocated objects did not prove significant.

Our results provide strong evidence for the knowledge of what-when and some implications for future research.

P116 Cue Dimension and Strategy Use in the Mid-Session Reversal Procedure

Neil McMillan, Western University, Canada
Chelsea Kirk, William Roberts

In a visual discrimination task with a reversal of reward contingencies at the session midpoint, pigeons make anticipatory and perseverative errors near the reversal due to interval timing from the start of the session. Fewer errors are made in a spatial task, suggesting the pigeons are using a more

optimal strategy, and we have shown similar results in rats. In a new task, pigeons responded on a three-choice discrimination (either visual or spatial) task, over 90 trials with two reversal points (after trials 30 and 60) during the session. This procedure allowed us to observe how pigeons learn the structure of the task. In probe sessions, the first correct stimulus was correct until trial 60 and the remaining two stimuli were correct after trial 60; birds could thus opt to use either order (the second correct stimulus) or time (the third correct stimulus) on these probe sessions. The results will be discussed in the broader context of choice behavior on the midsession reversal procedure.

P117 Role of artifacts and niche construction in learning to use tools: Nut-cracking in Wild Bearded Capuchins

Yonat Eshchar, University Of Georgia
Briseida de Resende, Patricia Izar, Elisabetta Visalberghi, Kellie Laity, Michele Verderane, Carlos Carvalho, Dorothy Fragaszy

Wild bearded capuchins (*Sapajus libidinosus*) use stones to crack palm nuts on anvils. Juveniles spend years engaging with nuts, stones and anvils, before they master this skill. We are conducting a longitudinal study to determine the influence of others' percussive activity, including physical remains of cracking, on juveniles' behavior. We present data from our first period of data collection. We have recorded the percussion activity and other activities of 11 young monkeys, and concurrently the nut-cracking activities of other group members. We report an age-dependent increase in different aspects of nut-cracking behavior – *e.g.*, manipulating the nuts in any way ($R^2=0.777$, $p<0.005$) or striking the nut with a stone ($R^2=0.626$, $p<0.004$). No such age-dependency was seen regarding manipulation of other objects ($R^2=0.054$, $p=0.490$).

Linear regression showed that activities related to handling nuts and percussion occur at higher rates near an anvil, where nut debris as well as suitable hammer stones can be found, than away from it ($p < .001$). Given that nut shells are easily portable, the results suggest that the sites and the artifacts present at these sites specifically promote activity relevant to cracking nuts. We suggest that artifacts play an important role in helping juveniles master tool use.

P118 Can parrots generalise conceptual information across novel transfer tasks?

Jayden Van Horik, Queen Mary University Of London
Nathan Emery

Parrots possess disproportionately large brains for their body size, suggesting enhanced cognitive capacities. We therefore investigated whether captive black-headed caiques (*Pionites melanocephala*) and red-shouldered macaws (*Diopsittaca nobilis*) use higher-order cognitive mechanisms to solve a battery of foraging tasks that could either be solved spontaneously or learned associatively. Each task involved a novel transfer problem, revealing whether conceptual information learned from one task was generalised across analogous problems.

Both species spontaneously solved a means-end connected problem, but showed impaired performances when presented with unfamiliar materials. Using a novel Trap Gaps paradigm, subjects required substantial experience to initially discriminate between pulling food-trays through gaps, while attending to the respective width of the gaps and size of the trays. Yet some individuals spontaneously solved the transfer task. In a serial reversal-learning paradigm, subjects trained to high criterions made fewer post-reversal errors than low criterion subjects. High criterion subjects were not impaired by the enhanced associative strength of the conditioned stimuli, but instead used abstract rules to respond to reversals.

Overall, our findings reveal that parrots can generalise conceptual information across novel tasks; suggesting that relatively large brains afford higher-order cognitive mechanisms that allow animals to rapidly respond to novel problems through abstractive experience.

P119 Recognition of individual humans differs between urban and rural house sparrows

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Animals coexisting with humans may benefit from reduced fearfulness and the ability to recognize persons. In this study, we observed the behaviour of captive house sparrows (*Passer domesticus*) in presence of a human to investigate if birds react differently to humans representing different levels of threat, indicating an ability to recognize persons; and whether this ability is related to habitat urbanization. We used latex masks to manipulate the appearance of the experimenter, acting hostile in one mask and non-hostile in another during a training period. In the following tests, we recorded

the birds' responses to these two familiar masks and a third, unfamiliar mask. We found that risk-taking behaviour was highly consistent within individual birds across the three trials, and rural birds were more fearful than urban birds in presence of an unfamiliar person. Rural birds were less fearful from the non-hostile person than from the other two, whereas urban birds made no distinction. Birds from the habitats with lowest human population density showed the greatest difference in response to the three persons. These results indicate that house sparrows can recognize individual humans and this ability is more expressed in rural habitats where people are relatively few.

P120 Planning in 4- to 10-year-old children: the paddle-box paradigm

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The ability to plan an appropriate sequence of actions might be particularly useful during complex problem solving. We used the 'paddle-box', a task originally designed to test the planning skills of non-human great apes, to investigate the development of planning ability in 4- to 10-year-old children (n=172). To succeed, children had to plan an appropriate sequence of 1, 2 or 3 actions (paddle rotations) to retrieve a reward (sticker) from a goal location. Two tasks were presented (6 trials of each) with the order counterbalanced. In the sequential-planning task children could always rotate the paddle with the reward on first and still succeed. In the advance-planning task, children had to pre-position some paddles *before* rotating the paddle with the reward on. Most children of all ages succeeded in the sequential-planning task, as did the non-human great apes we tested previously. In the advance-planning task, only 20.0% of 4- to 5-year-olds solved any 3-step trials, compared with 51.7% of 6- to 7-year-olds and 80.8% of 9- to 10-year-olds. Contrary to our predictions, introducing measures to reduce the inhibitory demands of the advance-planning task (imposing a delay or replacing stickers with tokens) did not improve the children's performance.

P121 Dogs detect human emotions in a two-way choice situation

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Flora Szántha, Ádám Miklosi, Erika Kubinyi

The ability to detect human emotions is among the most popular beliefs about dogs. Studies showed that dogs are able to obtain some information from human emotional expressions, however, only a few studies addressed how these information affect the dogs' behaviour. In our study 80 dogs could choose between two uniform plastic bottles and fetch one of them to the owner after observing their owners' emotional reaction (happy, disgust or no particular emotion: 'neutral') to each of them. The happiness and disgust were expressed by facial, verbal and body gestures, whereas the neutral was expressed only by a blank facial expression. The dogs were assigned to four groups according to the emotion-pair they received: happy-neutral, happy-disgust, neutral-disgust and neutral-neutral (control). Dogs in the control group performed on chance level, whereas dogs in the other groups preferred to fetch the bottle marked with the more positive emotion to the owner. However, their first approach to the targets suggests that they found the happy and disgust expressions equally attractive. According to our results, dogs recognize the valence of human happiness and disgust, and revise their own interest (what they first approach) by fetching the owner's preferred item.

P122 Feathered primates? Performance on the Hamilton Search Task by *Amazona amazonica*.

Victoria Cussen, University Of California, Davis
Joy Mench

Parrots may possess cognitive abilities similar to nonhuman primates, although use of standardized tests would increase comparability of results. We tested *A. amazonica* (n=12) on a spatial memory test used for primates, the Hamilton Search Task, with 3 test phases: pseudo-random location baiting (HST) to assess trial-and-error learning, fixed baiting (SB) to test cognitive flexibility, and single-choice fixed baiting (FSB) to distinguish motivation from inflexibility in SB. The parrots were re-tested after 6 months. Parrots did not select evenly across locations during HST ($X^2 = 228.28$, $p < 0.001$), indicating that, like primates, they fail to learn the pseudo-random baiting rule. However, within-trial error rates decreased across days ($z = -3.6$, $p < 0.0005$). The proportion of SB trials with multiple selections decreased across days ($p < 0.001$) indicating the new baiting rule was acquired, but location avoidance hindered performance ($z = 4.1$, $p < 0.001$). Parrots overcame this location avoidance when there was only one opportunity per trial (FSB) to obtain the reward (exact binomial test, 0.92, $p < 0.0001$) and remembered the task when re-tested ($t = -1.1$, $p = 0.29$). Although individuals differed in

their performance, as a group they were able to learn and retain the task, and showed more cognitive flexibility than primates learning the new baiting rule in SB.

P123 Sequential organization of stone-aided nut cracking by tufted capuchin monkeys.

Eduardo Ottoni, University Of São Paulo
Clara Corat

Stone-aided nut cracking requires the coordination of three elements: the agent must assemble nuts and hammer stones by a suitable anvil. Under naturalistic settings, nut cracking sites, constituted of anvil-like surfaces already containing a hammer stone, can be fairly stable. In an experiment with a semi-free ranging group of tufted capuchin monkeys (*Sapajus* sp), though, we separated these elements, positioning nuts, hammers and anvil in a 10m-radius equilateral triangle. Under such conditions, the monkeys systematically employed a Nut-Hammer-Anvil vertices' visit sequence, first collecting a nut, then the hammer, then carrying both movable items to the anvil, one of the shortest and more cost-effective possible routes. To check whether it resulted solely from a "nut first" strategy or if the monkeys were also taking hammer transport costs into account, in the following experiment we offered a choice between two hammers, one closer to the nuts, but far from the anvil, the other, farther from the monkey, beyond the anvil - but closer to it. The latter, which was the less immediate but more economic choice - was significantly preferred by our subjects (Funding: FAPESP, CNPq, CAPES).

P124 How chimpanzees (*Pan troglodytes troglodytes*) learn to complete sequences of arbitrary symbols

Matthias Allritz, Martin-Luther-Universität Halle-Wittenberg
Joseph Call

Sequence learning has been a widely used experimental paradigm in animal cognition research over the last 30 years. Studies in this field typically seek to inform theories of the cognitive representation of serial order, transitive inference, planning and memory. While many previous studies have aimed at illustrating *what* it is that animals have learned when they successfully perform such tasks (e.g. a chain of stimulus-response units vs. a positional representation of stimuli), this study attempted to document in detail *how* chimpanzees (*Pan troglodytes troglodytes*) gradually learn to

master such tasks. Four chimpanzees (three adult females and one subadult male) were trained to complete sequences of Arabic numerals of different lengths on a touch screen monitor. We investigate which types of errors (i.e. selecting a certain numeral too early) are made at which stage while subjects learn to complete sequences of increasing lengths. Results suggest that many errors can be attributed to a lack of inhibition (e.g. incorrectly selecting the numeral that is closest to the last numeral that was correctly selected) rather than a lack of stimulus discrimination. These results are complemented with reaction time data that suggests that subjects employ a serial rather than a collective search strategy.

P125 Object-object combinations during unrewarded play behaviour in corvids and parrots.

Alice Auersperg, University Of Vienna
Jayden Van Horik, Thomas Bugnyar, Auguste von Bayern

Combinatory actions during unrewarded object play are often considered ontogenetic and phylogenetic precursors of functional behaviour. We established play profiles for three corvids: jackdaws, common ravens and New Caledonian crows (NCCs) and for three parrots: Hahn's macaws, black capped parrots and Goffin cockatoos. One of the corvids, the NCC is a habitual tool user and one of the parrots, the Goffin has the capacity to innovate tool manufacture and use in captivity. The same four activity plates (holes, poles, horizontal & vertical tubes) as well as the same wooden objects of different size, shape and colour categories were offered repeatedly to each species in a group context. We determined the frequency of object-object combinations, up to how many objects were combined, whether the combined items were chosen within same categories (size/color/shape) as well the motor complexity of the object relationships established (eg. free object-object combinations, ring-stacking, inserting, caching). All species except for Hahn's macaws occasionally combined two objects, NCCs and Goffins up to three. Combinations were most frequent and motorically complex in NCCs amongst corvids and in Goffins amongst parrots. During free object-object combinations Goffins combined objects out of the same shape and colour categories more often than expected by chance.

P126 Environmental influences on memory decline in aging mice and humans

Thais C.G. de Oliveira, University Of Western Ontario

Joao Bento Torres Neto, Daniel G. Diniz, Natáli V.O. Bento Torres, Fernanda C. Soares, Liliane D.D. Macado, Cristovam W.P. Diniz

Environmental and age-related effects on memory were analyzed and compared in mice and humans. Aged (20 month old) adult female albino Swiss mice were housed from weaning in either impoverished (I, n=14) or enriched (E, n=15) conditions and were given object recognition memory tests. All tests were video recorded and analyzed with the ANYMAZE tracking system (Stöelting). Time spent in exploration in “former”, “recent”, “displaced”, “stationary” and “context recognition” memory tests was expressed as a proportion of the total exploration time. Institutionalized aged humans, living sedentarily under conditions of poor cognitive and sensorimotor stimulation (IH, impoverished-like conditions, 76 ± 6.9 years old, n=25) were given neuropsychological assessments and compared with an aged control group living in the community with their families (EH, enriched-like conditions, 74.2 ± 4.0 years old, n=17). IH showed significantly lower scores compared to EH in MMSE, Nomination, Phonological Verbal Fluency, Narrative Principal Concepts and Narrative Efficiency. I-mice, similarly, were less able than E-mice to recognize objects in a spatio-temporal context. After six months of multisensory and cognitive stimulation, however, IH performance in neuropsychological tests no longer differed from that of EH subjects except on naming tests.

P127 Body surface area discrimination and quantity judgments by fish

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Both human infants and non-human animals have been shown to be able to discriminate between two sets of discrete elements that differ in number. However, the influence of non-numerical variables has not been always ruled out. Here, using angelfish (*Pterophyllun scalare*), the role played in the discrimination by the surface area of the fish in the stimulus shoals, a non-numerical variable often conflated with numerical assessment, was investigated. The contrasting shoals were constituted by large (5 vs. 10 fish) and small numbers (2 vs. 3 fish), and differences in body surface area of the stimulus fish was minimized using the tpsDig software. Results indicate that discrimination between shoals of different numerical size can be affected by the surface area of

the stimulus shoals. Without controlling for this variable, angelfish spent significantly more time near the larger shoal in both numerical contrasts. When equating surface area, however, fish exhibited no significant preference for either of the shoals (i.e. did not prefer the shoal with more fish). Thus, surface area of the shoals may drive shoal preference in angelfish. Converging with this finding, angelfish also preferred the shoal with the larger surface area when equal number of conspecifics was contrasted (5 vs. 5 fish and 3 vs. 3 fish). Sensitivity to the total surface area of the stimulus shoals indicates that angelfish can make decisions on numerical choices using this non-numerical cue.

P128 Corvids consider relative gain in delay maintenance tasks

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Thomas Bugnyar, Kurt Kotrschal, Claudia A.F. Wascher

Controlling impulsivity towards immediate gratification in favor of a more valuable but delayed alternative is considered a beneficial cognitive skill in foraging and social contexts. Common paradigms to investigate impulsivity are the accumulation and the exchange of food, where subjects can either take an immediately available but smaller/less-preferred food, or wait for a larger/more preferred option. Non-human primates performed well in both tasks, with subjects tolerating delays up to several minutes. Studies on carrion crows and common ravens revealed that they act comparably to primates for a more preferred food quality, but not quantity, in exchange tasks. Intending to examine a potential bias of methodology on performances, we applied both paradigms simultaneously, making results more comparable between birds, as no avian species was yet tested in both tasks. Independent of paradigm, the subjects (seven crows, five ravens) did wait up to ten minutes for a higher food quality but not quantity, and adapt their behavior according to the relative gain; in different combinations of exchangeable food qualities, their decision to wait, considers the loss of food that must not be eaten in order to receive a more valuable reward. Our results suggest specific cognitive capabilities for effective future-orientated decisions in corvids.

The project was funded by the START program (Y366-B17) of the Austrian Science Fund (FWF).

P129 Sex differences in the effect of landmarks on learning based on environmental geometry

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Matt Buckley, Shamus Smith

Men and women rely differently on proximal and distal cues for navigation. It was predicted that proximal landmarks would restrict learning based on distal geometric cues more strongly for women than for men. The presence of proximal landmarks did affect women's ability to learn with reference to geometry, but with additional training both genders learned to navigate using geometric cues. The presence of proximal landmarks restricted learning based on geometry for both men and women.

P130 Acquisitional Neophilia or Retentional Exploration in Birds

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Alice Auersperg, Auguste Bayern, Thomas Bugnyar,
Ludwig Huber, Berenika Mioduszewska, Anna
Wilkinson, Gyula Gajdon

Exploration and neophobia are important factors when it comes to testing cognitive abilities of animals. Especially when working with animals, which express extremes in the spectrum of these responsive behaviors, their impact may be crucial for how subjects react to certain tasks. In 2009 we introduced a learning box with touchscreen to the kea (*Nestor notabilis*), a very explorative and barely neophobe parrot species from New Zealand. This apparatus allowed us to investigate the animal's reaction towards novel stimuli within a two-choice discrimination task. The results revealed that the kea chose novel unrewarded stimuli more often than the standard unrewarded stimuli, during the beginning of the experiment. This kind of initial novelty seeking in a task we labeled "acquisitional neophilia". These results demonstrate the need for awareness about the state of exploration a subject is in, when transfer tests are applied. Depending on a species' social and ecological background we expect to find different response patterns towards novelty in such tasks. In order to test for this hypothesis we selected different species of corvids and parrots with regards to their social and ecological background and applied the same task as a part of a collaborative project.

P131 Landmark Learning in Wild Rufous Hummingbirds (*Selasphorus rufus*)

David Pritchard, University Of St Andrews
T. Andrew Hurly, Susan Healy

Although small-scale navigation is well studied in a wide range of species, there have been very few field experiments on landmark use in vertebrates. Three wild male rufous hummingbirds were trained to feed from a flower in a constant relationship with two artificial landmarks. In the first experiment, the landmarks and flower were either 100cm, 50cm or 25cm apart and always moved 300-400cm between visits. In the second experiment, the landmarks and flower were always 25cm apart and moved either 100cm or 25cm between trials. In tests, the flower was removed and the birds' searches were recorded on video. In all conditions the birds searched around the landmarks, but they searched closest to the flower location when the landmarks had been only 25cm away, regardless of the distance moved between visits. These findings suggest ways the hummingbirds use landmarks to relocate flowers, and provide an experimental method for testing these hypotheses in the wild.

P132 Chimpanzee Statisticians - Do chimpanzees use statistical sampling to infer preferences of others?

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Human children can use basic statistical information, namely violations of random sampling, to infer that another person has a preference for one toy over another toy. In recent years, chimpanzees were shown to be able to infer a competitor's choices in different contexts. Here we used the same basic competitive paradigm that was used successfully in earlier studies to see if chimpanzees, like human children, were also able to infer another one's preference based on a violation of random sampling. Chimpanzee subjects observed a human competitor choose several objects (= wrapped food) from a bucket in different conditions and thereby either violating random sampling (= showing a preference) or not. The chimpanzee subjects could then choose between two different types of objects but only after their human competitor had already chosen one of them in private before them. Subjects had to infer the human's preference in order to avoid the object that was already taken. Indeed, chimpanzees avoided one type of object when the human had shown a preference for it by violating random sampling but chose randomly when the human had not. However, they also did this in nonsocial control conditions, so that different interpretations are possible.

P133 Exploration of mirror and several comparative objects in Callitrichids

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Radka Pintova, Lucie Tolarova, Daniel Volak

Mirror is an often used object for tests of cognitive abilities in animals. We studied exploration of a mirror in comparison to three objects similar in size and form - an object covered by a textile (regularly used in the first stage of mirror tests), a glass sheet, and a plexiglass sheet. The differences between objects were tested in 7 species of Callitrichids (*Cebuella pygmaea*, *Callithrix geoffroyi*, *jacchus*, *Saguinus labiatus*, *graellsii*, *imperator*, *midas*). All the mentioned objects were exposed in zoo exposition rooms two times in a random order. Displayed behaviour of Callitrichids (3 - 8 individuals in each species) was recorded. We evaluated 10 minutes from the beginning of the object exposition in each animal individually. Aggressive reaction against the mirror image, as well as, interest in own body was not registered. The biggest interest was generated by the mirror and by the object covered by a textile, however, spectrums of behavioural elements were quite different. Explorations of the glass and plexiglass sheets were similar and less intensive. Reaction to the mirror in comparison to the glass sheet (difference in reflection only) showed interest in the space behind the mirror and increase of interest in the second test.

P134 Abstract rule-learning abilities of zebra finches and budgerigars

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Carel ten Cate

Language and the mechanisms used to acquire it are considered to be unique to humans. Nevertheless, studies on artificial rule-learning in non-human animals can show us shared rule-learning mechanisms and reveal insight into the cognitive mechanism that may underlie the evolution of language.

We study zebra finches and budgerigars in an artificial rule-learning task. Both species are trained to distinguish two structures -XYX and XXY- over various tokens and are tested on their abilities to generalize these rules to new tokens. During the test, XYX and XXY structures are presented both with tokens that were present in the training, but now appear in a novel order, as well as completely new tokens following the grammatical rules.

We compare the results of these two species with each other and with humans in a comparable task.

P135 Spatial Cognition in Horses

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David Sherry

The spatial challenges for grazing foragers differ from those of many other animals. Domestic horses are highly trainable, making them an ideal species to examine spatial abilities in grazers. Experiment 1 characterized equine search strategy in a spatial array. Buckets containing a single reward were placed in eight randomly selected locations in a testing arena. Each horse was released and allowed to search the buckets until all rewards were retrieved. Experiment 2 measured spatial ability in a modification of the radial arm maze, which requires animals to rely on spatial memory instead of systematic search strategies. As in experiment 1, eight locations were baited with a single reward. In each trial, horses were released from a central location and allowed to retrieve a reward from one of the eight locations. Following each choice, horses were returned to the central location. Performance in both experiments was measured by total number of visits needed to retrieve all eight rewards. Horses searched systematically in Experiment 1, moving from one bucket to next nearest bucket until all 8 locations had been visited. Error rate increased in Experiment 2 when horses were required to return to the central place before each choice.

P136 Rapid explorative learning and functional inferences on a five-step means-end problem in Goffin's cockatoos

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Alice Auersperg, Alex Kacelnik

To investigate cognitive operations during innovative problem solving, we confronted Goffin's cockatoos with a baited box locked by 5 different inter-locking devices. Subjects were either naïve or had watched a conspecific demonstration, and either faced all devices at once or incrementally. We combined these conditions factorially to achieve four different groups. One subject solved the problem without demonstration and with all locks present from start, in less than 100 minutes, while others did so after social demonstrations or incremental experience. Most birds showed a ratchet-like progress, rarely failing to solve a stage once they had done it once. In transfer tests some subjects reacted flexibly and sensitively to alterations of the locks' sequencing and functionality, as expected from the presence of

predictive inferences about mechanical interactions between the locks. Performance was aided by species-specific traits including neophilia, a haptic modality and persistence, and the ratchet-like progress suggests that they followed a goal-directed path to the solution.

P137 Is sickness in the rat paired with a 'pessimistic' judgement bias?

Victoria Hurst, Newcastle University
Melissa Bateson, Paul Flecknell

In humans, sickness is often paired with negative feelings comparable to symptoms of depression. In animals, however, it is unclear whether sickness is similarly accompanied by depressive symptoms. To investigate whether negative feelings are also present in sick rats we used an auditory, operant-based judgement bias paradigm previously used to assess pessimistic judgement biases characteristic of depression. Rats were initially trained that responding to CS+ delivered food reward, whereas responding to CS- avoided exposure to mild foot-shock. They were subsequently tested with sound cues intermediate between the CS+ and CS-, and their judgements recorded. Sickness was induced via lithium chloride (LiCl) injection. Rats experiencing LiCl-induced sickness tended to move around, rear and groom less, and also engage in pica. A pilot study demonstrated that LiCl did not affect motivation to obtain food reward on a progressive ratio task, and response latencies were conserved. With normal operant activity and classic sickness behaviours both present with the same dosage of LiCl, the above judgement bias task was considered suitable to measure cognitive symptoms of sickness. If sick rats also exhibit depression-like symptoms, we predicted a reduced anticipation of reward evidenced by choice of the CS-lever in the intermediate test trials.

P138 Advancing the understanding of Animal Sentience

Gemma Carder, World Society For The Protection Of Animals
Helen Proctor

Scientific understanding of animal sentience underpins the entire animal welfare movement. As a result in August 2012, WSPA launched an interactive website called the Sentience Mosaic (www.sentience mosaic.org), which acts as a resource for students, academics and anyone whose work may involve animals. The site promotes and

shares scientific research on animal sentience, and features interviews with leading scientists. The Sentience Mosaic also has a forum and monthly on-line debates featuring a variety of topics, and global experts discussing their research and views. The site is currently available in English and Spanish and will be launched in Portuguese soon.

The Sentience Mosaic reaches out not just to individuals and organisations working in animal welfare, but also to other sectors such as conservation, agriculture, and animal experimentation, for whom sentience is a key aspect of their work, yet is so often neglected. There is still a great deal to learn about the capabilities of non-human animals. We hope that future research explores sentience not just in vertebrates, but also in invertebrates, in an ethical and humane way.

P139 Where have I been? Where should I go? Working memory on a radial arm maze in a rat model of depression

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Disturbances in cognitive functioning are among the most debilitating problems experienced by patients with major depression. Investigations of these deficits in animals may help to extend our knowledge of human emotional disorder. We employ the "learned helplessness" rat model of depression in studying working memory using an 8-arm-radial-maze procedure with temporal delay. According to a 2x2 factorial design, memory performance of 31 congenitally helpless (cLH) and non-helpless (cNLH) rats was tested on eighteen trials, additionally imposing two delay durations, 30s and 15min, respectively. While not observing strain-specific cognitive deficits, the delay length greatly influenced maze performance. Notably, performance was most impaired in cLH rats tested with a 30s delay, suggesting a stress-related disruption of attentional processes in cLH rats (ANOVA, strain-by-delay-interaction: $F_{1,13} = 5.45$, $p = 0.036$). Furthermore, sigmoid functions were fitted to the time series of daily memory performance. While some subjects followed a very smooth gradual learning process, most learning curves were characterized by fast transitions from chance to optimal performance within just a few days. By applying this task, we provide direct animal homologues of clinically important measures in human research, and contribute to the non-invasive assessment of cognitive deficits associated with depression.

P140 Rehabilitation of an adult male chimpanzee with a disability using computer-controlled cognitive tasks

Yoko Sakuraba, Kyoto University
Masaki Tomonaga, Misato Hayashi

Rehabilitation of companion animals with disabilities caused by disease or injury can lead to improvements in functional ability. Wild animal species born in captivity can also become disabled, yet there exist few reports and little systematic data on rehabilitation and impact on welfare. An adult male chimpanzee Reo, housed at the Primate Research Institute of Kyoto University, developed acute tetraparesis. Thanks to careful husbandry he has improved function gradually, however his walking and locomotion remain impaired. He is highly motivated to perform computer-controlled cognitive tasks for food rewards. Therefore, to encourage him to move we placed the touch-screen monitor 2m from the reward-dispenser. Reo had to move to collect the reward, and to return to the screen for the next task. We collected and analyzed data on: amount of movement, locomotion pattern, and walking speed. After participating in this novel rehabilitation program, we found that Reo moved more often and his walking speed increased. Further, his locomotion pattern shifted from walking with physical support to brachiation and an approximation of knuckle-walking; demonstrating improvements in locomotor skills. Moreover, Reo performed this activity-program regularly for more than three years, suggesting that rehabilitation using cognitive tasks helped maintain his perseverance and motivation.

P141 Do potentially depressed horses lack attention? A differential temporal pattern of responses towards auditory stimuli.

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Martine Hausberger

A recent study described an inactive state in domestic horses, termed *withdrawn* hereafter and characterised by an atypical posture and low responsiveness to tactile and environmental stimuli. Aiming at determining the potential role of underlying depression in this state, we investigated whether the attentional state, frequently impaired in depressed patients, differ between withdrawn horses (n = 12) and control non-withdrawn animals from the same stable (n = 15). These 27 horses (5

mares, 22 geldings, French Saddlebred, 4-20 years old) were exposed once a day for 5 consecutive days to a novel auditory stimulus, broadcasted for 3 seconds in horses' home environment. We recorded standard measures of attentional state (e.g. time spent with ears, head and/or neck orientated towards the loudspeaker). Different temporal patterns of attentional responses appeared: withdrawn horses paid less attention to stimuli on the first day (Wilcoxon, $p < 0.05$), while control horses similarly paid attention to stimuli over the 5 days period (Friedman $p > 0.05$). Moreover, time focused on the loudspeaker was lower in withdrawn than in control horses on this first day (Mann-Whitney, $p < 0.05$). Withdrawn horses therefore seem to "switch off" from environmental stimuli compared to control horses, which might reflect lack of attention.

P142 Looking Back To Map The Future: A Review Of Animal Sentience Research

Helen Proctor, World Society For The Protection Of Animals
Gemma Carder, Amelia Cornish

The science of animal sentience is key to achieving positive change for animals. WSPA has undertaken a systematic review of the scientific literature in order to identify gaps in our knowledge, and to assess the acceptance of animal sentience within the scientific community.

Two journal databases were searched using a peer-reviewed list of 171 emotions, behaviours, and terms associated with, or indicative of animal sentience. Chi-square analyses were performed in order to address the following questions;

- What do we know? What is being explored and what is being assumed in regards to the subjective minds of animals?
- Who is being studied? How far does knowledge of animal sentience reach in the animal kingdom? Are there fundamental gaps in what we know?
- Why is research performed? How beneficial is animal sentience to disciplines outside of animal welfare?
- Where is the research taking place? In laboratories, in zoos, on farms?

The results of this systematic review will help animal welfare scientists and animal protection organisations understand what is already known and where gaps exist in our understanding of animal sentience. This knowledge is essential if we are to improve the lives of animals.

P143 Development of validated cognitive and behavioural indicators of welfare in pigs towards a predictive early warning system for poor welfare

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Statistics, physics, engineering and psychology utilise a wide-range of methods that can be adapted for use as animal-based welfare measures if only they could be validated in a model animal system. Validated indicators could then be used to develop a predictive early warning system to detect welfare problems in advance. In this study, categories of pigs of different welfare status are created using both physical and environmental factors to develop and validate novel welfare indicators. Using video footage, activity budgets are calculated weekly both at the individual and group level. In addition to this traditional approach, we measure two further types of behavioural indicator: cognitive indicators of welfare; and quantitative indicators of welfare, calculated and analysed from the video footage. For both types of behavioural indicator, we use traditional, well-tested methods to validate novel indicators that will tell us something new and different. This dual approach will produce a set of results that are not only novel and potentially producing exciting new tools for the study of animal welfare, but that are also supported by the traditional, well-tested methods. Here, we present the initial results from this study and discuss the potential application of methods to other species and scenarios.

P144 An active choice judgement bias test for mice

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We validated an active choice judgment bias test to assess affective states in two mice strains. Fourteen CD-1 and twelve C57BL/6 female mice were trained on a tactile discrimination task, where one grade of sandpaper predicted a more valuable reward (almond) and another grade predicted a less valuable reward (oatflake). All mice showed a preference for the more valuable reward as indicated by latency to choose ($F_{1,13}=13.76$, $P=0.001$). CD-1 mice learned the task faster than C57BL/6 (14.14 ± 2.77 vs 19.7 ± 5.85 sessions). Animals were then allocated to two groups, control group (CON) and treatment (STR) group, counterbalanced by strain. CON group was left undisturbed whereas STR group underwent a two

week unpredictable mild stress treatment, known to induce symptoms of depression-like state. Animals were then tested for judgment bias. During a testing session, mice were presented with three ambiguous unrewarded cues, and their response towards the more or less valuable reward's location was scored as optimistic or pessimistic, respectively. We found group differences in responses to the probe close to the positive cue, with STR group showing a more pessimistic bias (GLM, $F_{1,13}=4.06$, $P=0.07$). These results suggest that our test can be used to assess affective state in mice.

P145 Development of cognitive bias test for hens as a tool to estimate poultry welfare

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Cognitive component of emotion represents an important source of information about animal emotions. Affect-induced judgement bias has been suggested as possible indicator of emotional states in animals. Building on designs of cognitive bias testing in rats and quails we have designed a touch-screen operant chamber and automatic feeder for cognitive bias testing in hens. Twenty laying hens were trained to peck to positive stimulus (white circle in half of animals; 80% grey circle in other half) rewarded by mealworm. Five sessions (each lasting about 30 minutes) were needed to reach at least 75% of correct responses on three consecutive days. After reaching this criterion hens were trained to operant discriminative task - to peck to positive stimulus associated with a reward and to refrain from pecking to negative stimulus (80% grey and white circle respectively in one half of animals and the other way round in other half) to avoid punishment (white noise). After three Go/NoGo sessions 19 out of 20 hens discriminated the stimuli (proportion of responses to positive and negative stimuli was $98.5 \pm 0.57\%$ and $13.33 \pm 3.4\%$ respectively; $\chi^2=0.716 \pm 0.01$). Our preliminary data indicate that the touch-screen operant chamber is a promising design of cognitive bias testing in laying hens.

P146 Acoustic features of piglet "scream" calls reflect level of situation urgency

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Marek Spinka

Vocalizations have been getting attention recently as possible indicators of animal emotional states. It

has been already shown, that piglets (*Sus scrofa domestica*) increase number of “scream” calls in stressful or painful situations. Question remains, however, whether the specific acoustic features of these calls could reflect the level of situation urgency.

We restrained piglets on their backs and recorded their behaviour and vocalizations during one minute. Restrain was done on scales and piglet was kept at the position with the smallest force possible. We recognized three situations based on apparent urgency level: low urgency (LOW; piglet is lying still), medium urgency (MED; piglet is fighting for escape), and maximum urgency (MAX; piglet is fighting with maximum force; force was assessed based on weight read from scales). One “scream” call from each situation was analysed per piglet and 50 piglets were tested overall. MAX screams were loudest, longest, they had the highest pitch and the lowest tonality. Moreover, maximum fighting force in MAX situation correlated positively with scream “harshness”.

We show that calls in piglets reflect situation urgency level. Our results are consistent with other studies suggesting that urgency is encoded similarly across studies.

P147 Calling by domestic piglets during simulated crushing: signal of need or condition?

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The study examined whether piglet distress vocalizations vary with age, body size and health status, according to the predictions of the honest–signalling-of-need and honest–signalling-of-condition evolutionary models. Piglet vocalizations were recorded during manual squeezing (a simulation of being crushed by mother sow) on Days 1 and 7 after birth in piglets from 15 litters. We predicted that during squeezing, younger and lighter piglets would call more because of the higher risk of dying during crushing (honest signalling of need) and healthy piglets would be able to vocalize more intensely than sick piglets (honest signalling of quality). Calls were analyzed in their time and frequency domain. Piglets which experienced ‘squeezing’ on Day 1 produced more intense acoustic distress signalling than on Day 7. Lighter piglets called more during squeezing than heavier piglets. Health status did not significantly affect any of the indicators of intensity of vocalization during squeezing. In summary, the model of honest signalization of need was confirmed in the squeezed situation, but no evidence for honest signalling of health condition was found.

P148 Is laterality in sheep predictive of behavioural stress during separation of lambs from their dams?

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Abruzzo E Molise

Lindsay Matthews, Stefano Messori, Luca Candeloro, Michele Podaliri Vulpiani, Nicola Ferri

Laterality reflects emotional responsiveness in many species. Our aim was to determine if laterality in sheep was predictive of reactivity during a simulated common farming practice (i.e. isolation and forced separation of ewes and their lamb during artificial weaning).

Laterality was assessed in 43 ewes and their singleton lambs by recording the direction of turn in a Y-maze when rejoining flockmates. Behavioural reactivity of lambs and dams was assessed over 5 minutes when they were physically separated by an open-mesh fence in adjacent pens. Time spent near the fence (within 80 cm), vocalisations and number of times the animal moved toward and away from the fence were recorded. Nineteen ewes (44.2%) and 35 lambs (81.4 %) showed individual laterality (binomial test, $p < 0.05$). An ANOVA showed that lateralized lambs spent significantly more time near the fence than non-lateralized animals ($F = 8.02$; $p < 0.01$), but were not more active or vocal. The data show that laterality is a potential novel predictor of separation stress and/or the degree of alleviation provided by the mother. Laterality offers the advantage of a non-invasive and relatively easy way to measure stress.

P149 Domestication effects on stress recovery in chickens

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Amir Fallahshahroudi, Per Jensen

During the process of domestication, changes in several aspects of the behavioural repertoire have emerged. In the chicken (*Gallus gallus*), previous behavioural comparisons between the wild ancestor, the Red Junglefowl, and domesticated breeds have displayed differences in fearfulness, foraging and exploration. We hypothesize that also the behavioural and hormonal responses to an acute stressor has been altered. Female Red Junglefowl ($n = 13$) and White Leghorn ($n = 13$) were compared. Baseline behaviour was recorded, followed by three minutes of restraint stress. An additional hour of behavioural recordings took place to obtain the recovery behaviour, complemented

with blood samples for corticosterone analysis. A repeated measures ANOVA reveal a significant difference between the breeds over time in feeding ($p=0.05$), drinking ($p=0.03$) and relaxed behaviour ($p=0.008$), as well as in corticosterone levels ($p=0.002$). White Leghorn displayed a more subtle HPA-axis and behaviour response, but a longer recovery period whereas the Red Junglefowl showed an immediate behaviour and HPA-axis response followed by a fast recovery after to the stress. A fast recovery could be a fitness benefit in the wild, whereas the relaxed selection pressure in domestic breeds has altered the stress recovery.

P150 Temporal dynamics of social modulation of sickness behaviours and associated impacts on immune defences

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Dwight Springthorpe, George E. Bentley

Sick animals experience a number of physiological changes in order to potentiate the organism in fighting the pathogen. This response is accompanied by a behavioural component, known as “sickness behaviour”, consisting of a generalized reduction in physical activity. It is thought that the energy resources saved by reducing activity can be reallocated into mounting an immune response. However, a conflict exists in situations in which being active might yield higher benefits than investing in immune response, such as in the presence of mates or intruders. In fact, several reports have demonstrated plasticity in sickness behaviour response. Here, we assessed whether this plasticity is temporal, using captive colonies of zebra finches (*Taeniopygia guttata*) and developing a miniaturized device that could be attached to the birds and quantify activity remotely. Simultaneously, we tested whether immunity was positively correlated with the intensity of the sickness behaviour response.

We found that, while time does not impact the plasticity of the behavioural response, the intensity of the immune response was reduced in immune challenged animals that remained more active. Reduction of sickness behaviours may thus impose costs that need to be balanced against the potential benefits of remaining active in social circumstances.

P151 Hippocampal Markers of Depression and Chronic Stress in Restricted Broiler Chickens

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G. Cirillo, M. Bateson, T. Boswell, P.W. Wilson, I.C. Dunn, T.V Smulders

Commercial broiler breeders are feed-restricted to avoid negative health outcomes including obesity and reproductive unviability. Beyond knowing these chickens are hungry little is known about how this severe restriction impacts the animals' affective state. We investigated potential correlates of the subjective affective state of broiler chickens by quantifying neurochemical changes to the hippocampus thought to be markers for depression and chronic stress. Alterations in hippocampal morphology are found in humans suffering prolonged and recurrent episodes of depression and chronic stress where decreases in both hippocampal volume and neurogenesis can occur. The purpose of this study was to determine if chronic hunger creates a state of chronic stress or depression leading to an overall negative subjective experience for the chicken. Hippocampal morphology was investigated for evidence of chronic stress using the following measures: i) hippocampal volume, ii) total number of neurons in the hippocampus, iii) proliferative activity (as measured by the presence of 5-bromo-2'-deoxyuridine (BrdU), and iv) incorporation of new neurons into the hippocampus (as measured by the presence of BrdU in neurons), to give a complete overview of the neurogenic process in these chickens.

To measure chronic hunger chickens were either feed-restricted or fed *ad libitum*. Hypothalamic AgRP expression confirmed that feed-restricted chickens were hungry, and elevated corticosterone levels in blood plasma suggested feed-restriction did place the chickens under stress.

Markers of depression were found in the hippocampus: the density of BrdU-positive neurons was significantly reduced in the feed-restricted condition as compared to chickens fed *ad libitum*. Feeding condition did not affect hippocampal volume, or the total number of new neurons. Another marker of depression-like state (IL-6 expression in the spleen) was also higher in feed-restricted than in *ad libitum* fed chickens.

These results indicate that feed-restricted broiler breeder chickens do experience symptoms of chronic stress, and therefore, likely a negative affective state.

Funded by DEFRA AW1141

P152 Heart rate and heart rate variability of dogs (*Canis lupus familiaris*) during physical movement and mental stimulation

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Heart rate and heart rate variability are influenced by a variety of factors with heart rate probably being more affected by physical activity and heart rate variability being more affected by psychological processes. The current study compared differences in heart rate and heart rate variability of dogs in three situations: (1) a leash walk (normal movement and limited mental stimulation), (2) a two-choice task working on a touch-screen (limited movement and mentally challenging), (3) a two-choice task that included physically active (stepping towards the right object) and passive periods (waiting for the two objects to be put down) and was considered to show an interaction between physical and mental activity. The experiments were carried out with six adult mongrel male dogs and all dogs were tested four times per test situation; but within a test situation, each session was carried out with a different trainer. We recorded all behaviours of the dogs and used the non-invasive Polar RS800CX heart rate belt to measure heart rate and heart rate variability. This is one of the first studies to investigate the influence of different factors (e.g. trainer, test situation, behaviour) on the heart rate and heart rate variability of dogs.

P153 Can we still justify the use CO₂ for killing laboratory rodents? A comparative study to inhalant anaesthetics

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Carbon dioxide (CO₂) can still be used for killing laboratory rodents but the method is strongly criticised. Inhalant anaesthetics are recommended as an alternative, but their application is not sufficiently validated.

We investigated distress induced by 100% CO₂ with different filling rates (20% (CO₂20), 60% (CO₂60), CO₂ 100% (CO₂100) of chamber volume/min) or isoflurane and sevoflurane in different concentrations (Iso2%, Iso5%, Sevo4.8%, Sevo8%) in NMRI and C57Bl/6 mice. We evaluated all gases for their effectiveness and reliability to induce general anaesthesia within 300s. We observed the behaviour during the induction of narcosis and measured plasma concentrations of adrenaline and noradrenaline immediately after surgical tolerance was reached.

Only CO₂60, CO₂100 and Iso5% induced general anaesthesia in all animals of both strains within the given time. Surgical tolerance was reached faster by CO₂100 compared to Iso5%. All NMRI mice but not all C57Bl/6 mice exposed to Sevo8% were anaesthetised within 300s. Behavioural analysis

revealed no distinct signs for distress during the induction of narcosis. Adrenaline and noradrenaline concentrations were significantly increased in CO₂ treated animals compared to animals exposed to isoflurane or sevoflurane.

CO₂60, CO₂100 and Iso5% effectively and reliably induced general anaesthesia, whereas sevoflurane was not as effective. However, the raise in adrenaline and noradrenaline plasma concentrations after CO₂ exposure points towards distress, so CO₂ alone is not the first choice for killing laboratory mice. Isoflurane should be used with maximum concentration to provide a safe stage of surgical tolerance.

Supported by the Bundesinstitut für Risikobewertung-ZEBET (FK 3-1328-429).

P154 Synchronization of stress coping between owner and dog? Evidence from heart rate, heart rate variability and behavior.

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Humans and dogs engage in mutual social relationships. The quality of such a partnership is also characterized by positive effects of “emotional social support”, which is may be manifested in synchronic behaviour and physiology during a stressful situation. Thus 120 owners, aged 18 to 60 years, with their intact dogs 1.5 to 8 years of age, were tested during and after a mild threat situation. Heart rate (HR) and heart rate variability (HRV) were measured from owners and dogs by using non-invasive HR monitoring belts (Polar-RS800CX). We investigated whether there is a synchrony in owner and dog HR and HRV and how owner personality, measured with the NEO-FFI, influences both. Owners and dogs positively correlated in their decrease of HR after the threat situation (Pearsons: $r=0.716$, $p=0.02$). Conscientious (Neo-FFI dimension 5) owners further had higher pNN50 values during the threat situation (Spearman's: $r_s=0.646$, $p=0.044$), whereas their dogs had higher SDNN values during the threat situation (Pearsons: $r=0.670$, $p=0.034$). Our results support the idea that owners and dogs can be synchronized in their stress coping during an emotional arousal and that owner personality plays an important role. Further results, including owner-dog interactions will be presented.

P155 Basal Ganglia Dysfunction and Equine Learning Ability

Linda Greening, Hartpury College

Domestic equine husbandry practices enable nocturnal ingestion in the stable through provision of forage. Little evidence exists relating to nocturnal ingestion and preferences of the stabled horse between ingestion from hay-nets or from the floor. The current study aims to establish nocturnal patterns of feeding behaviour, comparing two different methods of presenting the forage ration. The study observed six mixed breed geldings, ranging from seven to twelve years of age for six nights each, using an infrared CCTV system. For nights 1&2 horses received hay (10kg) in a net. For nights 3&4 hay was provided on the floor (10kg). For nights 5&6 horses received hay in both a net (5kg) and from the floor (5kg). Duration of ingestion behaviour from hay-net and from floor provision was recorded.

Average total duration of ingestion will be compared between N1&2 and N3&4. Average total duration of ingestion behaviour from the hay net provision and from the floor provision was compared for N5&6. The results from this study will be used to discuss nocturnal ingestion patterns, the influence of the method of provision on nocturnal ingestion of the forage ration, and also whether preferences are shown towards a more natural foraging posture.

P156 The effects of environmental enrichment on feather corticosterone content in captive wild-caught birds

Marju Männiste, University Of Tartu
Tuul Sepp, Richard Meitern

Behavioral stereotypies are well known to occur in most mammals and birds kept in barren cages. Environmental enrichment is thought to alleviate these abnormal behaviors. However it is unclear how enrichment relates to stress levels in captive wild-caught birds. We performed an experiment with captive wild-caught greenfinches (*Carduelis chloris*) performing long-term environmental enrichment with hay, pine- and fir cones in cages of half of the birds. We hypothesise that environmental enrichment reduces feather corticosterone content. In order to evaluate individual stress levels we removed one of the outermost tail feathers and measured corticosterone content of feathers grown during the experiment. Feather corticosterone content reflects individual stress level during feather growth integrating long-term changes in variation in baseline level, magnitude of the stimulated response, time course for the stress response and the number of stressors experienced. These results

help to elucidate underlying causes and mechanisms of abnormal behaviour in caged animals.

P157 Taking cows body dimension when designing housing system: A way to improve dairy cows wellbeing

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and L. Mounier

Dairy cattle spend most of the winter time indoors. Appropriate housing facilities-especially resting areas-are important to their welfare. As the selection for high milk production was accompanied by an increase in cows' size, it is important for farmers to take into account cows' dimensions when designing housing equipment in order to allow their adequate movements/positioning. The aim of this study was to investigate the links between specific characteristics of resting areas (e.g. size), cows dimensions and skin damages. A total of 131 farms (55 deep-bedded systems; 76 cubicle systems) were visited, resulting in 4254 cows on which height and width were measured and skin damages were recorded. Cows median height was 143 cm (1st-3rd quartile:143-147cm) and cows median length between point of shoulder and pin bone was 160 cm (1st-3rd quartile:155-164cm). Cows housed in deep-bedded systems had less hairless patches, lesions and swellings on the hindlegs, quarter and forelegs than cows in cubicles (P<0.05). In cubicles, we found evidences of the importance of taking cows dimensions into cubicles designs in order to avoid skin damages. For instance, more cows had hairless patches on their hindlegs when the ratio cubicle length/cow length was below 1.6. Such results shall help design ergonomic housing facilities.

P158 Development Of An Automated Measure Of The 'Defence Cascade' In Pigs

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W.J. Browne, M Mendl

Truly accurate assessment of on-farm welfare requires validated proxy measures of animal affect. Behavioural startle/freeze ('Defence cascade' (DC)) responses to a startling stimulus have been shown to reflect affective states in both humans and rodents. This study compares force plate, direct observation, and computational image analysis (IA) measures of DC responses in pigs. Twelve pigs individually experienced four test sessions when young (20-40kg) and again when

older (50-80kg). Each session comprised up to five startle stimuli giving 286 DC responses in total. Force plate and IA measures were compared to observer scores of magnitude of startle and occurrence / duration of freeze.

The force plate ($\chi^2 = 148.324$, $p < 0.001$) and IA measures ($\chi^2 = 136.859$, $p < 0.001$) increased in line with the observer score of startle magnitude. Magnitude scored by force plate and IA measures were significantly positively correlated ($r_s = 0.714$, $p < 0.01$). IA measures demonstrated high specificity (0.754) and sensitivity (0.711) in detecting freezes. Observer values of duration of freeze were more highly correlated with the IA ($r_s = 0.781$, $p < 0.001$) than with the force plate measures ($r_s = 0.671$, $p < 0.001$). Overall the IA measures were successful at quantifying DC responses in pigs and have potential for on-farm welfare assessment.

P159 How do different fluid reward schedules motivate macaques in behavioural neuroscience?

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Fluid control protocols are widely implemented in primate behavioural neuroscience to motivate individuals to perform cognitive tasks for fluid rewards. Whilst successful for motivating primates to perform in tasks that often require many hundreds of trials each day, fluid control protocols are contentious due to the potential negative effects on the animals' welfare. In this study we investigate whether giving rhesus macaques (*Macaca mulatta*) a preferred fluid or a choice of fluid rewards increases their motivation to perform a task, allowing fluid control to be relaxed. We systematically measured fluid reward preferences using a simple saccade task and found that Ribena was preferred over water. We then measured the number of daily trials an animal performed in a more complex cognitive task when rewarded for correct performance with either: water only, Ribena only, water and Ribena (with 50% probability) or allowed to choose between water and Ribena as a reward after successful completion of a trial. Our findings suggest that reward schedules that are more motivating to the animals could enable a reduction in the severity of fluid control protocols experienced by macaques in behavioural neuroscience research, while retaining scientific data quality and quantity.

P160 Automated testing of activity and learning in mice in IntelliCage

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The genome sequencing of many species and identification a large number of genes raise questions about their functional significance. New technologies have been developed to analyse the complex behaviours and to detect even small change in the phenotype, and consequently determine the relationship between the gene and behaviour. Here, we present application of the one of such systems, namely IntelliCage. The IntelliCage is fully automated apparatus used to study mouse behaviour, including the characteristics of mutant mice phenotype. Animals live in social groups in conditions similar to those prevailing in a home cage.

The IntelliCage functionality was investigated by: 1. measuring parameters difficult to examine in standard tests and 2. comparing learning performance in the IntelliCage with Morris water maze. Addressing the first issue, we found that mice exhibit significant changes in activity associated with circadian cycle. Second, wild-type mice were able to acquire place learning and reversal learning. Mutant mice showed either deteriorated or enhanced learning abilities in place learning/reversal tasks that were further confirmed in Morris water maze. We show the utility of IntelliCage system for testing the selected parameters of behaviour. Also, the results confirm the usefulness of the system to behavioural phenotyping of genetically modified mice.

P161 Cortisol analysis from hair of captive chimpanzees: methodological validation and application to social management

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Assessments of long-term stress are important given that prolonged stress can alter animal behaviors. The use of hair cortisol as a marker of long-term stress has been increasing, but there has not been any report on the use of such methods with chimpanzees. The purpose of this study was to establish a methodology for analyzing hair cortisol in captive chimpanzees. First, we removed hair from the arms of nine chimpanzees living in the Kumamoto Sanctuary, Kyoto University (KS) and sampled the regrown hair 3 months later. The aggressive behaviors during the hair growth period

were recorded. The result showed that hair cortisol levels were positively correlated with the rates of receiving aggression. Thus, hair cortisol may reflect long-term stress in chimpanzees. Second, we investigated factors affecting hair cortisol concentrations. We cut hair from the arms, sides, and backs of 27 chimpanzees living at the KS and the Primate Research Institute, Kyoto University. The results revealed that cortisol varied based on source body part, hair whiteness and institutions. Therefore, we recommend that hair should be collected from the same body part and that white hair should be avoided. Based on the results, we discuss the possibilities to apply for social management.

P162 Impact of artificial weaning of foals on HR increase in mares

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Jitka Bartonová, Martina Komárková, Jana Dubcová

Artificial weaning was found to be stressful for the females of domestic ungulates. We investigated changes in heart rate (HR) in domestic horse mares associated with abrupt weaning of their foals following a routine weaning procedure in group housed 9 mares. Ten non-lactating mares served as a control. The foals were led away from the group (they aged from 4 to 7 months). The mares stayed in the stable for 4 hours and then were joined with control mares and moved by foot to the other facility 3 km far from the home stable. Weaning of the foals significantly affected both, mean and maximal HR recorded in particular time periods (during and after weaning, before moving, during moving, after moving in a new facility; $P < 0.001$, general linear model). "Weaned" mares compared to non-lactating ones showed higher mean as well as maximal HR during and after weaning. The difference was still apparent in resting HR before moving as well as in a new environment. We found individual differences among mares in HR reaction to weaning which will be further investigated. Our results indicate at least short-term negative effect of abrupt artificial weaning on domestic mares. Supported by AWIN project (FP7-KBBE-2010-4)

P163 The social structure of farmed collared peccaries (Mammalia, Tayassuidae)

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Stella Calazans, Thaise Costa, Hélder Peregrino, Selene Nogueira

There is no consensus if a linear dominance hierarchy characterizes interactions among individuals in collared peccary (*Pecari tajacu*) groups. Therefore, this study described the social structure of three farmed peccary groups, composed of two males and four females each, kept in paddocks of 360 m². All occurrences of agonistic behavioral patterns were recorded during 50-minute observation sessions at feeding time, totaling 20 hours of data collection per group. Landau's corrected linearity index (h') was calculated through SOCPROG (2.4) software, which also provided the individuals' rank order. The subjects' live weights and the faecal glucocorticoid metabolite concentrations were correlated (r_s) with their rank positions. The h' ranged from 0.2 to 0.7 ($P_s > 0.14$), irrespective of including data on males in the analyses or not. There were no correlations between animals' live weight ($P > 0.05$) or faecal glucocorticoid metabolite concentrations ($P > 0.05$) and their rank positions. Although the dominance relationships in captive peccaries did not fit a linear hierarchy, the observed ritualistic agonistic behavioral patterns attenuated inter-group competition, preventing injuries and helping to maintain the group's cohesiveness. Moreover, the obtained results indicate the possibility of introducing unfamiliar individuals into an established peccary colony to avoid inbreeding in peccary farming projects.

P164 The Effects of Horse-Human Contact Prior to Riding Sessions

Jessica Lampe, University Of Bern

Natalie Waran

This study reports evidence that a phase of intensive contact between horse and rider (grooming) has a positive effect on a following riding session. It was not only confirmed that equine heart rate (HR) as an indicator of stress and anxiety decreases *during* grooming but also shown that grooming by the rider positively affects both the difference between horses' HR at the beginning and end of the subsequent riding session and the difference between horses' baseline HR before grooming and HR at the end of the riding session. With a familiar person other than the rider these effects did not surface. Contrary to horses' HR, riders' HR was not affected in a similar way. With regard to behaviour, grooming by the rider (but not by another familiar person) had a significant positive effect on riding session behavioural scores of horse-rider pairs. Rides were calmer and more harmonious, presenting more compliant horses and more relaxed

riders. These findings, based on a sample of 15 horse-rider pairs, suggest that intensive contact time with the riders themselves (touch, voice, visual and olfactory exposure) prior to riding sessions can improve horse welfare and performance in riding sessions.

P165 Equine Gatekeepers: Animal Narratives and foxhunting landscapes

Alison Acton, Independent

Firstly, this paper analyses the dynamic between horse, rider, culture and landscape. Secondly it considers non-human animals as active elements within the research process. My fieldwork involved seven years of ethnographic research into foxhunting culture, from the position of a rider within foxhound packs. The equine focus emerged unexpectedly as I originally participated as a rider/ethnographer in order to understand the nexus between foxhunting culture and the landscape. However, I became drawn into a collaboration with an unanticipated character in this network; the "made hunter," a horse seasoned for hunting. These animals acted as my equine gatekeepers literally incorporating me into this alien world. I conclude that social science can incorporate epistemic and often ancient elements of cultures that draw on animals as co-actors. Understanding traditional modes of social action, such as hunting, which are centred upon human-animal interaction can enable us to recover more-than-human views of the world and can lead to an enhanced understanding of our super-human experience with space. Additionally, the unexpected contribution of these horses to my research leads me to suggest that there is scope to recognise animals not simply as subjects to study, but as co-participants in the understanding of our embodied relationship with space.

P166 Preliminary results on the behaviour of Iberian piglets housed in three different systems in the South of Spain

Miriam Martinez-Macipe, Uab

Eva Mainau, Pedro Rodriguez, Xavier Manteca, Antoni Dalmau

The postnatal behaviour of Iberian piglets in three different systems was studied: crate system (CS); fence system (FS), where piglets were nursed inside a "camping house" in an individual fenced paddock; and group system (GS), where several sows and their litters were kept in a field with many "camping

houses". Piglet behaviour (86 piglets in CS, 37 in FS and 40 in GS) from 26 sows was recorded by scan sampling 1 hour/day from day 0 to day 30. At weaning (day 40), the number of fights between all weaned piglets (194 in CS, 90 in FS and 240 in GS) was counted.

Suckling behaviour from day 7 to 15 accounted for 18.47% of the time in CS, 6.45% in FS and 11.45% in GS, and time exploring from day 7 to 30 accounted for 13.60% in CS, 29.36% in FS and 40.61% in GS. At weaning, fighting ratio was 0.68 fights/piglet/hour in CS; 0.04 in FS and 0.03 in GS. The results suggest that the CS system results in more suckling behaviour and less exploratory activity after one week of age in piglets and has a clear social stress factor added to the separation of the sow at weaning.

P167 Crashes of laying hens in aviary systems.

Ariane Stratmann, Universität Bern

Ernst Fröhlich, Hanno Würbel, Sabine Gebhardt-Henrich

In aviaries, most laying hens roost on elevated perches, with the highest perches being most attractive. This entails the risk of hens falling and crashing with perches and other structures, which may cause keel bone fractures. We therefore compared movements, falling events, and crashes during the dusk period and the early dark period between different designs of an aviary system. Video recordings at weeks 18 and 43 were taken and the number of downward movements and falling events was recorded. Falling events were analyzed in detail including height, reason of falling and occurrence of collisions. Falling occurred significantly more often during darkness than dusk ($Z = 10.171$, $P < 0.0001$). The number of falling events was not reduced by a certain design, but additional platforms reduced the height of falling ($X^2 = 8.931$, $df = 3$, $P = 0.0302$). More downward movements but fewer falls were shown in pens equipped with ramps than without ramps ($X^2 = 18.319$, $df = 3$, $P = 0.0003$). In pens with additional perches more falling events were caused by landing accidents than in pens with fewer perches ($X^2 = 17.52$, $df = 3$, $P = 0.0005$). The design of aviaries may influence the movement and accidental crashes of laying hens.

P168 Adolescents and animals - A systematic review on animal perception and cruelty

Melanie Connor, Sruc

Joanne Williams, Alistair Lawrence

Children's interactions with animals and their beneficial developmental outcomes have been investigated in various disciplines. However, strong links have also been made between child abuse, animal abuse and domestic violence, which are also present in adolescents. The purpose of the present study was to systematically evaluate the literature to specifically investigate adolescents' relationships with animals to identify knowledge gaps. Two separate systematic literature reviews on adolescents' perceptions of animals and cruelty towards animals were conducted by obtaining articles from six electronic databases (Scopus, PubMed, Medline, PsychInfo, Web of Science, ScienceDirect). Results indicate that few empirical studies have been conducted on adolescents' perception of animals (N=5) and animal cruelty (N=5) with most either investigating clinical samples of adolescents or measuring animal cruelty retrospectively with adults having committed serious crimes. The reviews reveal that most adolescents reported or witnessed at least one act of animal cruelty. Dogs, cats and rabbits were among the most common victims of adolescent animal cruelty but also the most liked animals. Strikingly, animal cruelty is retrospectively evaluated as a part of growing up and seems to be extenuated by perpetrators. This needs to be addressed and implications will be discussed for the welfare of the animals.

P169 Co-housing mice with different coat colours as a simple, valid, and non-invasive means of individual identification

Carole Fureix, University Of Guelph
Michael Walker, Rupert Palme, Georgia Mason

Standard practice typically requires that group-housed mice are marked for individual identification. This might compromise welfare, and also cause spurious results. Mixing strains with different coat colours within a cage would allow them to be readily visually identifiable, negating needs for invasive marking techniques. Here we test the impact of mixed strain housing on the phenotypes of female C57BL/6 (black) and DBA/2 (brown) mice, and the variability of the data they yield. Fifty-six mice were housed in mixed strain or single strain pairs for 19 weeks, from weaning into adulthood, and their phenotypes assessed using 23 different behavioural, morphological, haematological, and physiological measures (including several relevant to welfare). Mixed strain housing did not increase the variation in data obtained, nor have negative effects on the

phenotypes of either strain. Differences and similarities between strains were typically as expected from previous studies. Only two main effects of housing type occurred, both cautiously suggesting benefits: mixed strain pairs were less stereotypic, and had smaller red blood cell distribution widths. Female DBA/2 and C57BL/6 mice can thus be housed in mixed strain pairs for identification purposes with no apparent negative effects on their welfare or the data they generate.

P170 How congruent are tests for anxiety and fear in the domestic chicken?

Inga Tiemann, Bruno-Dürigen-Institute
Mareike Fellmin

Domestication can be seen as a process which leads to the adaptation of an animal to the human environment. An intrinsic goal of this relationship is to reduce stress e.g., anxiety and fear, and to maximize coping strategies. The aim of the study was to test for possible genetic (breed-specific) or individual differences in the chicken's behavior. We observed 16 breeds of the domestic chicken (minimum n = 5) in two tests, looking for anxiety in the open field and for fear in the tonic immobility test. In the open field, distance covered within 15 min was analyzed. In the tonic immobility test, animals were manually restrained on their back and released after 15 sec. Duration of time until the animal turned was analyzed. Results of the open field and the tonic immobility test were not completely congruent ($r = -.232$). In addition, we found major breed-specific differences in both tests (open field $p < .001$; tonic immobility $p = .006$). These ethological findings invite further genetic identification of desired characters which could reinforce coping and, therefore, adaptive strategies in domestic animals.

P171 Pain in fish? Behavioural responses to fin-clipping in zebrafish (*Danio rerio*)

Clare Andrews, University Of Edinburgh
Craig McLaren, Ignacio Vinuela-Fernandez, Gidona Goodman

The taxonomic distribution, evolutionary function and practical assessment of pain in animals poses questions for pure and applied ethologists. Recent anatomical, neurophysiological and behavioural evidence suggests several fish species are capable of experiencing pain. Zebrafish are amenable models for behavioural genetic, neurobiological and endocrinological research, and their use is rapidly

expanding, often being viewed as a replacement for mammalian models. Tissue samples for genetic analyses are obtained through fin-clipping (surgical removal of part of the caudal fin) under anaesthesia but without the provision of analgesia. Tail fin-clipping has been shown to induce pain-associated responses in various fish species. Here, we examine for the first time the potential of fin-clipping in zebrafish to be painful. We compare behaviour of fin-clipped, anaesthetic-control and handling-control groups of zebrafish, examining swimming activity and anxiety-related behavioural responses in novel object and light-dark tests. We also investigate physiological parameters of respiratory rate and holding-water cortisol concentration as potential indicators of pain. Our results are important for pain monitoring in this common laboratory model and contribute to the future refinement of procedures in order to improve animal welfare and scientific validity. We also discuss implications for the understanding of fish sensory abilities and behavioural evolution.

P172 Additional foraging elements reduce fur-chewing and stereotypic behaviour in farmed mink (*Neovison vison*)

Jens Malmkvist, Aarhus University
Steffen W. Hansen

We studied 200 juvenile mink (half males and females) during the 5-month growth period with plenty of feed and subsequently adult females during the 2-month period of feed restriction before mating. The mink were distributed in four equal-sized groups: FARM, farm feeding without foraging enrichment; ROPE, access to biting ropes; CHNK access to chunky feed; BOTH, access to both biting ropes and chunky feed. In growing mink, biting rope access reduced fur-chewing (16 % vs. 29 % of mink without biting ropes; $P=0.044$), and chunky feed reduced both fur-chewing (16 % vs. 33 % of females without chunky feed, $P=0.019$) and the low amount of stereotypic behaviour (0.1 % vs. without chunky feed: 0.8 %; $P=0.038$). During the season of feed restriction, the wear/tear of biting ropes increased. In the restrictively fed adult females, fur-chewing was reduced both by access to biting ropes ($P=0.005$) and chunky feed ($P=0.007$). Consequently, 54 % of group FARM mink showed fur-chewing reduced to 21 % in group BOTH. In conclusion, stereotypic behaviour was reduced by provision of chunky feed, increasing the consummatory element in daily foraging. Fur-chewing was reduced upon access to either biting ropes or chunky feed in mink females throughout the study.

P173 Effect of providing additional drinkers on alleviation of moderate heat stress in broiler chickens: a behavioural study

Oluwaseun Iyasere, Newcastle University
Melissa Bateson, Jonathan Guy, Andrew Beard

Heat stress is a worldwide problem in broiler chickens. We investigated whether provision of additional drinkers can alleviate heat stress. Since birds exposed to heat stress use thermoregulatory behaviours such as wing drooping to maintain core body temperature, we used the frequency of these behaviours to measure the effect of our intervention. A total of 64 Ross broiler chickens participated in a 2 × 2 factorial experiment with two environmental conditions; normal or moderate heat stress (MHS), and two levels of drinker provision, standard (SD) or additional (AD). MHS was imposed for 6 hours/day for 3 days. During the 6th hour of heat stress, birds were scan sampled each minute for nine categories of behaviour, namely wing drooping, panting, drinking, feeding, preening, lying, standing, foraging and sitting. MHS increased the proportion of birds' wing drooping, panting and drinking, but decreased those preening, lying and foraging. AD increased the proportion of birds feeding. There was a significant interaction between environmental condition and drinker provision on wing drooping behaviour: provision of AD to birds exposed to MHS reduced wing drooping. Therefore, provision of additional drinkers reduces signs of heat stress, and could be used as an intervention to combat this welfare problem.

P174 Indicators of playfulness in rats

Luca Melotti, University Of Bern
Jessica Lampe, Oliver Burman, Hanno Würbel

Play is a universal feature of behaviour among higher vertebrates and is regarded as a promising indicator of animal welfare. To study play behaviour and its consistency across contexts, we investigated potential indicators of playfulness in adolescent male Lister Hooded rats ($n=21$) by measuring conspecific and heterospecific play. At 6 weeks of age, group-housed rats (three per cage) were socially isolated for 3.5 hours per day for three consecutive days. After each isolation period, a different pair combination of cage-mates was returned to the home cage and both social and solitary play were scored for 20 minutes. Scores from different pair combinations were combined to form individual play scores. At 7 weeks of age, rats were individually tickled by the experimenter

through bouts of gentle, rapid finger movements on their underside, during which approach towards the experimenter's hand and vocalisations were recorded. We found that conspecific play was longer when play roles were more unequal, and was unrelated to solitary play. Positive vocalisations emitted during tickling positively correlated with approach behaviour. Both conspecific and heterospecific play revealed high individual variability within and between cages, and were not related suggesting the existence of independent factors within the playfulness dimension.

P175 Red Junglefowl (*Gallus gallus*) selected for low fear of humans have improved welfare and fitness in captivity

Beatrix Agnvall, Linköping University
Anser Ali, Per Jensen

Reduced fear of humans is a major component in domestication of animals. It has been suggested that many of the traits associated with domestication could have developed as correlated responses to such reduced fear. To investigate this, Red Junglefowl (ancestors of domestic chickens) were selected on high or low fear response towards humans, generating three strains, High (H), Low (L) and Intermediate (I) fear. We investigated possible correlated effects on social behaviour and social dominance, and changes in other, non-behavioural traits relating to welfare and fitness. Birds from the third generation were tested in three different social tests, and growth and plumage condition, as well as size of eggs and offspring were recorded. Animals selected on low fear response towards humans (L) had a higher weight, laid larger eggs and generated larger offspring than H and I. They also had a better plumage condition. L-birds performed more and received less aggressive behaviour in a social dominance test and were more food motivated in all tests. The results indicate that social dominance was affected by selection on reduced fear of humans, and the welfare and reproductive ability was improved under the housing conditions applied in this experiment.

P176 Public attitudes to stray dogs and dog rescue shelters - a pilot study

Simona Normando, Padua University
Sara Gianotti, Antonio Mollo, Rebecca Ricci

Different countries have adopted different policies concerning dog overpopulation, but the public perception of these regulations has seldom been

investigated. In the present study, 227 answers to an online Likert-like scale survey on the public attitude to unwanted dogs and related regulations were analysed. Gender and dog-ownership of the respondent were independent variables in U-Mann Whitney tests. The Italian no-kill policy for dog shelters was completely agreed upon by 61% of the sample, with women (n°149) agreeing more ($p=0.016$) than men. Sixty-five% of the sample completely disagreed on the culling of stray dogs bands, with men agreeing more ($p=0.0006$) than women and non-owners than owners (p from 0.02 to 0.003). Only 23% agreed (11% partially and 12% completely) on a trap-neuter-release for stray dog bands, while most respondents agreed (22% partially and 37% completely) on moving them to shelters, with women agreeing more ($p=0.006$) than men. Fifty-one% of the sample completely agreed that a more efficient public control of shelter dogs' welfare was needed, women agreeing more ($p=0.002$) than men and dog owners than non-owners ($p=0.01$). In conclusion, given the general agreement on housing unwanted dogs in shelters, more studies on factors affecting the welfare of shelter dogs are needed.

P177 Does the volume of intraperitoneal injections affect the welfare of laboratory rats?

Rachel Peden, Centre For Behaviour And Evolution, Institute Of Neuroscience, Newcastle Univers
Dominic Dwyer, Paul Flecknell, Matt Leach, Candy Rowe

Current guidelines recommend volumes for intraperitoneal injections in the rat of between 10-20mL/kg, although volumes administered during research are often greater. As there are no scientific data to support these guidelines, we investigated whether commonly administered volumes cause pain or discomfort to laboratory rats. Three groups were allowed to drink a novel sucrose solution prior to being given either: a sham intraperitoneal injection (needle insertion only), or either a 25mL/kg or 50mL/kg saline intraperitoneal injection. Pain and discomfort were assessed by comparing the exhibition of validated pain behaviours before and after the procedure. Consumption of sucrose was assessed 24 hours later to provide a measure of any conditioned taste aversion (CTA) produced by the procedure. We found that increasing injection volumes were associated with behavioural indicators of discomfort, such as increased abdominal grooming and reduced high-rearing. Furthermore, although the sham group significantly increased their consumption of sucrose the following day, rats injected with 25mL/kg and

50mL/kg of saline were less inclined to increase their consumption. Overall, our data provide the first scientific evidence to suggest that larger intraperitoneal injection volumes are associated with discomfort and produce CTAs in rats, which could lead to evidence based changes in current guidelines.

P178 Behavioural assessment of disease progression in laboratory mice using radio-frequency identification homecage technology

Claire Richardson, Newcastle University
Melissa Bateson, Paul Flecknell, Caroline Wilson, Fiona Oakley

Developing our capacity to objectively measure disease progression can help us to improve laboratory animal welfare by identifying periods in a study when pain and distress are likely to occur. In this study behavioural assessment was carried out on 16 socially housed male mice within their 2 homecages. Prior to the induction of disease each mouse was implanted with 2 subcutaneous radiofrequency identification transponders to measure both behaviour and temperature. Under isoflurane anaesthesia with buprenorphine administered as an analgesic, all animals underwent surgery and had liver disease induced by bile duct ligation. Minipumps were also implanted during this surgery; mice in the treatment group received a therapeutic compound and control animals received a vehicle. In the 2 week study period animals' body temperature decreased significantly by a mean of 2.4°C. Change in body temperature did not vary between treatment groups. Severity of liver disease determined by histological staining of collagen in the liver was significantly greater in the control group compared to the treatment group and correlated with the individuals' pattern of drinking within their homecages. These findings support the hypothesis that subtle changes in behaviour can be used to objectively and non-invasively study disease progression in mice.

P179 Play behaviour is affected by early human tactile stimulation in pigs

Manja Zupan, Swedish University Of Agricultural Sciences

Therese Rehn, Daiana de Oliveira, Linda J. Keeling
It is known that tactile stimulation (TS) during ontogeny modifies the brain plasticity and enhances motor and cognitive skills of animals, but there is no documentation on how this type of handling correlates with play behaviour in pigs later in life.

Piglets from 13 litters were subjected to gentle stroking (from 5-35 days of age) according to one of four treatments: all piglets in the litter were handled (H), none of the piglets were handled (NH), half of the piglets in the litter were handled (50/50H) or not handled (50/50NH). After weaning, the pig's locomotor, solitary object and social object play was observed in pairs in a novel environment.

Locomotor play was greatest in handled piglets (H and 50/50H) but the total amount of play, and social object play in particular, was higher in piglets from 50/50 litters, irrespective of whether they were handled or not (Glimmix procedure; overall, $P < 0.05$). We propose that while TS did affect motor skills, as predicted, handling half of the piglets in the litter may have triggered a series of socio-emotional interactions that were beneficial for the whole group.

P180 If ontogenesis scale of wolf pups (*Canis Lupus*) contains features were unknown before?

Anna Yachmennikova, Russian Academy Of Sciences
Ekaterina Blidchenko, Andrey Poyarkov

The present study is concentrated on the group behaviour development; mutual social influence of cubs particularly. The time-period of wolf pup social system establishment is under analysis. The main question: when we analyze development of social animals in the group all together if we could catch period when primary social grouping practically appears as a holistic unit? A simple social group of four not tamed growing pups which were kept in captivity were used as a test model, the sample is 2 groups. We reared pups by using recommendations for re-introduction into the wild. Data processing: old ethological methods; (indexes of individuals association, of synchronization their activity, distances between sleeping individuals, sociograms, the variability of contact intensity) and relatively modern method of T-patterns in group behaviour detection, Theme (NOLDUS) was used. For physical changes we measured the weight gain in the wolf pups and the ratio of different types of activity. As a result, we assume the existence of a period of multi-aspect transformation in the ontogenesis showed on the scale scheme. During this non-linear and sharp change were found in the amount of activity, activity synchronization, rates of growth, rates of development and social structure in the wolf pups.

P181 Play development in three felid species

Anastasia Antonevich, A.N. Severtsov Institute Of Ecology And Evolution

Galina Alekseeva, Ekaterina Pavlova, Yulia Loschagina, Maria Erofeeva, Sergey Naidenko

Social development in felids is mostly studied for domestic cat, but its social life is different than in other felids. Social play with littermates is essential for cub's social skill development and may act as an adaptation for further interactions. We analyzed the differences in social play development between three felid species: Eurasian lynx (*Lynx lynx*), Far East wild (FEW) cat (*Prionailurus bengalensis*) and domestic cat (*Felis catus*). The study was conducted at the biological station Tchernogolovka in Russia. Litters were raised with their mothers. Observations were made using continuous recording method. Although play behavior developed similarly in three species, species specific traits were found. Lynx kittens had lower variability and frequencies in play than domestic and FEW kittens. We classified play elements by dimensions "activity" and "contact". Lynx kittens had higher percentage of active contact play than FEW and domestic kittens. Domestic cat differed from both solitary species in the lower frequencies of active contact and non-active non-contact play. Species specific differences in play behavior could be related to differences in social activity of adults or adjusted to particular needs of kittens in each age period. The study was supported by RFBR 12-04-32028.

P182 The effect of juvenile and adult density on the developmental plasticity of behaviour and genetic variance

Chang Han, University Of New South Wales
Robert Brooks

Both juvenile and adult environment can change developmental trajectories and interactively shape behaviour in later life. However, within a population, the developmental response of behaviours to environments can vary among genotypes. Here we use a full-sibling, split-brood experiment design and random regression model to understand the variation in developmental plasticity across juvenile/adult density conditions in four behavioural traits of water striders: exploration, dispersal, same-sex behaviour and remounting attempts. Our results showed that both juvenile and adult density affected behavioural development, and that there was modest level of genetic variation in all behavioural traits. In contrast, there was little variation in genotype-environment interactions (G×E) across density conditions observed in all traits other than same-sex behaviour. We suggest that experiences at different life stages can interact to affect the behavioural expression of families (G×E×E,

genotype-multiple environment interaction), but variation in G×E or G×E×E depends on traits. Hence we highlight how genetic variation in behavioural plasticity is related to experiences at different life stage and how the effects of experience at those life stages combine.

P183 The development and individual lateralization of prey delivery in a bill load-holding bird

David Craig, Willamette University

Laterality is widespread among vertebrates and has been documented among some birds. Bill load holding or the delivery of whole prey in a bird's beak is common among terns (Charadriiformes) and many other birds. We recorded more than 200 hundred hours of Caspian tern, *Hydroprogne caspia*, chick-feeding events for analysis of individual lateralization of prey within the bills of adult birds, size and shape of prey items delivered to chicks in relation to chick age, and the development of prey-handling skills among chicks. No initial lateralization of prey head position was found as adults flew into the colony, but head position of successful feeds was found to be significantly lateralized in individual chicks with a bias to the right side for the entire population. Lateralization was most obvious in the first week of a tern's life and some individuals were more strongly biased than others. Adults appeared to modify their delivery behaviour to respond to individual chick laterality biases. Bill load-holding birds are excellent subjects to study lateralization of feeding behaviour in the wild and they may allow integration of lateralization with developmental changes.

P184 A comparative study between newborns placed in institution, foster family or infant-mother centre: Behaviours and states of awakesness during bath

Edwige Ducreux, Université De Sherbrooke
Odile Tessier, Guadalupe Puentas-Neuman

The present study used an ethological approach to explore the behavioural adjustment of nineteen newborns from their arrival through the first six weeks of their placement in institution, in foster family or in infant-mother centre. Direct observations were conducted once a week during bath. Observed behaviours were: motor activity, facial expressions, vocalisation, feeding-related behaviours and states of awakesness. Data were analyzed with SPSS as a function of modality of

placement. Results show that babies placed in institution, regardless of their age, spent the least time in alert state the most time in crying, the most time in inertness and showed the highest frequency of feeding-related behaviours and the lowest frequency of vocalization. Moreover, in institution the duration of the bath was the shortest. Babies placed in infant-mother centre showed the highest frequencies of motor activity, facial expressions and vocalization. According to these results, babies placed in institution were less awake and active in discovering their physical and social environment. This difference can be partly explained by the lesser time spent by caregivers in babies' care. In opposition, the placement in infant-mother centre seems to be the most favourable for the development of babies and would deserve to be promoted.

P185 Development of personality in corvids and the role of conspecifics

Rachael Miller, University Of Vienna
Thomas Bugnyar, Christine Schwab

Stable individual differences, referred to as "personality", are of interest in animal studies as they impact on learning, performance and behaviour. In a social context, personality traits may be facilitated or inhibited, due to the identity of the conspecific(s) present. However, most studies test in an individual or group context only, so are unable to investigate the influence of a specific individual's personality on another. Furthermore, we know relatively little about how personality develops in non-human animals. Here, we tested 10 carrion crows *Corvus corone* and 9 common ravens *Corvus corax*, comprising 6 sibling sub-groups, housed in species groups at Haidlhof research station, Austria. Subjects received a range of response to novelty and familiar control tests, run repeatedly from fledging until 9 months old, in sibling dyads, individual and group context. We predicted that behaviour during individual tests would be fairly consistent over conditions and time, though anticipated an influence of becoming neophobic. We further predicted that social context would influence individual behaviour, dependent on the personality of the focal and conspecific(s) present. Results generally confirm the predictions. We discuss the strength of the effects and how our findings may inform research on personality in general.

P186 Ontogeny of consistent individual differences in behaviour in a wild-type rodent

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Expérimentale Et Comparée
Heiko G. Rödel

During the last decades, interest has been grown sharply in the study of individual differences in behaviour that are consistent across time and context. However, little attention has been paid to the developmental origins of such differences, usually referred to as temperament or animal personality. The goal of our study was to describe the ontogeny of consistent individual differences across successive life stages using standard behavioural tests. Experiments were conducted with wild-type mound-building mice (*Mus spicilegus*), a small rodent from Central and Eastern Europe. We found clear consistencies in certain behavioural responses across different life stages, indicative for the existence of temperamental traits. However, there was huge individual variation during early juvenile life stages, and in particular the current state of the animals (e.g. differences in juvenile body mass) was an important source of such variation. On-going studies will show whether such differences are reversible or if early developmental differences have long-lasting and priming effects on the animals' behavioural profiles.

P187 Collective Decision Making And Interindividual Variability In The Aggregation Process In *Periplaneta Americana* (L.)

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Grégory Sempo, Céline Gibon, Jean-Louis
Deneubourg

Aggregation is one of the most widespread social behaviors among animals. Collective decisions which lead to aggregation emerge from the interactive network within the group. The global understanding of these collective decisions require the integration of two levels of analysis: the individual and the collective one. In this respect, most of the studies on collective decision making neglect or underestimate individual idiosyncrasies.

Through the use of the RFID tagging method, we have shown a strong variability between individuals within a group in terms of responses to environmental heterogeneities (e.g. resting sites where individuals aggregate). The differences between individuals are maintained through time over successive experiments. Beyond this inter-individual variability, we have observed that some key-individuals act as initiators of the aggregation process and that the level of exploration varies among experimental groups. We have theoretically

analyzed how idiosyncrasies affect the dynamics of the collective response and individual fitness. Finally, based on our experimental and theoretical results, we argue that similar influences of idiosyncrasy on collective response may be present in other social species, as well in many collective activities.

P188 Do nervous cows produce more milk? The relationship between production and personality in dairy cows

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Hanne Lovlie

Variation in animal personality (i.e. behavioural responses consistent within individuals over time and/or across contexts) is predicted to be related to life-history traits, such as growth rate and investment in reproduction. How this translates into relationships between personality and milk production in dairy cows is however scarcely investigated and previous studies are showing contradicting results. To further investigate this relationship, we studied intra-individual consistencies in behaviour in relation to milk production in two breeds of dairy cows (Holstein and Swedish red and white cattle, SRB). We found variation among the breeds in consistency of behaviours. In both breeds were stepping behaviour during milking (a measure of nervousness) and frequency of performed abnormal behaviours highly correlated over time. Variation in neophobia and responses to social separation were more flexible, both among breeds and over time. Nevertheless, most behaviours showed limited relationship with milk production; Holstein cows producing generally less milk displayed more abnormal behaviours and SRB cows producing less milk early in life were more nervous when socially separated. To conclude, the tests here carried out are useful in describing personality in cows; however, personality showed limited relationship with milk production encouraging future studies to explore this further.

P189 Coping styles and welfare in farmed fish: current understanding and future directions

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Maria Filipa Castanheira, Marcelino Herrera, Sandie Millot, Marco Cerqueira, Luis Conceiso

Individual variation in behavioural and neuro-endocrine responses to aversive stimuli in fish is no longer recognized as noise around a mean. Instead such variation seems to represent adaptive

responses that are crucial for survival in a continuously changing environment. In fact, individuals of the same fish species can display consistent responses in stressful situations, i.e. they exhibit coping styles. Over the past 10 years the interest on understanding coping styles in farmed fish has increased because many studies have established links between coping styles and welfare problems. This study will review 1) the methodological approaches used to identify coping styles in the most relevant farmed fish, 2) the main behavioural, neuro-endocrine, cognitive and emotional differences between reactive and proactive coping styles in fish and 3) how the knowledge on coping styles may contribute to improve the welfare of farmed fish. This review will show that 1) methods are already available for fast screening of coping styles at the farm level, 2) behavioural, neuro-endocrine and cognitive characteristics of coping styles in fish share many similarities with other vertebrates and 3) coping styles influence a number of welfare relevant issues such as performance traits, disease resistance, aggression, cognitive ability and affective states.

P190 Is personality a lame excuse in horses?

Carrie Ijichi, Queen's University Belfast
Lisa Collins, Hugh Suffern, Robert Elwood

Tissue damage may result in pain and induce protective behaviour, such as limb guarding. Because we cannot directly measure an animal's subjective experience, veterinary assessment and pain research rely on these behavioural indicators when quantifying pain. This assumes pain expression is proportional to damage but this has not been tested in animals and ignores the possible effects of personality and coping style. Our first aim was to assess if lameness accurately predicted the severity of tissue damage, or whether there is variance in how stoical individuals are. An experienced equine vet scored horses for lameness then severity of damage using either x-ray or ultrasound during the course of normal diagnostics in a clinical setting. Surprisingly, we found no relation between scores for lameness and severity. Consequently, stoicism was calculated as *severity score - lameness score*. Our second aim was to assess whether personality might be linked with Stoicism and pain behaviour. Personality was quantified using a validated questionnaire, completed by owners. Owners also gave their subjective opinion on how tolerant the horse was to pain using a 1-5 likert scale. This is the first paper to assess the relationships between severity of tissue damage, pain behaviour and personality in animals

and we found novel links between personality and pain behaviour. Future work to clarify these findings and major implications for accurate assessment of damage and pain in animals are discussed.

P191 'Personality' in Laboratory Mice: A Way of Understanding Standardisation-Resistant Variability?

Lars Lewejohann, University Of Muenster
Benjamin Zipser, Norbert Sachser

The mouse, including countless lines of transgenic and knockout mice, has become the most prominent model organism in biomedical research. Behavioural characterisation is often conducted in batteries of short tests on locomotion, anxiety, learning and memory, etc. In such tests, any individual differences within groups are usually considered to be disturbing variance. Hence, in order to reduce this variance in experimental animal research, enormous efforts of standardisation have been made. Fundamentally, the genetic variability of mice has been minimised by means of inbreeding for many generations. While a substantial reduction of variability has been reached compared to the earlier years of experimental animal studies a considerable amount of inter-individual differences still seems to escape all efforts of standardisation. This effect is demonstrated and evaluated by recent data from highly standardised experiments conducted with inbred mice. Interestingly, behavioural patterns of individual animals seem to be correlated across contexts and time. In evolutionary biology, 'animal personalities' have been discussed recently to comprise such stable patterns. We argue here, that non-random behavioural correlations across contexts and time might underlie the variability commonly found in highly standardised experiments such as biomedical mouse studies.

P192 Your face says it all: red and white bill markings signal quality and identity in the black swan, *Cygnus atratus*.

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Kaspar Delhey, Raoul Mulder

Birds display colourful beaks in a wide variety of social contexts. Yet in contrast to plumage, we know little about the function of bill colour. Colourful bills may broadcast information about individual quality or identity. Models of these signal types predict that signals of quality should be costly and condition-dependent, whereas identity signals should be

cheap, independent of physical condition and vary more between- than within-individuals to remain effective. We tested these predictions on the red and white bill markings of the black swan, *Cygnus atratus*. Each swan had a unique white bill stripe in shape and size that did not change over time. Furthermore, white stripe area did not correlate with body condition or brood size. These findings are consistent with an identity signal. Intriguingly, both red and white bill patches were condition-dependent, but only for males. Red and white patches were also correlated with brood size, but in opposite directions for males and females. These findings are consistent with quality signals but suggest that the costs of maintaining bill colour differ for each sex. Thus, models suggest bill markings in black swans indicate both identity and individual quality.

P193 Singing behaviour of male great tits suggests personality and phenotypic quality

Kaarin Koosa, Tartu University
Vallo Tilgar

Behavioural differences between individuals as well as intra-individual consistency of behaviours are believed to reflect the nature of an animal. In songbirds, rival's song overlapping rate has been found to be a stable behavioural trait over time and is therefore assumed to reflect singer's personality. We conducted playback experiments on male great tits (*Parus major*), and found that song overlapping rate was repeatable over time but unrelated to subject's body parameters or reproductive performance. However, we found that male's song overlapping was positively correlated with female's risk-taking behaviour towards artificially imitated nest predator. Furthermore, we discovered that females produced larger clutches when paired with males of less variable song overlapping between consecutive trials. We conclude that males' behavioural consistency is a reliable indicator of individual quality in terms of good territory or sexual attractiveness to females. Moreover, if the high rate of song overlapping is an indicative of male dominance or aggressiveness, this result demonstrates that males are paired with females alike.

P194 To sing or not to sing: personality is associated with singing activity in wild great tits (*Parus major*).

Erica Van Rooij, Wageningen University
Lysanne Snijders, Kees Van Oers, Marc Naguib

Sexually selected signals like birdsong, vary among individuals often signaling individual quality or motivation. Additionally, part of the variation in singing activity among individuals may reflect consistent intrinsic differences (personality), as well as social and environmental factors. Yet, the interaction between these factors is not well understood even though this interaction most likely drives the decision to sing and thus act as potential selection agents on song. Using a personality-typed field population of great tits (*Parus major*) we show how personality affects singing activity at different reproductive stages and times of day. Additionally, we examine how singing activity among neighbours affects song content and sharing. Current findings indicate that individuals differing in personality have different strategies in using sexually selected signals, allowing conspecifics to extract personality-information from the song. These singing strategies indicate that males differing in personality partly use different signaling windows, possibly reducing direct social interactions with males of different personality. Such temporal segregation in singing also would facilitate females to assess male personality. These findings highlight that multiple factors including personality need to be integrated, when assessing causes of variation in the expression of such highly variable sexually selected signals.

P195 Personality and Survival of Translocated, Wild and Rehabilitated, Juvenile European Hedgehogs (*Erinaceus europaeus*)

Sophie Lund Rasmussen, Copenhagen University, The Behavioural Ecology Group
Torben Dabelsteen

An increasing number of orphaned hedgehogs are brought to rehabilitation centers where they stay for a period before being translocated back into the wild. Their survival has rarely been studied, but likely depends on clinical condition as well as personality. We tested this in 10 juvenile, wild-caught and 14 rehabilitated hedgehogs. Their behaviours were observed in a novel arena (NA) and two novel object (NO) tests. The NO test setups were a ball and a stuffed animal toy combined with badger feces.

The tests showed that it was possible to divide the hedgehogs into relatively shy and relatively bold individuals. The number of shy and bold individuals did not vary between wild and rehabilitated hedgehogs, but the latter had a longer approach time to the novel object with the badger setup. After a week in arenas, the hedgehogs were released into the wild wearing radio transmitters.

They were radio tracked, and their clinical condition and survival was monitored. Personality did not influence survivability. More wild than rehabilitated hedgehogs survived in captivity, but the post release and general survivability between wild and rehabilitated individuals did not differ, indicating that rehabilitated juveniles are capable of surviving post release despite their background.

P196 Are behavioural differences of scavenging wild common ravens (*Corvus corax*) related to age class, experience, bonding and social status?

Sabrina Reimann, Department Of Cognitive Biology, University Of Vienna
Matthias-Claudio Loretto, Thomas Bugnyar

In a human influenced landscape ravens often use anthropogenic food sources year round. The Cumberland game park in our study area is such a food source, which, depending on the season, attracts 40-100 ravens per day. Here we focus on behavioural differences between individually marked ravens foraging at the enclosures of wolves (*Canis lupus*) and wild boars (*Sus scrofa*). Specifically, we investigate if age class (juvenile, subadult, adult), experience with the situation (regularly visiting 'local' bird, infrequent visitor), bonding status (with/without partner) or social status (breeder, non-breeder) affect the birds' use of enclosures. We predict that younger and/or inexperienced birds should have a preference for participating at feedings of boars rather than wolves, since the latter poses a high risk for getting injured or even killed. Birds with local knowledge and/or high social status, however, should prefer wolf over boar feedings due to the differences in food quality. Bonding status should mainly affect the ravens' opportunities to get food from conspecifics via tolerated theft and sharing and thus might only indirectly influence their choice of enclosures. Our preliminary results support most of these predicts. How the observed patterns fit the assumption of foraging ravens being flexible Machiavellian players is discussed.

P197 Variability In Morphological Traits As A Reproductive Strategy In A Lizard Model

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Cecilia Blengini, Sergio Naretto, Gabriela Cardozo

Sexual selection is an important force driving the evolution of morphological traits. We aimed at

elucidating the variability of morphological traits as a reproductive strategy in the context of sexual competition in lizards. As a model of study we focused on two phylogenetically sister Tegu lizards, *Tupinambis merianae* and *T. rufescens*, which are phenotypically similar and exhibit male-biased sexual size dimorphism. We quantified the variation in sperm traits between species, among males and within males in both species. We also quantified sexual differences of the Pterygoideus jaw muscle, the relationship with male reproductive condition and temporal variation throughout the reproductive period. We found substantial within-male variation for all sperm traits. Moreover, we also observed significant variation in the mean values and within-male variation of sperm traits among males of both species. Furthermore, we detected differences between species in all sperm components. These results suggest that within-male variation in sperm traits may be a strategy to afford sperm competition. Moreover, in both species males had larger jaw muscles than females, mainly during the reproductive activity. Seasonal increment of muscle mass at maturity suggests that jaw muscle might be a secondary sexual character acting as an honest signal of reproductive condition.

P198 The effect of parasitism in the evolution of consistent individual behavioural differences

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Ann Hedrick, Anssi Vainikka

Consistent, individually characteristic, expressions of behavioural traits (i.e. personalities) and their evolutionary and ecological importance are currently a topic of intensive research interest. We, together with other researchers, have suggested that parasites and pathogens may provide an ultimate explanation for the evolution and diversification of animal personalities. This proposition is based on the negatively frequency-dependent selection generated by parasites and pathogens - which are ubiquitous. By inducing and maintaining genetic variation in host immune function, parasites affect the optimal behaviour of individuals. This occurs if the fitness benefits and costs of different behavioural types are dependent on individuals' immunological capacity. In this scenario (that contradicts recent ideas based on the structure of pace-of-life syndromes), individuals that are genetically resistant or able to improve parasite resistance through high food intake rate behave more boldly than less resistant individuals. Moreover, the stronger is the risk of parasitism, the more strictly individuals are predicted to follow their optimal behavioural trajectories. Therefore,

consistent individual differences in behaviour should most commonly be detected in highly parasitized populations.

P199 Personality in the African Striped Mouse *Rhabdomys pumilio*: a combination of competing interests?

Megan Mackay, University Of The Witwatersrand
Neville Pillay

Personality traits are not often considered in investigations of adaptive diversification, yet personality types are often a product of environmental selection pressures. The genus *Rhabdomys* is widespread in southern Africa, characterised by marked climate and vegetation variation. *Rhabdomys pumilio*, occurring in desert areas, is usually bolder and more exploratory than the grassland-inhabiting *R. dilectus*. Recently, *R. pumilio* has been found in the northern grasslands of South Africa, sympatric with *R. dilectus*, but the personality profile of the grassland *R. pumilio* is unknown. We studied the personality profile of grassland *R. pumilio* and thus whether personality is determined by phylogeny or ecology. We tested the personality of *R. pumilio* from the desert and grassland, and *R. dilectus* from the grassland using the open-field/novel object test, the modified plus-maze, the light-dark/startle response test, and a closed exploratory maze. Grassland *R. pumilio* has an intermediate personality profile on the bold-shy continuum between the highly explorative and bold desert *R. pumilio* and the shy *R. dilectus*, possibly indicating that there is selection for an intermediate personality form, that the environment modulates gene expression of a phylogenetic signal, and/or possible character displacement between *R. pumilio* and *R. dilectus* in the grassland.

P200 Personality relates to measures of oxidative stress in captive greenfinches

Richard Meitern, University Of Tartu
Tuul Sepp, Marju Männiste, Ulvi Karu, Peeter Hõrak

The existence of different animal personalities reflects that there are various ways of coping with stressors. Coping with stressors may result in changes in oxidative status of the animal. Therefore the personality of an organism may be linked to its oxidative status. However, to date the connection between behavioral traits and markers of oxidative stress has not yet been firmly established. We address this question by relating measurable behavioral traits shown to be consistent in time with both measures of oxidative damage (to lipids,

proteins and DNA) and antioxidant defenses in wild-caught captive greenfinches (*Carduelis chloris*).

P201 Chronic exposure to 17 α -ethinylestradiol reduces behavioral consistency in male Siamese fighting fish

Teresa Dzieweczynski, University Of New England
Kimberly Hentz, Brittney Logan

The occurrence of consistent individual differences in behavior within a species both over time and across contexts has received much attention. Endocrine-disrupting chemicals (EDCs) pose a serious threat to aquatic organisms and can have behavioral, morphological, and physiological effects on exposed individuals. 17 α -ethinylestradiol (EE2), the active component in birth control pills, is prevalent worldwide and is known to decrease both courtship and aggression in exposed males. However, how exposure affects behavioral consistency over time is not commonly addressed. To address this, male Siamese fighting fish were presented with a dummy male and dummy female simultaneously both before and after chronic exposure to a nominal dose of EE2. In general, male-directed and female-directed behaviors were reduced after EE2 exposure. Repeatability values were marked lower and level of response was no longer correlated after exposure, suggesting that exposure disrupts behavioral consistency. These results cannot be explained by a temporal effect as they were not found in the control group of unexposed males. This study demonstrates that EE2 exposure may have effects beyond a reduction in overall response. In addition, it implies that males in this species may differ in their sensitivity, an important area for future research.

P202 Time for personality? On the trade-off between effort and information gain in personality tests for the field

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Christine Schwab, Rachael Miller, Thomas Bugnyar, Tecumseh Fitch

Stable individual behavioural differences between animals of the same species have proven to be a fundamental factor influencing animal behaviour. These differences should therefore be taken into account when studying wild populations with regards to their social structure and ecology. Many species have been subjected to personality tests in captivity. However, testing personality in the

field is often challenging due to extensive time effort, practicability of tests and requirement of test-equipment in the field. In order to reduce stress for the animals and increase feasibility of testing, it is desirable to limit the number of tests to those necessary to obtain reliable data on the behavioural type. We therefore aim for "indicator" tests, which make additional tests redundant, yet strongly show an individual's behavioural tendencies.

We present five different personality tests, which we have conducted on 70 wild carrion crows (*Corvus corone*), focusing on boldness. We show correlations among these tests and compare their informational value for the behavioural type of a bird.

We discuss the tradeoff between practicability and information gain of these tests, ranging from the novel room, an extensive but good indicator for behavioural type in our species, to the short but least informative tonic immobility test.

P203 Investigating the link between 'personality' and mate choice in a polygynous pinniped.

Sam Hardman, Durham University
Sean Twiss

Research has shown that male and female grey seals, *Halichoerus grypus*, exhibit a continuum of behavioural types along a proactive-reactive axis. Proactive females tend to show little behavioural flexibility across situations and exhibit high levels of aggression. Reactive individuals tend to show more behavioural plasticity and are generally less aggressive. Recently analysed data suggests that proactive females spend more time in aggression with other adult females, while reactive females show more aggression towards males. High levels of aggression shown towards males by reactive females may be explained by their tendency to be found in low density areas of the colony where they are subject to transient male incursions and harassment; alternatively it may indicate a greater degree of choosiness of potential mating partners. In contrast, proactive females may be able to secure preferred pupping sites in high density areas of the colony which tend to be occupied by more dominant males. Since proactive females have access to dominant males by default they have little need to be choosy about their mating partners and are less aggressive towards males. This situation suggests that female grey seals express mate choice and that there are consistent individual differences in their levels of choosiness.

P204 Are personality traits consistent in fish? - The influence of social context

Maria Filipa Castanheira, Centre Of Marine Sciences - CCMAR

Marco Cerqueira, Sandie Millot, Rui A. Gonzalves, Catarina Oliveira, Luis E.C. Conceisso, Catarina I.M. Martins

Previous studies in Seabream *Sparus aurata* (Castanheira *et al.*, 2013) suggested that individual differences in behaviour reflect distinct coping styles or personality, contrasting consistent traits associations. Here, we investigate the consistency of coping styles in fish kept under different social contexts. Individually tagged juvenile Seabream (n=360; 70.18 ± 11.44 g; mean ± SD) were subjected to a restraining test that consisted of keeping each fish in an emersed net for three minutes. Behaviours measured in the net (latency to escape; escape attempt and total time spent on escape attempts) were collapsed into first principal component scores using Principal Components Analysis (PCA). Using the PCA scores the individuals were divided into homogeneous groups (n=30 each group) of proactive, reactive and intermediate. Control groups consisted of mixed groups with 1/3 of each coping style. After one month the same individuals were exposed to the same test (restraining test) to assess consistency of behavioural responses. Results show that homogenous groups of proactive ($p=0.173$) and reactive ($p=0.152$) groups did not exhibit consistent behavioural responses as opposed to the intermediate ($p=0.010$) group. In conclusion, this study shows that the social context in which fish are kept significantly influence personality traits.

P205 The causality of the relationship between personality and social dominance in the domestic fowl, *Gallus gallus domesticus*

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Olof Leimar, Hanne Lovlie

Individuals in social species commonly form dominance relationships, and are often observed to differ in behaviour depending on their social status. However, whether such behavioural differences are a consequence of the social position, or at least partly a cause of it, is not known. We have investigated the causality of the relationship between social dominance and personality in male domestic fowl (*Gallus gallus domesticus*), which forms relatively stable dominance hierarchies. We found that high exploration and aggression independently predicted a dominant social position. Further, by experimentally changing the social

status between repeated personality assays we found that boldness and territorial crowing appeared as stable individuals properties, independent of social status, but that social status influenced the expression of vigilance and activity. A fairly large part of the observed variation in these behaviours was explained by social status. Together, our results reveal a two-way causality between social position and individual behaviour. We conclude that social position should be taken into account when investigating and interpreting variation in personality.

P206 Puppy personality: The association between observed and reported behaviour

Naomi Harvey, The University Of Nottingham
Peter Craigon, Rebecca Somerville, Caroline McMillan, Martin Green, Lucy Asher

The ability to measure stable and consistent traits in dogs would facilitate selection and assessment of working dogs, such as guide dogs. This study investigated the construct validity of a dog personality questionnaire by comparing trait scores against observed behaviour in controlled tests. Ninety-three guide dog puppies (52 female; 41 male) were tested at 5 (mean 4.78; SD ± 0.729) and 8 (mean 7.98; SD ± 0.775) months of age. The dogs were exposed to a sequence of 11 tests designed to assess the dogs' reactions to: meeting a stranger; obedience commands; body sensitivities; scavenging; animal and human distractions. The behaviour of dogs was videoed and analysed using a scoring protocol which incorporated both continuous counts of behaviour and specific reactions to each test situation. A questionnaire completed by the dogs' puppy walkers and training supervisors comprised 56 items, scored on a visual analogue scale, categorised into 8 'traits': Excitability; General Anxiety; Chasing; Body Sensitivity; Distractibility; Attentiveness; Trainability and Energy. Random effects models were used to analyse associations between questionnaire traits and observed behaviour. Most traits showed some degree of association with predicted aspects of observed behaviour. Results suggest the questionnaire has potential in measuring personality traits in puppies.

P207 Stability and causality of animal personality

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Andrew Grimmer, Craig Walling, Alastair Wilson

Many studies have demonstrated behavioural repeatability consistent with personality variation in animals. However, several gaps remain in our knowledge regarding such variation, e.g. are behavioural differences stable over lifetimes and to what extent is personality determined by genotype and early-life environment?

Using a captive population of the tropical poeciliid, *Xiphophorus birchmanni*, we address these questions in relation to boldness, commonly defined as the reaction of an individual to risky but not novel situations, (Reale et al 2007). We assayed a suite of behaviours across two trial types - open field and emergency and exploration - with repeated observations collected over long and short time periods on two generations of fish.

Using multivariate modelling approaches, including quantitative genetic animal models, we demonstrate repeatable variation for individual behaviours and moderate-high between-trait correlations consistent with an axis of boldness variation. Although there was evidence for individual personality over long periods, short-term repeatabilities were higher than those estimated over lifetimes. While both genetic and early environment effects contribute to personality, much of the among-individual variance in behaviour still remains to be explained.

Real et al (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews* 82, 291-318.

P208 Locusts show handedness during goal-orientated movements

Adrian Bell, University Of Sussex
Jeremy Niven

Handedness in limb control has been well-documented across a wide range of vertebrate taxa, including humans. Studies of handedness have been linked to asymmetries in the nervous system known as lateralisation. In contrast to vertebrates, there has been relatively little research on handedness in invertebrates. We investigated whether desert locusts (*Schistocerca gregaria*) show a preference for a particular forelimb whilst crossing a gap in the substrate upon which they are walking. Locusts must reach with their forelimbs across the gap. We found that locusts exhibit a leg preference when crossing the gap. This preference varies between among individuals; some show prefer to use their right forelimb, others their left. We also recorded leg movements before the initiation of gap crossing to determine whether an individual's preference was the product of a decision making process or simply a continuation of the walking pattern. These results show that small insect nervous systems,

which lack pronounced lateralisation, are capable of generating handedness in limb control. The results also shed light into the evolution of handedness in limb control, which was previously thought only to exist in vertebrates.

P209 A brief review of comparative human-animal personality and areas for future study

Elodie Briefer, Na
James Oxley

Research on animal temperament has increased significantly over recent years. Animal temperament is very similar to human personality, and is defined as individual differences that are consistent over time and between situations (Reale *et al.*, 2007). There is some evidence suggesting that dogs physically resemble their owners (Roy and Christenfeld, 2006). However, to our knowledge, despite some studies having measured the personality of both pets and owners (e.g. Gosling and Bonnenburg, 1998), no study has investigated directly and objectively the potential match between pets and owners' personalities. Furthermore, such comparisons would be biased if pet personality is assessed by the owners, as is often the case (Gosling and Bonnenburg. 1998; Gosling *et al.*, 2003). We suggest that owners' personality may also impact on pets' personality. Alternatively, when selecting a pet, humans could choose one that matches their own personality. This review discusses studies which could include volunteer workers at rescue centres and farms to investigate how humans select their favourite animal, according to both animal and human personalities. This paper reviews current work relating to personality comparisons/matches/resemblance between humans and animals and suggests potential for future work using methods recently developed to accurately measure animal personality (Reale *et al.*, 2007)

P210 Does eggshell pigmentation pattern signal female and egg quality in the Great Tit (*Parus major*)?

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Zoltán Nyiri, Zsuzsanna Eke, János Török

Many bird species lay eggs speckled with protoporphyrin-based brown spots, however, for most of them, the function of eggshell spotting is unknown. Protoporphyrin shows a pro-oxidant activity, so it has been hypothesized that eggshell

pigmentation may signal the female's oxidative status. In this study, we examined variation of eggshell pigmentation pattern in relation to female traits, egg weight, and the antioxidant concentration of the egg yolk of Great Tits (*Parus major*). We found that heavier eggs had darker pigment spots, which suggests that female body condition and food availability during laying may influence pigment deposition into the eggshell. However, there was no evidence that eggshell pigmentation pattern indicates egg quality in terms of the antioxidant concentration of the egg yolk. Furthermore, we failed to observe any relationships between eggshell pigmentation pattern and several morphological and physiological traits of the female. However, we found that females that laid eggs with a concentrated spotting ring at the blunt end of the egg (coronal ring) showed higher level of oxidative stress. This result suggests that a higher production and deposition of protoporphyrin into the eggshell may have a cost on the female's oxidative balance.

P211 Exploratory strategies in European tits (*Paridae*).

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Eliska Beranova, Alice Exnerova

There is copious evidence that individuals differ consistently in exploratory behaviour. Research has mostly been focused on differences among individuals of a single species, but interspecific comparisons have been neglected. We studied exploratory behaviour and reactions of hand-reared juveniles of three species of tits (great tits *Parus major*, coal tits *Parus ater*, blue tits *Cyanistes caeruleus*) in several types of tests: exploration of novel environment, exploration of novel object, neophobia and reactions towards aposematic and non-aposematic prey of novel appearance. We found significant differences between the tit species in most tests including reactions towards novel and aposematic prey. Blue tits hesitated longer than great and coal tits before attacking novel prey (larvae of house cricket, *Acheta domestica*, with blue coloured sticker) and coal tits hesitated longer than great tits to attack adult aposematic firebug *Pyrhocoris apterus*. Blue tits refused to attack aposematic prey in most cases. In great tits, there was also positive correlation between results of exploration and neophobia tests, while in other two species these two behavioural traits did not correlate. Nevertheless in blue tits we observed positive correlation between exploratory tests and also test of novel object exploration and reaction to novel prey. Funded by CSF-grant P505/11/1459.

P212 Individuality takes all: behavioural plasticity is related to personality type and influenced by social environment

Klara Sichova, University Of South Bohemia, Faculty Of Science

Gabriela Urbankova, Nella Mladenkova, Jan Riegert, Frantisek Sedlacek

Intraspecific variation in the behavioural phenotype, animal personality, represents an omnipresent phenomenon. It has been proved that these behavioural differences are partly heritable, closely related to individual fitness, and show considerable rank order consistency over time and/or across a variety of situations and contexts. However, latter rank order consistency does not necessary denote absolute stability of behavioural values at an individual level. It has been proposed that behavioural plasticity may vary in different personality types of animals. Despite the importance of this presumed relationship, only a few empirical attempts have yet been completed. Using the behavioural reaction norms approach, we assessed personality types and the individual behavioural plasticity of 61 common voles (*Microtus arvalis*). "Exploration activity" of the same aged individuals was quantified in five experimental sessions. The findings confirmed the prediction that, at least at the phenotypic level, animal personality is linked to a variation in behavioural plasticity. Voles with high initial scores of "exploration activity" tended to decrease their value across repeated sessions and vice versa, both independently on the length of inter-session gap. Moreover, a substantial influence of the amount of siblings on individual behavioural plasticity was detected, despite the fact that voles were reared individually since their weaning.

P213 Consistent Individual Differences in Common Marmosets (*Callithrix jacchus*)

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Animal personalities (or behavioural syndromes, tendencies, constructs, temperaments) refer to groups of correlated behaviours, i.e. a consistent way in which different animals of the same species behave throughout time, contexts and situations. Whereas studies on most non-human animals are based on behavioural and/or physiological data, those on non-human primates are often based on questionnaires. In this study we analysed

personality traits in captive common marmosets (*Callithrix jacchus*) on a behavioural level. We tested 21 subjects from three family groups in five different tasks (general activity, novel food, novel object, predator and foraging under risk) and on two occasions. We analysed behavioural parameters (e.g. latencies, manipulation time, vocalisations, foraging, locomotion) from videos and extracted four principal components, explaining 82.28% of the variance. Three components consisted of traits relating to boldness-shyness (39.53%), activity (19.52%) and exploration-avoidance (14.75%); the fourth component consisted of the duration of calls given (8.48% of the variance), possibly indicating a trait with a social character. Taken together, our findings support the idea that personality traits can be found in common marmosets. Whether or not the social context plays a role in expressing these traits is discussed.

P214 Personality and behavioural plasticity across three populations of the wild wood mouse (*Apodemus sylvaticus*)

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Personality research has greatly advanced over the last decade, with repeatable behavioural traits identified in a wide range of species. However, the number of studies measuring personality traits of wild animals *in-situ* is limited, leading to questions regarding the validity of applying lab based findings to animals in the wild.

In this study three populations of wild wood mice were tested *in-situ* using a portable open field and novel object test. Two behavioural traits were extracted, 'Activity' and 'Boldness', using factor analysis. Linear mixed modelling was then used to quantify individual consistency and behavioural flexibility over repeated tests.

All three sites demonstrated consistent individual differences in activity, but only two of the sites for boldness. Although there were no significant inter-individual differences in habituation, the populations significantly differed in their response to repeated testing, possibly indicating population-level variation in behavioural plasticity. Activity and boldness were correlated across all three sites suggesting a behavioural syndrome.

Further analysis confirmed these artificial behavioural variables relate to real world traits; Mice that entered a trap previously occupied by a conspecific were significantly more bold, and activity levels were significantly greater during

overcast than clear conditions, as has been previously observed in the wild.

P215 Does the travelled distance in Open field test provide reliable information about personality traits in common vole?

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Klara Sichova, Nella Mladenkova, Frantisek Sedlacek

Study of intraspecific behavioural variability has recently attracted substantial attention. The complex of unique characteristics, labelled most often as animal personality, is temporary and contextually consistent and distinguishes the individual from its conspecifics and influences its learning abilities, social and parental behaviour and its reproductive success. The personality traits are commonly described by behavioural tests. One of the most used tests is the Open field test (OFT), represented by an empty apparatus without any odour or visual cues. Individual behavioural profile is often quantified by coding of animal's behaviours or by recently very popular measuring of the travelled distance in testing apparatus. However, measuring of travelled trajectory may bias obtained results (e.g. long travelled distance may refer to neophilia but also to panic reaction). This potential source of results inaccuracy has not been studied yet. In our study we repeatedly tested 61 individuals of common vole (*Microtus arvalis*) in OFT. Subsequently, we analysed travelled distance and chosen types of behaviour (locomotion, immobility, freezing, rearing, grooming and jumping). The first results of our study indicate that there is only a weak accordance between used methods of Open Field behaviour assessment and indicate the importance of further study of this topic.

P216 Behavioural consistency in *Rana temporaria* tadpoles: strong personalities, lack of syndromes, and link to life-history

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Interest in evolutionary behavioural ecology has turned towards understanding individual variation in behaviour, manifesting either as animal personality or behavioural syndrome. Further, behavioural variation has been linked to life-history trait variation currently, possibly forming integrative pace-of-life syndromes (POLs). Here, we tested, using agile frog (*Rana dalmatina*) tadpoles as model, if POLs could be detected in the larval stage of

amphibians based on a common garden experiment targeting two ontogenetic stages and measuring three behavioural traits. Activity was consistent in the early stage and was negatively related to age at metamorphosis. In the later stage, activity, exploration and risk-taking were all consistent, but their relationship with life-history depended on whether the studied individuals were tested in the earlier stage or not. Already tested individuals showed no POLS, but both activity (negatively) and risk-taking (positively) was related to age at metamorphosis in their previously untested conspecifics. We detected only one behavioural syndrome: activity and risk-taking was strongly negatively correlated in the previously tested (i.e. disturbed) group. Our results provide evidence for (i) animal personality in tadpoles, (ii) an activity – metamorphosis-timing POLS and (iii) an unexpectedly strong effect of moderate disturbance related to standard behavioural testing on the emergence of different syndromes later.

P217 Amygdala functioning to psychic trauma and behavior in human

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Objective: A new multidisciplinary research project studying developmental brain damage in medical and educational settings and using the Miyazaki perinatal network system has been supported by a Grant from the Japanese Government (website:www.med.miyazaki-u.ac.jp). This work explores what is known about cognitive processes involved in emotion and temperament and at the same time it clarifies the processes and anatomical structures involved in emotion, temperament and behavior. We aimed to clarify if emotion and its neural substrates require further study.
Method: Social communication in nonhuman primates and humans is strongly affected by facial information from other individuals. Many cortical and subcortical brain areas are known to be involved in processing facial information. In this study we used a long-term incentivized experiment to study this experience of emotion derived from observation of facial information in others.
Results. Nearly 1,000 participants were enrolled. Data showed that there was a gender difference in the conscious experience of emotion (and therefore in amygdala functioning) induced by facial information (joy, anger, and pathos) and this gender difference appeared when the participants are aged

older than 3 to 20 years. About one-fourth of the gender difference of psychic trauma can be explained by differences in education (age).
Conclusion: In this study, we summarize the process of emotion generation, the functions of the amygdala, the conscious experience of emotion, its regulation, dysregulation, and a proposed approach to child psychic trauma. Our projects extended to this work by comparing the relationship between child neurogenesis (Nature 429,761,2004; Trends-Neurosci. 33,121,2010).

P218 Developmental changes of neural activities associated with infants' own-cry perception

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Human infants cry soon after birth, and much more than any other animals. Their cries can attract their caregivers' attentions. We hypothesized that human infants' crying behavior also strengthen their aural-oral loop for abilities to imitate others' vocalizations. In this study, we analyzed infants' own-cry perception to reveal the importance of hearing their own-cries by comparing to others' cries. Healthy infants at 1-6 months of age were presented four types of sound stimulations (infants' own-cries, two types of modulated their own-cries, other infants' cries) for 8 seconds five times each in pseudorandom order, and their brain activities were measured by near-infrared spectroscopy. The mean oxy-Hb concentrations during sound stimulations were calculated, and compared statistically by ANOVA. In 1-2 month of age, the oxy-Hb concentrations to their own-cries were significantly higher than others' cries. But after 3 month of age, there were no significant differences between them. Infants' crying behaviors increase during first two months, then decrease until four months. Our results suggest infants' crying behavior and their own-cry perception have an important function in 1-2 month of age. After that, infants may pay their attention to others more. These results support our hypothesis of human infants' crying behavior.

P219 Very Early Development of Nucleus Taeniae of the Amygdala

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The avian nucleus taeniae of the amygdala (TnA) corresponds to part of the mammalian medial amygdala. Like its mammalian counterpart, it has

been shown to be involved in the control of social function. According to behavioral observations, such control is already necessary early in the ontogenetic development of a bird. If so, TnA should be one of the earliest differentiating brain structures of the telencephalon. Our anatomical study shows TnA can already be delineated at posthatching day one. The volume of TnA exhibits a growth spurt between days 1 and 8, developing at a faster rate than the entire telencephalon. Our results suggest that between days 1 and 8 the growth of neuropil exceeds the enhancement of neuron number and an addition at the same pace of new neurons and neuropil thereafter. A plateau is reached at day 30. The development of TnA precedes that of the song control nuclei and is similar to the early growth of thalamic and telencephalic sensory areas. This adds to the idea this structure may already be involved in social control at the time of hatching. A proximate cause of the early development of TnA might be the direct afference from the olfactory bulb.

P220 Reward-related behaviour in Japanese quail: the effects of environmental enrichment and dopamine and opioid receptors blockers

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Andrea Kohutova

Sensitivity of animals to announced reward, reflecting previous experience and measured by anticipatory behaviour, has been suggested as a possible indicator of welfare status. Induction of anticipation of a positive rewarding stimulus has been shown to have stress-reducing effects. The aim of this study was to define the anticipatory behaviour induced by classical trace conditioning in Japanese quail. Quails were trained to anticipate in the conditioning chamber by gradually increasing the conditioned stimulus (CS) – unconditioned stimulus (US) interval from the 1 to 30 s. Anticipatory behaviour consisted mainly of rapid head movements and standing alert. Frequency of the anticipatory behaviours increased during the interval between CS (flashing green spot, 5 s) and US (food, 10 s), as compared with the same interval before CS and after US. Anticipatory behaviours were affected by housing conditions. Quails housed in wire cages were more sensitive to reward than those housed in the deep litter pen, as reflected by lower anticipatory behaviour in an enriched housing. Treatment with dopamine antagonist haloperidol (0.5 mg/kg i.m.) as well as opioid antagonist naltrexone (5 mg/kg i.m.) suppressed certain part of anticipatory behaviours during the

CS-US interval suggesting the role of dopaminergic and opioid mechanisms in their control.

P221 Stress-induced antinociception in fish: endocannabinoid modulation

Carla Wolkers, Fmrp/usp
Anette Hoffmann

This study evaluated the participation of the endocannabinoid system in restraint-induced antinociception promoted by 3 and 5 minutes of restraint (RES) in the fish *Leporinus macrocephalus*, using the AM251 (3 mg.kg⁻¹), a CB1 receptor antagonist. For this purpose, 80 fish were divided into 10 experimental groups (n=8, per group): Saline (SAL); Formalin (FOR); SAL+RES+SAL; SAL+RES+FOR; AM251+RES+SAL; AM251+RES+FOR. The behavior (speed and distance traveled) was videotaped and analyzed for 5 minutes (baseline), followed by intraperitoneal injection of AM251 of saline. After 30 minutes, animals were submitted to restraint (3 or 5 minutes), and were submitted to subcutaneous injection of saline or formalin 3% (20 µl) in the adipose fin. The behavior was videotaped and analyzed for 5 minutes after the injections. The results are presented as the difference between the post treatment and the baseline data, and were analyzed by One Way ANOVA, followed by post-hoc test of Tukey (P<0.05). The previous treatment with AM251 blocked the antinociception induced by 3 and 5 minutes of restraint stress (P<0.001). Our results provide unprecedented evidence about the participation of the endocannabinoid system in nociception modulation in fish, suggesting that fish possess an analgesic endocannabinoid system that can be activated by environmental factors, similar to what is observed in mammals.

P222 Biogenic amines as mediators of spider behaviour

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Biogenic amines, such as serotonin and octopamine, are important mediators of behaviour in both vertebrates and invertebrates, with remarkably consistent patterns apparent over vast taxonomic ranges. Spiders are popular model systems for behaviour research, but little is known about physiological mediators of spider behaviour and especially little is known about the role of biogenic amines. We quantified base-line levels of biogenic amines at different life stages of the jumping spider

Seruaea incana, and considered the role of biogenic amines as mediators of intraspecific interactions. Base-line levels of biogenic amines might be linked to resource holding potential such that winners and losers tend to differ in base-line levels at the beginning of contests. Alternatively, the winning or losing of contests might induce changes in base-line levels such that winners and losers might be similar in levels of biogenic amines at the beginning of a contest but differ at the end. To address this, we staged contests between size-matched *S. incana* males and measured levels of biogenic amines either immediately after the contest or three days later as well as in control groups that did not experience contests.

P223 Altitudinal modulation of the stress response in Black Redstarts

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Birds breeding in extreme environments with short breeding seasons typically can raise only one brood while individuals breeding in more benign habitats manage to rear several broods. As a consequence, each nesting attempt is more valuable for breeders in extreme environments as it is likely to be their only opportunity. Facing an external stressor, birds respond with the release of corticosterone, the prominent avian stress hormone. High concentrations of corticosterone, however, can suppress parental behaviour and lead to nest abandonment. Therefore, individuals breeding in extreme environments are thought to adaptively suppress their adrenocortical responsiveness during reproduction in favour of the current effort. We tested this hypothesis in European Black Redstarts (*Phoenicurus ochruros*), which breed across an elevation gradient up to 3000 m. We assessed adrenocortical responsiveness by taking blood samples according to the capture stress protocol and established a temporal pattern of corticosterone release in birds breeding at high and low elevations. As predicted, individuals breeding at high elevations had significantly lower baseline corticosterone levels compared to low-elevation breeders. Moreover, baseline corticosterone levels showed significant variation between life history stages (migration, pre-breeding, incubation, and feeding). Our results are in line with studies on birds breeding in Arctic or desert environments.

P224 Cellular scaling rules for brains of passerine birds

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Many passerine birds, particularly corvids, are known to express complex cognitive skills comparable to those observed in primates. In order to examine how these similarities are reflected at the cellular level we counted neurons and nonneuronal cells in passerine brains using the isotropic fractionator method. We show that, in these birds, neuronal numbers scale almost isometrically with telencephalic size, i.e., the average neuron size shows little increase and neuronal density decreases minimally as brains get larger. Neuronal densities in the passerine telencephalon exceed those observed in the primate cerebral cortex by a factor of 3-6. As a result, the number of telencephalic neurons in the Common Raven *Corvus corax*, the largest extant passerine bird, equals those observed in the cerebral cortex of small monkeys. The cerebellum features similar scaling rules. However, because the relative size of the cerebellum is smaller than in mammalian brains, cerebellar neurons make a much smaller proportion of total brain neurons than in mammals. In contrast to the little variation in neuronal densities in telencephalon and cerebellum, the density of neurons rapidly decreases with increasing structure size in the optic tectum. For all examined brain structures, the densities of nonneuronal cells remain constant regardless of structure size, a finding congruent with data from mammals. Our findings strongly suggest that high neuronal numbers and hence high brain's computational capacity underpin the behavioural and cognitive complexity reported in passerine birds.

P225 Homiothermy in giant honeybees (*Apis dorsata*). Occurrence of convection funnels.

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Giant honeybees (*Apis dorsata*) are native to Southeast Asia and build their open nests on tree branches, rocks or buildings. The nest consists of a central comb, which is covered by colony members in multiple layers. The open nesting behaviour is particularly prone to environmental changes. Therefore, giant honeybees have evolved strategies to keep the inner nest atmosphere stable regarding brood temperature, humidity and content of

oxygen. They display thoracic heating if ambient temperature is low, and cool the nest by evaporating water when ambient temperature is high. The present study focuses on the appearance of so-called convection funnels, which are distinct areas on the nest with a local temperature gradient of several centigrades below the surface temperature. The study was primarily carried out on two different nest sites near Chitwan National park (Nepal). Infrared imaging, high definition video recording and image analysis techniques (ImagePro) allowed the detection and characterization of convection funnels over the day, in particular their appearance during mass flight activities. In correlation with ambient temperature, we assessed position and temperature profiles of each funnel over time, and were able to provide evidence that the existence of a funnel is associated with the presence of venting bees.

P226 Testosterone decreases the color expression of carotenoid-based plumage trait of male Serins (*Serinus serinus*)

Sandra Trigo, University Of Coimbra
Paulo Mota

Secondary sexual traits are assumed to have evolved as honest signals of individual quality and an assumption of models of sexual selection is that androgens regulate male secondary traits and reproductive behavior. In the Serin, *Serinus serinus*, carotenoid-based plumage coloration is a sexually selected trait dependent on carotenoid intake of animals during molt. In this experiment, we wanted to test if the plumage coloration expression is affected by testosterone circulating levels. We manipulated testosterone during the single postnuptial molt, by implanting males with an empty or testosterone filled capsule. After molt, the control and T-implanted males had no differences in the extension of the yellow patch and in body condition. However, T-implanted males had less saturated plumage coloration than control males. Our results suggest the existence of a trade-off in the use of carotenoids, since that T-implanted males had to allocate carotenoids in stimulating the immune system to counteract the negative effects of testosterone and, thus produced a drabber plumage coloration.

P227 Role of an avian basal ganglia-forebrain circuit in seasonal song plasticity

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Benoit Le Bec, Arthur Leblois, Catherine Del Negro

Human speech is a complex motor skill and vocal learning is one of the most striking cognitive abilities of the brain. While various brain areas are involved in speech learning and production, cortical and basal ganglia (BG) networks and their dynamic interactions are known to be centrally involved in sensorimotor learning in general, and in vocal learning both in humans and in songbirds. The BG-thalamus-cortical loop is known to be important for song learning in juvenile songbirds. Some bird species, like the canary (*Serinus Canaria*), relearn their song every year, adding new syllables. We take the advantage of this animal model to investigate the role of BG in adult networks reorganization and plasticity. We first provide an extensive quantitative analysis of seasonal song changes. We study the effect of bilateral lesions on the output of the BG-thalamus-cortical loop (the IMAN nucleus) on syllable and sequence variability of adult male canary song. Preliminary results have indicated the IMAN lesions alter both acoustic syllable structure and song sequence in the variable autumn song.

P228 Effects of amygdala lesions on male mouse ultrasonic vocalizations and sexual behavior

Yui Matsumoto, University Of Tokyo
Kazuo Okanoya, Yoshimasa Seki

Mice produce ultrasonic vocalizations (USVs) in several behavioural contexts. Especially, male mice articulate a series of long and various sounds, like a birdsong, to females during courtship and mating. Here, we report functional roles of the amygdala, an important neural module in emotional behavior, on the USVs. We recorded mice vocalizations with presentation of females and categorized those vocalizations into several types like 'upward', 'harmonic' and so on. Then, we created lesions on the amygdala of both hemispheres of the mice while half number of the subjects received a sham-operation. We found altered vocal behaviour between pre- and post-surgery only in the lesion group. After the surgery, appearance rate of 'upward' increased while that of 'harmonic' decreased dramatically. These results could be interpreted in two ways, which are not mutually exclusive. First, the amygdala lesions might cause a kind of persistent approach to females with loss of emotionality, such as vigilance, resulting in increase of 'upward' syllables during courtship. Second, the decreased production rate of 'harmonic' syllables, which often appear during mounting, would be caused by an impairment of the neural pathway for mating behaviour made from the amygdala lesions.

P229 Assessing Vocal Flexibility in a Female Songbird: Does social stress modify the vocal behavior of female zebra finches?

Avelyne Villain, ENES, Université Jean Monnet
Nicolas Mathevon, Clémentine Vignal

One important problematic regarding animal vocal signals is to know how much they are shaped by individual experience (plasticity) and whether they can be momentarily modified in response to the context of emission (flexibility). Birdsong has been a primary model on these questions. Songbirds emit two types of vocal signals: songs -complex successions of notes generally emitted during reproduction or territorial defense- and calls -single notes used in a variety of social interactions. Knowledge about vocal flexibility in birds has developed on songs and barely anything is known about the degree of flexibility in calls, representing the large majority of birds' vocalizations. Moreover, as song has been studied in songbird species whose females do not sing, there is a serious gap of knowledge on vocal communication in females. We focused on domestic female zebra finches to study flexibility in calls. Using playback experiments, we investigated the impact of a powerful stressor – social isolation- on both the female vocal behaviour and the acoustic structure of the evoked distance calls. Results show that calls' acoustic structure is modified by social isolation compared to control (females were accompanied by conspecifics). Specifically, calls recorded during isolation were longer, higher pitched and more broadband.

P230 Gestural signalling in wild chimpanzees (*Pan troglodytes*): development and underlying cognitive complexity

Marlen Fröhlich, Max Planck Institute For Ornithology
Simone Pika

Advancing gestural and neural research on non-human primates over the past decades has led many theorists to emphasize the role gesture might have played in the evolution of language. Although the flexible and intentional use of gestural signals in great apes is well established, the development and underlying cognitive complexity of these communicative means are to date poorly understood. By conducting the first longitudinal study on gestural development and complexity in two subspecies of free-living chimpanzees (*Pan troglodytes*) we will expand upon the pioneering

study conducted by Plooi (1978). Apart from systematically retesting his results on intentional signalling in infant chimpanzees we will use newly developed methods to also include features crucial for human language such as communicative meaning, referentiality and learning. To do so, the communicative behaviour (i.e., gestures as well as co-occurring vocalisations and facial expressions) of chimpanzee infants between the ages of 9–42 months and their mothers were observed in the communities of Kanyawara, Kibale National Park, Uganda, and Tayÿ, Tayÿ National Park, Cÿte d'Ivoire. Here we will present preliminary data on gestural and socio-cognitive development after the first field seasons at Tayÿ and Kanyawara and discuss them with regard to infant age and social environment.

Plooi, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture and symbol* (pp. 111–131). London: Academic Press.

P231 Relationship between song traits and long-term life history in the Java sparrow (*Lonchura oryzivora*)

Nao Ota, Hokkaido University
Masayo Soma

Birdsong is a sexually selected acoustic ornament, which is assumed to serve as an indicator of male quality. Recent studies on the developmental stress hypothesis revealed that early rearing conditions affected neural development of song control systems, and determined learning-based song traits, such as repertoire size. Especially in age-limited song learners, song features crystallized early in life are less subject to changes in adulthood, in sharp contrast with age-dependent repertoire increase in open-ended learners. However, less attention has been paid to and little is known of age-related lifelong song changes in closed-ended learners. We investigated among-individual song variations and within-individual song changes in a closed-ended songbird, the Java sparrow (*Lonchura oryzivora*), with the aim of shedding light on the relationship between song phenotype and long-term life history. We found that song performance related to motor skills (i.e., song duration and tempo) increased with age, while syllable repertoire and song complexity not. Female preference for older male is a common phenomenon among animals. Therefore, our results suggest that song performance reflects male quality with aging.

P232 A method for automated individual, species and call type recognition in free-ranging primates

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Klaus Zuberbühler

The ability to reliably identify individuals is often a key prerequisite for animal behaviour studies in the wild. In primates, recognition of other group members can be based on individual differences in the voice, but these cues are typically too subtle for human observers. We applied a combined mechanism consisting of a call feature extraction (Mel-Frequency Cepstral Coefficients) and pattern recognition algorithm (Artificial Neural Networks) to investigate whether automated caller identification is possible in free-ranging primates. The mechanism was tested for its accuracy in recognising species, call type and caller identity in a large population of free-ranging blue monkeys (*Cercopithecus mitis stuhlmanni*) in Budongo Forest, Uganda. Classification was highly accurate with 96% at the species, 98% at the call type, and 73% at the caller level. It also outperformed conventional discriminant function analysis in the individual recognition task. We conclude that software based on this method will make a powerful tool for future animal behaviour research, as it allows for automatic, fast and objective classifications in different primate species.

P233 Skype birds; Audio-visual online communication in budgerigars (*Melopsittacus undulatus*)

Yuko Ikkatai, Riken Bsi
Kazuo Okanoya, Yoshimasa Seki

Is the human unique species which is capable of wielding audio-visual online tools such as Skype or FaceTime? Establishing an animal model for this kind of modern communication would help us to understand what communication is, but it has not been systematically examined. Some birds could be a better model for this purpose than rodents because of the similarity of sensory modality to humans; visual and auditory dominance, similar range of normal hearing, and so on. Budgerigars (*Melopsittacus undulatus*) might be one of the best candidates because they have higher sociality; imitation of vocalizations in affiliated groups and modification of behaviours even by video playbacks of other budgerigars. Therefore, we put two budgerigars separately in each experimental box, equipped with a monitor, a speaker, a camera and a microphone, to enable them to establish real-time

“online communication”. We observed their behaviours in three conditions; paired (two-way, interactive), pseudo-paired (one-way, non-interactive) and solo (no bird in one side). They showed more “interactive” behaviours in the paired condition and the behaviours were different from the pseudo-paired condition. Our data quantitatively revealed that budgerigars are capable of making communication via monitors and speakers like humans.

P234 Automatic classification of rat ultrasonic vocalizations.

Shoko Yuki, University Of Tokyo
Yosimasa Seki, Ryosuke Tachibana, Kazuo Okanoya

Ultrasonic vocalizations around 50 kHz (USVs) of rats are recently suggested to contain ecological signals reflecting their emotional states. USVs containing many frequency modulations (FM) are hypothesized to indicate positive affect. In previous studies USV types were manually classified by visual inspection of the spectrograms. Because of this convention, it was not possible to compare studies done based on different classification schemata. The present study proposed an automatic clustering method for the rat USVs with acoustic similarity indices. First, we applied unsupervised random forest algorithm on acoustical features related to amplitude and frequency modulations that were extracted from recorded USVs, and calculated a similarity matrix of them. Then, we conducted a hierarchical clustering using the similarity matrix by Ward method. The number of cluster was determined as the most consistent value among four indices that suggested estimated best number, and the result was confirmed by supervised decision tree to be satisfied a classificatory criterion. Five clusters were successfully derived from our procedure. They were named as Short, Middle, Long, Complex, and Step, according to their acoustical features. The proposed method provides a robust index of USV and should contribute to studies on the emotional states of rats.

P235 The Effects of Dufour’s and Poison Gland Pheromone Extirpation on Emigration Efficiency in the Rock Ant *Temnothorax albipennis*

Jonathan Stuttard, University Of Bristol
Daphna Gottlieb, Nigel Franks

Temnothorax albipennis typically inhabit rock crevices. Such crevices are often ephemeral and their fragility compels frequent emigrations.

Emigration to a new nest site is an energetically and metabolically costly process. Thus, efficient emigration to an improved nest site is essential. Recruitment by *T. albipennis* encompasses tandem running and social carrying. Such behaviour improves emigration efficiency and is therefore likely to be of primary importance to colony fitness. This study aimed to evaluate the effect of pheromones secreted from the Dufour's and poison glands on colony recruitment and emigration progression. Emigrations performed by colonies with both extirpated Dufour's and Poison gland pheromones and natural pheromone secretions were monitored and compared. The results of this study suggest that tandem running in *T. albipennis* does not occur without pheromones secreted from the dufour's and poison glands. Furthermore, the results indicate that colonies with extirpated pheromones decreased their acceptance thresholds of the new nest sites whilst maintaining usual scouting behaviour and emigration performance time. This provides an interesting example of ant behavioural plasticity.

P236 Do Rusty blackbirds moult some feather patches in spring to change their UV pattern?

Claudia Mettke-Hofmann, Liverpool John Moores University
Gerhard Hofmann

Sexual colour dichromatism has often been linked to sexual selection with males usually being brighter coloured in the visual and ultraviolet spectrum. Colour can be an honest signal of fitness and females prefer brighter over duller males. The Rusty blackbird (*Euphagus carolinus*) is sexually dichromatic with black males and brown females in summer but mainly sexually monochromatic in its winter plumage. Sexes become dichromatic in spring primarily through feather wear but some plumage parts, particularly head feathers, are moulted in spring. As head feathers and UV often play a role in courtship display we tested whether this moult relates to changes in UV patterns that cannot be achieved with feather wear. Feather patches known to be moulted in spring were measured with a photospectrometer in museum specimens collected either in summer or winter. UV reflectance was stronger in winter than in summer and stronger in females than in males, particularly in summer, speaking against a role of UV in courtship display. Interestingly, in Icterids females show a higher degree of mutations to brighter visual colours than males which has been linked to a possible social role of plumage brightness in female-

female interactions. The current finding expands this to ultraviolet colours.

P237 Carotenoid-based colour ornamentation predicts social dominance in serins, *Serinus serinus*

Ana V. Leitio, Cibio
André C. Ferreira, Caterina Funghi, Gonzalo C. Cardoso, Paulo G. Mota

In gregarious animals, social interactions frequently take the form of dominance hierarchies that maintain stable relationships between individuals and settle disputes without extra-costs. Traits that function as signals of status can play important roles in mediating interactions among individuals. We used European Serins (*Serinus serinus*), whose plumage has carotenoid-based yellow ornamentation, to experimentally analyse feeding order and aggression in same-sex groups of unfamiliar individuals. We constructed a dominance hierarchy to each group and tested whether ornamentation (colour saturation), age, or morphology (size and condition) predict dominance. Dominance hierarchies were stable/repeatable, and ornamental colouration, particularly the male yellow crown patch, rather than age or morphology, was related to dominance status. We argue that carotenoid-based colour differences in agonistic encounters can be a reliable predictor of social status in male serins.

P238 Response to Pup Ultrasound Calls by Nulliparous Mice

Elizabeth Hill, University Of Detroit Mercy
Leslie Becerra

Maternal motivation of mice has been studied using their retrieval response to ultrasound distress calls by pups. This study investigated response to such calls by nulliparous female mice that had been exposed to differing conditions during the first week after birth. It was expected that those reared in a predator exposure condition (PE; fox urine odor) would be less likely to approach the USV calls than females in the control group. Swiss Webster mice (CD-1; n=14 PE, n=10 Control) were tested in a choice apparatus -- two tubes extending from a center box. Recorded calls from a 7-day old pup were broadcast for 10 minutes. Contrary to predictions, those reared in the predator-exposure condition appeared to spend *more* time near the USV speaker than the control females (M=174.7 [128.6] vs 119.9 [84.0]), but the difference was not significant (p=.214). They were significantly more

likely to scratch at the screen near the active speaker ($M=8.9$ [4.4] vs 6.2 [3.6], $p=.047$). Nulliparous females did not show a strong preference for the choice arm near the USV broadcasts, and the implications of scratching the screen are unclear. Tests with lactating females will be conducted, to determine the typical maternal response in this apparatus.

P239 Structure of dance sequences in the red-crowned crane

Kohei Takeda, The Graduate University For Advanced Studies
Hisashi Ohstuki, Mariko Hasegawa, Nobuyuki Kutsukake

A coordinated mutual display (i.e., dance) is often seen in monogamous birds, but its structure and function remain unclear. The structure of dance can be complex as its sequences vary both within an individual and within a pair. Although several studies described behavioral components of dance structure, quantitative analyses have rarely been done. We investigated behavioral characteristics of the dance in wild red-crowned cranes (*Grus japonensis*) in Japan. Based on a detailed video analysis, we classified 15 types of behavioral components. The proportion of "stoop", a behavioral component not seen in other contexts, was high, occupying >25% of the total components. As a result of sequential analysis within an individual, we found that probabilities of some key transitions between different behavioral components were higher than expected values based on random transition. Within a pair, those key transitions occurred synchronously. In addition, behavioral components commonly used as a threat signal were involved in the key transitions of dance sequences. These suggest that specific rules exist in a dance sequence and that the order and synchrony of behavioral components may function as signals within a pair. Our research has implication for the understanding of mutual communication in animals.

P240 Airborne odor of Blue Petrel described by unraveled thermal desorption method

Marianne Gabirot, Cefe-Cnrs
Nana Hesler, Aurélie Colomb, Sylvia Campagna, Francesco Bonadonna

Birds' chemical communication is an emergent topic of research. Majority of studies have focused on either uropygial secretions or feather lipids. However, screening secretions or feather lipids for

volatile signals might overlook the various degradation processes, which may exogenously convert secreted lipid precursors into their biologically active forms. The blue Petrels (Procelariiforms) living in burrow-nesting in the Kerguelen archipelago, have a well developed olfactory system and good associated capabilities which are used for foraging, homing and nesting. Behavioural choice experiment with body odour showed a sex-specific and individual recognition. Thus, our current research is examining the airborne volatiles to further elucidate which particular compounds play a key role in the final conduction of petrels' olfactory signals. Due to the difficulties of collecting body odor samples and extracting volatile molecules from biological samples for chromatographic analyses, we provided novel techniques of airborne volatiles by thermal desorption. Results described the molecules involved in Blue Petrel odor. We noted chemical differences between secretions, feathers and airborne volatiles rather suggest that these variations might result from various bio-chemical processes. Finally, this unraveled thermal desorption method shed light on the real potential of these airborne volatiles to convey information about specie, sex and identity.

P241 Geographic variation in the signalling behaviour of the Jacky dragon, *Amphibolurus muricatus*

Marco Barquero, Macquarie University
Martin Whiting, Richard Peters

Animal communication systems are extremely complex and diverse. Signal diversification is often the product of sexual or natural selection and may be accompanied by genetic differentiation or simply reflect a plastic response to environmental variables. We use an agamid lizard endemic to Australia, the Jacky dragon (*Amphibolurus muricatus*), to examine relationships between genetic structure, morphology and signaling behavior. We also investigate the consequences of this variation on the ability to discriminate conspecifics. We used three populations separated by over 280 km, two of which belong to the same genetic clade. We found that individuals from the more closely-related populations exhibited more similarities both in morphology and signaling behaviour than lizards from the third, more distant population. In addition, animals from all populations showed different levels of aggression if confronted with individuals from the same or different populations. We discuss the significance of this

concordant pattern between genetic structure, morphology and behaviour.

P242 What sons get from fathers? Song repertoires in the pied flycatcher

Helene M. Lampe, University Of Oslo
Antonieta Labra

Songs constitute a significant component of the behavioural repertory of birds, particularly for males, who use songs in different contexts involved in sexual selection. Different song features are honest signals in male pied flycatchers that can convey important information about the quality of the signaller such as body condition and age. If song complexity is a good proxy of the singer quality, one might expect that the feature can be transmitted to the next generation. Here we investigated the similarities between fathers and sons several song components that can be considered part of the complexity of the songs: repertoire size measured as different syllable types in 25 songs, number of different syllables per song and number of syllables per song. We studied more than 20 pairs of fathers and sons, but did not find a clear relationship between the songs of fathers and sons. However, birds that breed when one year old have sons with smaller syllable repertoires than older breeders. We discuss the causes and consequences of these results.

P243 Propagation and degradation patterns of acoustic signals in frogs of the austral temperate forest

Mario Penna, University Of Chile
Felipe Moreno-Gomez, Matias Musoz

Propagation patterns of acoustic signals and auditory sensitivity provide insights into the evolution and adaptation of sound communication systems. Calls produced by 16 *E. calcaratus* males and 17 *E. emiliopugini* males recorded at 0.25–8.0 m show larger average amplitudes at 0.25 m for *E. emiliopugini* (83.5 dB SPL) than for *E. calcaratus* (75.9 dB SPL), and the amplitude of both signals decreases with distance (ANOVA $F_{(3,75)} = 314.50$, $P < 0.00001$). In the tonal calls of *E. calcaratus*, the amplitude ratios: harmonic 2/harmonic 1 and harmonic 2/harmonic 3 decrease with distance. The pulsed calls of *E. emiliopugini* show a decrease in amplitude modulation depth from about 90% at 0.25 m, to 70% at 4 m. Auditory thresholds for conspecific vocalizations measured with midbrain multi-unit recordings are about 60 dB SPL for *E.*

calcaratus and 44 dB SPL for *E. emiliopugini*. These results combined reveal remarkable differences in active spaces: *E. emiliopugini* communicates beyond 8 m, while *E. calcaratus* is restricted to distances of about 2 m, implying different communication strategies in these anurans. Males give similar vocal responses to degraded and non-degraded conspecific signals, which may contribute to maintain chorusing in different aggregation densities. Supported by FONDECYT Grant 1110939.

P244 Sing, and we will know everything: Advantages of individual acoustic monitoring in a songbird

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Iveta PiÅívejcová, Anna Kinitová, Tomáe Brinke,
Michael Weiss, Adam Petrušek

Individual identification of studied species is often necessary for fieldwork. Colour rings are commonly used to mark birds; however, rings might be difficult to observe, especially in small species and dense habitats. Our study species, tree pipit *Anthus trivialis*, belongs among such taxa but we show that acoustic monitoring may be a useful alternative: singing males can be reliably identified from their repertoires and song syntax based on a recording containing 20–30 songs (approx. 5 minutes). Males banded with colour rings were repeatedly recorded throughout the season, and syllable repertoires were determined from spectrograms for each recording. Individual repertoires (2011: 29 males, 186 recordings, 2012: 23 males (9 returning), 185 recordings) were stable within as well as between seasons, and males with very similar syllable repertoires distinctly differed in syntax. This allowed us to identify all singing males in studied population, including non-ringed ones, by song only. Acoustic data revealed dynamic within-season changes in territory occupancy that would otherwise be missed, and allowed matching individual song characteristics with success in territory holding. Furthermore, we detected returning birds that actively avoided approaching humans. Individual acoustic monitoring seems a valuable tool bringing new insights on behaviour and ecology of studied species.

P245 The structure of vocal duets at the nest reflects separation time between mates in zebra finches.

Ingrid Boucaud, ENES, Université Jean Monnet
Mylene Mariette, Clémentine Vignal

The monogamous pair-bond in birds is a partnership that relies on coordination between mates. To understand this coordination it is necessary to study communication between mates. In Zebra finches, partners coordinate most of their activities, and rarely separate except during the breeding period. Both partners participate in incubation and take turns in the nest, each mate foraging separately. The relay between partners in the nest is a time of reunion during which the pair performs a vocal duet. In this study, birds bred in a large aviary equipped with an acoustically and visually isolated feeder that mimicked the separation between partners due to distance in the wild. Separation time was manipulated by trapping males in the feeder. Duets were recorded before the closure of the feeder and after the reopening for two treatments: when the male had been trapped in the feeder and when both partners had remained outside. With increasing separation time zebra finches performed shorter duets with higher call rate, but the duets' core structure was not modified. These results suggest that the content of the duet is of importance for zebra finches partners: even when they increase the speed of the duet, they maintain its organization.

P246 Domestication may change innate predispositions for song learning

Hiroko Kagawa, Jst
Kenta Suzuki, Miki Takahasi, Kazuo Okanoya

Songbirds acquired their own song by imitating their tutor's song, but some parts of species-specific song features are developed based on innate predispositions. Bengalese finches are the domesticated strain of wild white-rumped munias. The songs of domesticated strains have more tonal sounds and variable sequences than those of the wild strains. We hypothesized that innate predispositions for song learning have been altered between the strains. We recorded songs that were produced by normal, isolation-reared and cross-fostered birds and compared these songs between white-rumped munias and Bengalese finches. Principal component analyses were conducted based on 19 song measurements. We found that there were significant differences in the first component mainly including frequency and entropy between the strains, regardless of rearing condition. The second component showed isolated songs of both strains differed in temporal features from normal and cross-fostered songs. Our results suggest some genetic aspects of song learning could be changed through domestication, although general features of songs of both strains vary depending on rearing conditions.

P247 Avian Communication in Anthropogenic Noise

Rupert Marshall, Aberystwyth University
Emily Mockford

Acoustic signals are fundamental to avian communication, having evolved under pressure from both natural and sexual selection. Recently, an association has been demonstrated between key temporal & frequency (pitch) characteristics of avian signals and the noise level of the signaller's habitat. However, data addressing the effects such variation has upon the ability of conspecifics to successfully communicate remains scarce. Male birds display a stronger response to song recorded on territories with noise levels similar to their own than to song recorded on territories with different noise levels. Using playback experiments, we examine the role of low frequency song on response behaviours among great tits (*Parus major*). We also compare song output and frequency during counter singing, relating this to variation in background noise. Finally we discuss communication and dispersal between urban and rural populations, asking the extent to which noisy urban areas can be described as ecological traps.

P248 Female Infants Express Sympathetic Cry More

Hiroimi Nito, Riken Bsi
Reiko Hoshi-Shiba, Yulri Nonaka, Kazuo Okanoya

Vocal communication with emotional sympathy is fundamental for breeding or survival among animals. In this study, we focused on human infants' crying reaction evoked by peers' cry to clarify the primary features of emotional sympathetic vocalization.

Healthy full-term infants aged 1-6-month-old were presented four types of stimuli; infants' own cries, other infants' cries, frequency-modified sounds and time-reversed sounds of own cries, in pseudo random order.

From the video-recorded data, utterances under displeased facial expression were assessed as "sympathetic cry", and total amount per 8-seconds' stimulus presentation and 8-seconds' rest was calculated. ANOVA with gender, types of the stimuli, and group of age (1-2, 3-4 and 5-6-month-olds) revealed significant main effects for gender and group of age, but not for types of stimuli; female cried more than male, and 3-4-month-olds cried more than 1-2-month-olds in both gender.

Our results indicate that female infants are more sensitive to the emotion conveyed by the cry-related sounds, and vocalize more with sympathy. This tendency is observed in their very early infancy and may have some advantages for social

development. The increase of the sympathetic cry of 3-4 months of age suggests that period to be important for growth of infants' sociability.

P249 Colours of quality: condition-dependent signalling in male wall lizards

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Pau Carazo, Enrique Font

Chromatic signals result from the differential absorption of light by chemical compounds (pigment-based colours), and/or from differential scattering of light by integumental nano-structures (structural colours). Both structural and pigment-based colours can be costly to produce, maintain and display, and have been shown to convey information about a variety of individual quality traits. Male wall lizards (*Podarcis muralis*) display two conspicuously-coloured patches during ritualized inter- and intrasexual displays: ventral colours (perceived as orange, yellow or white by humans) are pigment-based, while blue outer ventral scales (OVS), located along the flanks, have their peak of reflectance in the ultraviolet (UV) and are structurally produced. We used spectrophotometric data from 372 adult males to examine, considering the entire visual spectrum of lizards, whether ventral and OVS colour variables can predict male quality. Results indicate that the UV chroma and hue of OVS are good predictors of body condition and fighting ability (size-independent bite force), respectively. This suggests that structural colour patches are condition-dependent and function as complex multicomponent signals in this species. Conversely, ventral colourations do not function as male quality indicators. We suggest that these colour patches may be social signals with different information content, possibly aimed at different receivers.

P250 Multiple sources of temporal variability in song of Bengalese finches (*Lonchura striata* var. *domestica*)

Ryosuke Tachibana, University Of Tokyo
Kazuo Okanoya

Birdsong provides a unique model for studying control mechanisms of hierarchically structured complex behaviors. In the present study we analyzed temporal aspects of song elements and silent intervals (i.e. notes and gaps) of Bengalese finches in various time ranges to address factors of temporal variability in the song production system. We found notable temporal properties in three time

ranges: circadian change, within-bout drift, and note-gap tradeoff. Note duration, but gap duration, was getting gradually shorter over time from morning to evening. Note duration was getting longer monotonically as the progress of singing in each song bout, while gap duration was becoming shorter at the beginning then was getting slightly longer. In originally shorter gaps, when the duration became shorter than usual, duration of the preceding note had a strong tendency to become much longer than usual, suggesting a trade-off relationship. However, the trade-off relationship was weaker when the gap was originally longer. The gap duration did not have much of the relationship with the following notes and gaps. These results appeared to support a view that there are distinct sources of temporal variability in multiple levels, and the entire song structure would be comprised of the interaction of them.

P251 Evolution of vocal cultures in two strains of Bengalese finches

Miki Takahasi, University Of Tokyo
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Bengalese finches (BF) have been domesticated in Japan for more than 250 years from white-rumped munias (WRM) living around East Asia. Through the domestication, BF courtship songs changed from those of the wild strain. BF songs have acoustically clear sounds and variable note sequences. WRMs sing more stereotyped songs with wide-band sounds. Cross-fostered experiment revealed that WRMs have strong preference for own strain songs in song learning and that this preference was weakened in BF. We hypothesized that the difference of song preference would lead to different song cultures. To investigate this, we compared the songs emerged within a closed colony in BFs and WRMs. An isolated male and three non-singing females were bred as founders of each colony. Song elements of founders were acoustically unstable and their songs were slower than that of normal reared birds. First generation tutees improved song tempo in both BFs and WRMs. Through several generations, songs of tutees were diverse in BF colonies. But tutees in WRM colonies tended to copy the founder song. Results suggest that the temporal organization is easily rescued by general auditory stimulation but syllable acoustics are gradually canalized through generations by perceptual filters.

P252 Acoustical basis of human emotion assessment of conspecific and dog vocalizations

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Attila Andics, Viktor Devecseri, Anna Kis, Márta Gácsi, Ádám Miklesi

Human non-verbal vocal bursts are evolutionary conservative emotional expressions. Humans can easily assess inner states of conspecifics based on these calls. Moreover, they can attribute emotions to non-human animal vocalizations too. However, whether the same acoustic cues are used to assess emotional content in conspecific and non-conspecific vocalizations is not clarified yet.

To test this, we compiled a pool of 100-100 various dog and human non-verbal vocalizations from diverse social contexts, and designed an online survey, in which every sample could be rated along emotional valence and intensity. We also measured within each sample the average length of calls, the fundamental frequency and the harmonics-to-noise ratio.

While valence ratings did not differ across species, human vocalizations were less intense. Linear regressions revealed that both shorter dog and human calls were rated as more positive. In contrast, subjects scored higher pitched human and dog sounds to be more intense. We also found dog vocalizations with shorter call length or with higher HNR were rated less intense.

In conclusion, acoustical parameters affected humans' emotional ratings independently from the source species of these vocalizations. These findings suggest that humans utilize the same mental mechanisms for recognizing conspecific and heterospecific vocal emotions.

P253 Polyspecific communication and association: birds and lemurs

Kit Stoner, Anglia Ruskin University

Some species in co-evolved communities may rely on others to access resources or avoid predation, with knock-on effects for their survival if the dynamics of mixed groups are changed. I used a controlled playback experiment to test responses of ring-tailed lemur (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi verreauxi*) to the following bird calls in different habitats: Madagascar magpie robin (control), green pigeon, white headed vanga and a crested drongo alarm call. The research was carried out at Berenty reserve in the south of Madagascar. Calls were presented in a counterbalanced order to 22 different troops of

lemurs, and I used instantaneous group scans to record lemur behaviour prior to and after playback. Preliminary data suggests the strongest pattern for both lemur species was in response to the drongo alarm call. Significant differences from the control were also found in the responses to the green pigeon but these were context and species dependent. I also investigated whether there is any evidence of interspecific association between the two lemur species and specific bird species, and explored the function and habitat context of any associations found.

P254 Presleep chorusing and unusual vocalizations at night in captive bottlenose dolphins

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Margarita Briseno Jaramillo, Martin Böye, Alban Lemasson, Martine Hausberger

Diurnal animals produce sounds at night. In roosting species, high vocal activity at roosting sites may be a prerequisite to sleep, suggesting a role of chorusing in coordinating resting. In other species, vocalizations during sleep are commonly reported, which in humans correspond to dream contents. Dolphins' nocturnal vocal activity has been rarely investigated. This animal model is interesting because: dolphin resting behaviour is associated with social synchrony (formation swimming/synchronous breathing), dolphins' daily social activities are primarily mediated by vocalizations, and dolphins are known to mimic sounds of their environment. Therefore, we recorded the nocturnal vocal and breathing activities of a captive group of dolphins. The temporal pattern revealed two peaks of intense whistling, followed by a decrease in vocal activity and low respiration rates, resembling the presleep chorusing in other species. Within the night, we also found non-specific vocalizations, which appeared to be vocal copies of whale sounds broadcast during daily public shows. This suggests a vocal rehearsal of day salient events. These findings are questioning the significance of nocturnal vocal activity in dolphins as, contrarily to most previous reports, these productions are clearly outside a feeding context. They shed new light on the potential cognitive/social significance of auditory communication.

P255 Neighbour-stranger discrimination and the trade off between repertoire size and within-song type variation

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Michał Skierczyński, Anna Wisniewska, Katarzyna Āosak, Paweł Podkowa, Aleksandra Jakubowska, Paweł Szymanki, Krzysztof Deoniziak, Lucyna Wojas,

Majority of bird species have small song repertoire. In birds with discontinuous song, males usually produce strophes, which could be easily classified to few categories based on visual inspection of sonograms. Males of such species often share repertoires, which means that neighbours may use at least some 'identical' song types. On the other hand, economically efficient territory defence requires at least ability to distinguish between neighbours and strangers (NSD). We studied the ortolan bunting (*Emberiza hortulana*), a small migratory passerine species in which males usually have small repertoires (2-3 song types), which is commonly shared (≤ 11 different song types per 100 males within population) but both repertoire sizes and level of sharing may highly differ between populations. Males of this species were found to distinguish between neighbours and strangers regardless of repertoire size and sharing level. It is possible, because shared song types are individually distinct because of frequency shift, which consistently discriminate particular males. Here we present data from a few different ortolan bunting populations (Poland, Norway, Finland, Germany) in order to test if the necessity of NSD enforced a trade off between song repertoire size and within song type variation.

P256 Body Slap: An innovative aggressive display by breeding male grey seals (*Halichoerus grypus*)

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Rob Lidstone-Scott, Paddy Pomeroy, Sean Twiss

Male aggression in polygynous pinnipeds such as the grey seal has been studied extensively but with little attention to the communicative behaviour that is used. Therefore our knowledge is limited and for male grey seals it is often simplistically assumed that threat signals are mainly cephalic in nature. We report on an undescribed and apparently innovative threat signal we term a Body slap. It is used exclusively by males in pre-fight displays at a breeding colony in England. The behaviour has been recorded at multiple breeding sites in this region since 1997 but has not been studied or reported on. The aims of this study were to describe the behaviour and how it is used. Body slaps were performed in 66.3% of interactions and by 57.2% of males. We found the Body slap was positively associated with intraspecific behaviours of Approach and Open-mouth treat but individual rates were not related to dominance rank;

nevertheless, display rates were greater for subsequent winners. We suggest that the Body slap display carries information about resource holding potential and is not a submissive behaviour. This study furthers our understanding of geographic variants of male threat behaviour and interspecific forms of non-vocal communication.

P257 How effective are acoustic signals in territorial defence in the Lusitanian toadfish?

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Paulo Fonseca, Marta Picciulin, Clara Amorim

Breeding Lusitanian toadfish males (*Halobatrachus didactylus*) use sounds (boatwhistles) to defend nests from intruders. Previous studies with territorial intrusion experiments suggest that boatwhistles function as 'keep-out signals'. To experimentally test this hypothesis we performed territorial intrusion experiments with muted Lusitanian toadfish. Subject males were assigned to three groups: muted, sham and control. Males were muted by making a cut and deflating the swimbladder (the sound producing apparatus) under anesthesia. Sham males suffered the same surgical procedure except from the actual swimbladder deflation and control fish were unmanipulated. Muted males suffered a higher number of intrusions than the remaining groups. Subject males reacted to intruders mainly by emitting sounds (only sham and control) and less frequently with escalated fights. There was no difference in the frequency of escalated fights among fish groups. When an intruder received a boatwhistle, the probability of fleeing was significantly higher than expected by chance alone either when they approached or intruded the resident's nest. Taken together, our results show that acoustic signals are effective deterrents in nest intrusions in the Lusitanian toadfish.

P258 YELLOWHAMMERS.NET: Citizen science projects uncovering mysteries of distribution of Yellowhammer (*Emberiza citrinella*) song dialects

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We present two citizen science projects focusing on mapping the geographic distribution of song dialects of Yellowhammer (*Emberiza citrinella*). This species is particularly suitable for such projects: its song is

easy to recognize, and consumer devices such as digital cameras and smartphones can be used to obtain recordings with quality sufficient for dialect identification. Thus, wide public can be involved in large-scale data collection. The Dialects of Czech Yellowhammers project (www.strnadi.cz) started in 2011 as part of the Bird of the Year campaign of the Czech Society for Ornithology. Its aim was to map distribution of dialects and to document a potential border between two European macrodialect groups in the Czech Republic. During two years, over 1700 recordings were obtained thanks to over 120 volunteers. We detected all so far known dialect types and also some local variants. In 2013, Yellowhammer Dialects project (www.yellowhammers.net) was launched, aiming to compare distribution of dialects in Great Britain and New Zealand where yellowhammers were introduced by British colonists in the 19th century. As the releases were documented, we hope to use data on dialect distribution in the newly colonised territory to assess impacts of founder effects and cultural evolution during a biological invasion.

P259 Vocal interactions in groups of captive Zebra finches (*Taeniopygia guttata*) during different stages of the breeding cycle

Lisa Gill, MPIO Seewiesen
Andries Ter Maat, Wolfgang Goymann, Manfred Gahr

Vocal communication has been extensively studied in many animal species and has very often proven vital for individual survival and reproduction. In songbirds, most studies to date have focused mainly on conspicuous song or alarm and contact calls. Although almost ubiquitous in many species, less is known about quiet calls that occur between individuals acting at close range.

This lack of information seems to be due to technical limitations. Firstly, it is difficult to capture quiet calls over a distance or through noisy environments and secondly, assigning those calls to the correct individual in the presence of more than one potential sender may be complicated. This information, however, is crucial for the understanding of ultimate and proximate factors shaping vocal communication.

In our study, we recorded different vocalisations including quiet ones from single individuals within four groups of eight captive zebra finches (*Taeniopygia guttata*) each. Using these individual acoustic recordings in addition to behavioural observations, breeding success and hormone data, we were able to describe temporal vocal interactions within a group and analyse their role

especially for pairs, at different stages of the breeding cycle and according to other social and environmental factors.

P260 Developmental differentiation in human infant cry through dynamic interaction with caregivers

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Jean-Julien Aucouturier, Kentaro Katahira, Kazuo Okanoya

The diversity of human infant cries is unique among primates. Two hypotheses compete to explain such complexity: For one, the cry is a graded signal reflecting an amount of e.g. neediness or pain; for the other, the cry is a categorical signal conveying discrete types of needs. We present data suggesting that it is, in fact, a mixture of both. We followed up 35 infants and caregivers during first year of age, recording cries and collecting verbal reports every month. Regression analyses from the reports indicated that, with development, caregivers increasingly attribute the cause of the cry to the infant's social (e.g. loneliness, shyness), rather than physiological needs (e.g. pain, hunger); and that the latter are identified less and less from the vocal content of the cries, while the former, more and more. Acoustical analyses of the cries revealed that each infant progressively adopts distinct vocal signatures of pitch and expiration rate for different social needs.

Together, these findings suggest that the infants communicate physiological states by a graded-signal portion of the cry which is stable through development, and social needs by a categorical-signal portion whose code which is learned conjunctly by the caregiver and the infant throughout development.

P261 Warbling is a highly contagious behavior in male budgerigars

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Imitation of both vocalizations and other behaviors in budgerigars has been widely investigated. Synchronization between artificial audio-visual stimuli and their movements was also reported, suggesting some behaviors of budgerigars are easily led by surrounding circumstances. Here, we report how warbling of a group member affects warbling of other members in budgerigars. We grouped four birds together from males and females for each experiment. The birds were put in one sound

attenuated chamber but were separately kept in each cage for 2 weeks. Each cage equipped a microphone and the sound inputs were recorded with independent channels. Warbling in each 10-minutes time-window was compared among the birds. In male groups, warbling of each bird was not independent from others' as followings; 1) the amount of vocalizations in each period had strong correlations among birds, 2) cross-correlation analysis revealed warbling was mostly accompanied with warbling of neighbors, 3) the probability of coincidence of vocal production by all four birds was higher than that by three birds or less, which means once a bird began to vocalize, others followed the first one and finally all of the birds were warbling together. However, those correlations were not observed in male-female groups.

P262 Chimpanzees, social bonds, urinary oxytocin and cortisol

Catherine Crockford, Mpi Eva
Tobias Deschner, Kevin Langergraber, Toni Ziegler,
Klaus Zuberbuhler, Roman Wittig

Evidence over the last decade shows that some mammals can increase their reproductive success by maintaining close social bonds with others. However, the mechanisms underlying this benefit are not yet clear. A contributing factor maybe that maintaining close social bonds with others leads to buffering of the negative effects of stress. To examine this hypothesis, we predicted that individuals who engaged in the same type of social interaction would experience different associated hormonal changes depending in their relationship with their interaction partner. Thus, we measured urinary cortisol and oxytocin levels in wild chimpanzees, Budongo Forest, Uganda, in the hours following target social interactions including grooming, food-sharing, neighbour-encounters and aggression. We found that, following a certain social interaction, like grooming, subjects' urinary hormonal levels were significantly lower for cortisol and higher for oxytocin when the interaction was with a bond partner compared with another individual. In contrast, little variation in hormonal levels was explained by other factors, such as the duration of the interaction. Our results showed that interactions with bond partners were qualitatively different from the same type of interactions with others. Interactions with bond partners may indeed buffer the negative effects of stress more than interactions with others.

P263 Acute 17-ethinylestradiol exposure on audience effects during male-female interactions in the Siamese fighting fish, *Betta splendens*

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Teresa Dzieweczynski, Krystal Mannion

It is increasingly evident that the presence of endocrine disrupting chemicals (EDCs) often negatively affects aquatic organisms. Behavioral effects often occur before morphological effects, yet the negative impacts of these behavioral changes can be just as severe. While it is apparent that the presence of EDCs affects courtship and aggression, the effects of chemical exposure on more complex behaviors are less well known. We recently established that short-term exposure to the estrogen mimic 17 α -ethinylestradiol (EE2) interferes with the ability of male Siamese fighting fish to modify their behavior when an audience is present. In this study, we examined whether acute EE2 exposure also interferes with the effect of an audience on male-female interactions. To address this, exposed and unexposed male-female pairs interacted in the presence of three different audience types (female, male, or no audience). It was hypothesized that acute EE2 exposure would negatively impact both overall level of response and the ability of individuals to modify their behavior in response to the sex of the audience individual. This study serves as an important addition to the exploration of population-level effects of EDC exposure as it demonstrates that EE2 disrupts the ability of individuals to communicate to multiple social partners.

P264 The role of dopaminergic system in the modulation of the Indo-pacific bluestreak cleaner wrasse *Labroides dimidiatus* cooperative behavior

Joao Messias, Ispa-lu
José Paula, Alexandra Grutter, Rui Oliveira, Redouan Bshary, Marta Soares

The cleaner wrasse *Labroides dimidiatus* is one of the best studied examples of cleaning mutualism, an interspecific interaction with positive payoffs for both sides of the involving parties. Although its behavioral basis is well-known, its physiological counterpart is less comprehended. The cleaner wrasse *Labroides dimidiatus* is a fish species highly specialized in these type of interactions, and given the extremely complex social network that these animals are exposed to, we assume neurotransmitter systems must be involved in the modulation of this animal's behaviour. Dopamine is a neurotransmitter involved in a variety of

behavioral modulating actions, that usually being tied with aggressive behavior and reward-related learning systems. Here we tested if the administration of exogenous agonists (SKF38393, Quinpirole) and antagonists (SCH23390, Metoclopramide) would produce any changes in their motivation for inter- and intra-specific interactions.

To our knowledge, our study is the first to link the effects of dopamine actions and mechanisms to cooperative behaviour, to which we expect have tremendous effects on the output behaviour of these highly social fish.

P265 Heart rate responds to familiar and unfamiliar individuals of different social statuses in the giant mole rat (*Fukomys mechowii*)

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We assessed stress indication during some dyadic interactions in a socially living subterranean rodent, the giant mole-rat (*Fukomys mechowii*). Heart rate of five submissive individuals (3 females, 2 males) was monitored in two different situations – exposure to an intruder and exposure to its odour. For this purpose we used transponders for heart rate telemetry developed by Respirationics Mini Mitter (USA). After surgical implantation into abdominal cavity the Mini-Mitter system enables watching heart rate online, without any movement restriction of the animal. Our experiments showed that during confrontation with an intruder (or its odour) heart rate increased from 200-350 beats per minute up to double values and the submissive males indicated greater response to unfamiliar submissive individuals than to dominant ones ($p = 0,0387$). The odour stimulus was also influenced by the order of its presentation. If the intruder preceded the odour stimulus, the heart rate reached higher values than during the opposite arrangement ($p = 0,0472$). However, the mentioned dyadic interactions never produced such high heart rates observed during e.g. an open field test. Based on the determined stress parameter we get more real insight into the social system of mole-rats.

P266 Serotonin Neuromodulation of Cooperative Behaviour in a Cleaner Fish

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Joao Messias, Alexandra Grutter, Rui Oliveira,
Redouan Bshary, Marta Soares

The cleaning behaviour has been used as a classic example of mutualism, with benefits to cleaners and clients. Although much has been studied on the behavioural aspects of these mutualistic interactions, little is known about physiological processes that underlie these interactions. The neurotransmitter serotonin or 5-hydroxytryptamine (5-HT) is involved in the regulation of vertebrate social behaviour while its activity is usually related with social status and aggressive behaviour. Here we tested if the serotonergic system is responsible for the modulation of cooperative behaviour, in the best studied cleaning mutualism, between the Indo-Pacific bluestreak cleaner wrasse *Labroides dimidiatus* and their visiting clientele. We've found that exogenous administration of 5-HT agonist 8-Hydroxy-2-(dipropylamino)tetralin (8-OH-DPAT) and selective serotonin reuptake inhibitor (SSRI) fluoxetine caused a substantial increase of cleaners' motivation to inspect clients without affecting their intraspecific interactions, which suggests a particular effect of 5-HT on interspecific behaviour but not of an overall effect on social behaviour. Additionally we've discovered that 5-HT antagonists WAY-100635 and p-chlorophenylalanine lead to a substantial decrease of cleaning inspections. To our knowledge, our study is the first to link the effects of neurotransmitter action (serotonin) to cooperative behaviour, beyond the usual focus of its influence on conspecific social behaviour.

P267 See you soon? Adrenocortical responses to experimentally induced fission-fusion dynamics in ravens (*Corvus corax*)

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Ravens exhibit a complex social organisation that in early life, when they form non-breeder aggregations, includes a high degree of fission-fusion dynamics. Within these groups, individuals have social relationships of varying quality and valence – “friends” provide benefits, such as social support during or after conflicts with others, presumably reducing corticosterone levels and alleviating stress. So far, little is known about the adrenocortical activity in the context of fission-fusion dynamics, where long-lasting separations of affiliated birds may occur. The present study aims to elucidate these endogenous effects by separating eight ravens individually from their group for four days and subsequently reintroducing them. To determine stress response patterns, we measured

amounts of excreted immunoreactive corticosterone metabolites (CM) in droppings using an enzyme immunoassay against $3\alpha,11\text{oxo-CMs}$, previously validated for ravens. Preliminary results suggest 1) that not only isolated individuals, but also “friends” that remain in the group experience stress, indicated by elevated CM levels, while “non-friends” are not affected by the separation of the conspecific; and 2) that the amplitude of the stress-induced corticosterone response most likely depends on the social integration of the bird, rather than on the hierarchical status.

P268 True and false positives in guppies: a field study in group decision making

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Jens Krause

Grouping behaviour has evolved due to a variety of benefits including defense against predators and collective foraging. Another benefit of group living is increased decision making quality, which can translate into faster and more accurate decisions. In the wild, making the wrong decision in the presence of potential predators and competitors can be extremely costly and have important ecological consequences. In this study, we quantified the response of Trinidadian guppies (*Poecilia reticulata*) in various group sizes to a true positive (edible) stimulus and a false positive (non-edible) stimulus in natural stream systems. We show that, for a randomly chosen individual, the number of pecks – but not the number of approaches – towards the true positive stimulus increases with group size.

P269 Decision making in ants - A threshold approach

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Social insect colonies provide some of the richest examples of complex systems in nature. They are an excellent model for experimental investigation into questions about how collective decisions are made since they allow direct manipulation of their components and observation of the collective behaviour. In *T.albipennis* ant colonies, workers need to perform many different tasks, for instance, foraging for food, patrolling or scouting for nest-sites. How these are allocated in response to colony needs is still poorly understood. One possibility is that workers have task response thresholds, meaning that they will perform a task when the

stimulus that elicits that task exceeds the workers threshold. But is there variability in thresholds among individuals? Or do they behave differently due to chance encounters with certain stimuli? To investigate this issue we move colonies to nests of different qualities and analyse the individual ants' willingness to leave the safety of the nest and scout for a new one. Each individual is marked and a tracking system provides information about their location. Using this information we will assess the existence of, and variability between, individual thresholds when all ants receive the same stimuli, nest quality.

P270 Comparing coordination by chimpanzees and 4-year-old children in a Stag Hunt Game

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Group living requires primates to coordinate their decisions with conspecifics in a variety of contexts (e.g. whether to hunt, which direction to travel). The ‘Stag Hunt Game’ is a tool used in game theory to experimentally simulate such coordination challenges: Players have to choose between acquiring a low-value reward independently or cooperating with a partner in order to acquire a high-value reward. But cooperation involves a risk, since a solo attempt at the cooperative option results in loss of all rewards.

In a comparative study, we presented both chimpanzee dyads and child dyads with a Stag Hunt Game, and examined their tendencies to cooperate, as well as the strategies employed to overcome the risk associated with cooperation. Both species were likely to risk cooperating in conditions in which they could easily monitor their partners. However, when visual access to the partner at the moment of decision was blocked, only chimpanzee cooperation was hindered, to some extent. Children, in contrast to chimpanzees, communicated with partners before making a decision regardless of condition, apparently reducing the perceived risk overall. Though both species are able to coordinate to some degree, these findings highlight the importance of communication in solving coordination problems.

P271 To cache or not to cache: do observers influence the decision to cache in Eurasian jays?

Edward Legg, University Of Cambridge
Nicola Clayton

When corvids cache in front of a conspecific they face both an immediate risk (the cacher is in a vulnerable position where they are prone to lose the item they are about to cache) and a future one (the observer may remember the location of caches and pilfer them later). Previous studies in our laboratory have shown that when cachers and observers are allowed to freely interact (*immediate* and *future* risk) both Western scrub-jays and Eurasian jays will suppress the overall number of caches made in the presence of dominant conspecifics. Studies in which observers were separated from the cacher by a barrier (*future* risk) tested cache-protection strategies by analysing where individuals chose to cache and not how much they cached. Indeed, cachers protected their caches by choosing sites not easily perceptible to observers. In the present study, we tested whether Eurasian jays will suppress caching when given only one cache-location and when a Perspex barrier prevented any immediate risk from the observer. Here, Eurasian jays did not alter their caching behaviour depending on being observed and on the observer's dominance status. We discuss these findings in light of the existing literature on cache-protection strategies in corvids.

P272 Name recognition by domestic cats (*Felis catus*)

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Yuki Ito, Kazutaka Shinozuka, Toshikazu Hasegawa

Domestic cats (*Felis catus*) have cohabited with humans for 10 000 years and seem to be able to communicate with them. However, this has not been extensively examined in the literature. Using the habituation-dishabituation method, we investigated whether domestic cats could recognise their names in a series of sounds in their owners' voice. In Experiment 1, with the owner out of sight, four different common nouns were presented sequentially, followed by the cat's name. The cats' reactions to the sounds were video-recorded. Researchers then rated the magnitude of the cats' responses. Of the 16 cats, 13 demonstrated a lower response magnitude to the fourth noun than to the first. These habituated cats showed a significant rebound in response to the subsequent presentation of their names. In Experiment 2, cats that lived with four or more other cats in the same house were tested. Four of the other cats' names were presented sequentially, followed by the name of the tested cat. In this experiment, only 5 of the 14 cats demonstrated habituation but all these five cats showed some rebound in response to their own

names. These results suggest that cats are able to distinguish their own names from other words.

P273 Social information and experience-pooling

Mike Webster, University Of St Andrews

Decades of research have shown that many animals use socially transmitted information to locate resources. What is less clear is whether groups containing individuals with incomplete but complementary information about resource distribution can effectively combine their experience. In this study, groups of stickleback fish (*Gasterosteus aculeatus*) were presented with a two-part foraging challenge, consisting of a navigation task and a feeder-access task. Some fish were trained in the navigation task, some in the feeder-access task and others were naïve to both. Groups contained either: (a) naïve fish only, or naïve fish plus (b) navigation-trained fish, (c) feeder-trained fish or (d) a mixture of both navigation-trained and feeder-trained fish. Navigation-trained fish arrived at the feeder soonest, while feeder-trained fish typically accessed the food first. In the naïve-only group, fish took the longest to find the feeder and were least successful at accessing the food. Crucially, fish in the mixed navigation-trained and feeder-trained groups were the fastest to access the food, and had the greatest proportion of feeding fish, including naïve individuals. These data suggest that in complex environments, individuals may benefit from exposure to social information from groupmates with diverse experience. Future research will focus upon the mechanisms behind this effect.

P274 Benefits of mother/offspring associations in eastern grey kangaroos

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Marco Festa-Bianchet, Graeme Coulson, Anne Goldizen

Eastern grey kangaroos are gregarious and females appear to be philopatric. Females are thus suspected to form kin clusters but the true social structure is largely unknown. We wished to examine mother/offspring associations and determine whether they correlated with survival, growth and reproduction of offspring. We observed 123 offspring aged 10 to 49 months with their mothers in a high-density population at Wilsons Promontory National Park, Australia. We marked young in the pouch or as young-at-foot and confirmed genetic relationships using 9 highly polymorphic

microsatellite markers. We quantified associations using half-weight indices (HWIs), which ranged from 0 to 100%. On average, mothers associated more closely with their daughters (HWI=33%) than their sons (HWI=23%) when offspring were aged 16 to 33 months but neither sex associated closely with their mothers at older ages (HWI=1%). HWIs of dependent offspring were not correlated with their survival, mass gain or reproduction, however both sons and daughters that spent more time with their mothers had faster skeletal growth than other offspring. Females thus do not form kin clusters with adult daughters in this population but mother/offspring associations before weaning have a beneficial effect on growth of both sons and daughters, which likely reflects maternal care.

P275 Social Structure in a South African population of Giraffe (*Giraffa camelopardalis*)

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The social structure of the giraffe (*Giraffa camelopardalis*) has only in recent years undergone inclusive investigations, and additional studies will be needed to further progress the understanding of the social system of this particular species. The aim of this study is to recognise the structure in the social organisation of a population of giraffe by means of network analysis. Between October 2012 and March 2013, association and interaction patterns were studied in the giraffe (*Giraffa camelopardalis giraffa*) population residing in Pilanesberg National Park, South Africa. Over this 4-months period, 451 giraffe groups were registered and approximately 170 individuals have been identified. The data will be analysed by use of specialised computer programs. The role of different types of individuals (e.g. sex, age groups) in the social network will explicitly be investigated, and the fission-fusion dynamics of the population are furthermore considered. Features of the social network will be tested statistically, such as whether females and young are making up the main kernels of the social network.

P276 Laying hens differ in their following behaviour depending on their companions' success in finding food

Anette Wichman, Slu

As a group living species it should be advantageous for hens to gather information about skills that

other hens in the group have and be able to benefit from this to get access to for example different food sources. To investigate this, adult laying hens (N=28) were trained in pairs (one demonstrator and one observer) in an arena with six food bowls. Each hen was trained in two different pair constellations. In one of the pairs the hens got access to the food when the demonstrator that had been selected to be skilled approached a food bowl whereas they got no food in the other pair constellation. At testing no food was provided for any pairs and behavior towards the other bird in the pair and towards the food bowls were observed. The observers followed the skilled demonstrator more (Wilcoxon Signed Rank test; $P=0.005$) despite the fact that the demonstrators behaviour towards the food bowls was independent of who they were paired with. This shows that laying hens are able to learn that one bird will give them access to food, not based on the demonstrators' specific behaviour at the time, but on the observers' previous experience with this bird.

P277 'I'm watching you!' Grey squirrels pay continuous attention to their conspecifics.

Pizza Ka Yee Chow, University Of Exeter
Lisa Leaver

Food-hoarding grey squirrels (*Sciurus carolinensis*) are sensitive to their conspecifics during caching. They showed more vigilance and implemented flexible food protection strategies to avoid food loss. However, it is not clear how the presence of their conspecifics also affect cacher's pre- and post-caching behaviours. We conducted two studies in four grey squirrels to examine the effects of social context on pre- and post- caching behaviours. The first study was using a social abstract design that obstructed visual access to environment while the second study was a control that provided full visibility of surroundings. Squirrels were allowed to cache their preferred nuts either in the presence or absence of a conspecific and they were then given 30 minutes to visit their caches. Both studies showed that cachers avoid their conspecifics before caching and they also oriented more towards the conspecifics during caching. Cachers also dug out their caches more often and selectively rehandled the nuts that had been observed by the observer during caching. Altogether, these results suggest that squirrels are continuously paying attention to their conspecifics. Discussion will relate to the social intelligence hypothesis and other plausible explanations.

P278 Repeated social interactions generate between-group variation, not between-individual variation in behavior in foraging groups of sticklebacks

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Alison Bell

Recent theoretical models have proposed a number of ecological factors that might generate and/or maintain between-individual variation in behavior, or personality. However, to date, empirical tests of these models are few. Several models have demonstrated the importance of conspecifics and group dynamics in generating personalities. Specifically, the presence of conspecifics can create the need for between-individual variation in behavior as this reduces competition. Then when groups repeatedly interact, individuals can benefit from behaving reliably. Therefore we would predict that groups of familiar individuals should exhibit greater between-individual variation in behavior compared to groups of non-familiar individuals. Here, we explicitly test this theoretical prediction using groups of sticklebacks in a patchy foraging environment. This context should favor between-individual variation in behavior as it can allow the group to achieve the ideal free distribution more quickly, thereby maximizing individual payoffs. However, contrary to our hypothesis, we found that familiar groups of sticklebacks did not show greater between-individual variation in behavior; but rather that groups of familiar fish diverged more from each other, than the groups of non-familiar fish. This suggests that repeated social interactions might instead increase group cohesion, which might be especially relevant in species that rely on group defenses.

P279 Cleaning stations, signalling and cleaning behaviour of Red Sea endemic shrimp *Ancylomenes longicarpus*

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The behaviour of endemic anemone shrimp *Ancylomenes longicarpus* was studied *in situ* in the Red sea. The signalling and cleaning behaviour was observed and analyzed. 3 different types of signalling behaviour were recorded: swimming towards object, swaying and rapid movements of pereopods ("clapping"). Intensity of signalling behaviour is significantly different during day time, the threshold distance of different signalling types is same during day and in 2 different habitats (grass vs coral).

Cleaning interactions with fish and complex cleaning behaviour was observed and analyzed (using direct observation and video analysis). In addition experiment with artificial fish and objects was conducted. Shrimps reaction was very similar among different presented objects (artificial fish, object with no fish characteristic, human hand) and cleaning of real presented fish client. The cleaning activity has two peaks: one high activity level during noon and second slight peak before sun set. Cleaning stations on coral reefs tend to have more visitors than cleaning stations situated on sea grass or sandy bottom. Cleaning interaction is longer when fish client is bigger and also shrimps are able to significantly prolong the stay of client in the station by using tactile stimulation.

P280 Do high ranking mothers produce high ranking babies? Dominance hierarchy in the mixed herd of Western Derby eland

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Adaptation of dominance hierarchies in social-living ungulates permits successful coexistence and determine the animals' access to resources and reproductive success.

Although dominance hierarchies have been examined in single-sex herds, studies of mixed herds are few. We examined the structure of social hierarchies in Western Derby eland in Bandia reserve, Senegal. We tested whether i) dominance hierarchies were linear or complex; ii) age and iii) sex influence the social rank of animals in mixed herds; iv) maternal rank inheritance appears in Derby eland offspring. Two herds (herd1, herd2) were observed in 2006, 2010, and 2011 ($N_{\text{herd1}/2006}=24$, $N_{\text{herd1}/2010}=22$, $N_{\text{herd1}/2011}=22$, $N_{\text{herd2}/2011}=13$). Total 615 and 198 dyadic interactions in herd1 and in herd2 were recorded, respectively. Frequency based dominance index revealed linear hierarchy in Derby eland ($h_{\text{herd1}/2006}=0.93$, $h_{\text{herd1}/2010}=0.68$, $h_{\text{herd1}/2011}=0.83$, $h_{\text{herd2}/2011}=0.89$). Dominance order was influenced by age ($r_s=-0.763$, $N=81$, $P<0.01$). Although the influence of sex on dominance order was significant ($H_5=48.25$, $P<0.001$), we revealed no difference between males and females in respective age categories: juveniles < 18 months, subadult animals – 18-42 months, adults > 42 months. There was no relationship between the rank of mother and offspring ($r_s=0.05$, $N=13$, $P=0.873$) probably arising from the adopted nursery herd system.

P281 Lateralization has no effect on social behavior in the domestic pigeon (*Columba livia f. dom.*)

Mareike Fellmin, Bruno-Duerigen-Institute
Inga Tiemann

The bird's visual system is highly lateralized. For this reason, many studies were aimed to learn more about the specialization of the brain hemispheres. For precocial chicks and quails it has been shown that social partner recognition is lateralized. In our study we observed altricial pigeons in standardized experiments to find out, if lateralization has an impact on imprinting, flocking and sexual behavior. Three different pigeon breeds were tested in a multiple choice arena, where they could choose from four live stimulus animals placed in the corners of the arena. Accordingly, one quadrant belonged to one stimulus animal. Time spent in the quadrants was analyzed using a multivariate analysis, followed by a t-test for dependent samples. Young pigeons showed a preference for their parents only when using both eyes and, therefore, both hemispheres for discrimination (N = 142; binocular: $p = .005$; monocular: $p = .36$). Similarly results were found in the two other experiments on flocking and sexual behavior. Our data suggest that there is no lateralization effect on the analyzed social behavioral patterns. Pigeons need visual input of both eyes and, thereby, information processing in both brain hemispheres for social discrimination behavior.

P282 Variation in reproductive investment in birds: links with life-history and sociality

Gretchen Wagner, University Of Zurich
Szymek Dobranik, Michael Griesser

Life-history theory suggests that species with a slow life-history can afford to adjust their annual reproductive investment depending on current conditions. This theory does not consider, though, that the parental investment of species is modulated by social lifestyles. For example, while some species invest in offspring only until they reach independence, others extend their care beyond this time. Additionally, in cooperative breeders the parental investment can be buffered by the presence of helpers. Using a comparative data set, we investigate the inter-annual variation in reproductive investment of more than 70 bird species with a wide range of lifestyles and life-histories to demonstrate that the annual investment

of reproductive effort is not solely life-history based. Specifically, we examine variation in reproductive investment, reproductive success relative to investment, and both of these factors relative to environmental conditions, to determine which environmental and lifestyle factors play the greatest roles in the fluctuation of reproductive investment across breeding seasons in the examined populations. Our results suggest that both life-history and social lifestyles modulate annual reproductive decisions.

P283 Sentinel System across the Breeding Cycle: How Individual Trade-offs affect Contributions to Cooperative Activities

Lindsay Walker, University Of Exeter
Andrew Young

The sentinel system, which has been observed in numerous social species, involves an individual assuming a conspicuous position while group members forage nearby. What if time available to forage had to be traded against other activities, thereby altering the value of individual foraging time? How would such individual and selfish trade-off decisions affect cooperative behaviour? Utilizing the cooperatively breeding white-browed sparrow weaver (*Plocepasser mahali*), I have investigated how individual contributions to the cooperative activity of sentinel behaviour are affected by the breeding stage of the group. Throughout the breeding cycle, individuals face distinct trade-off decisions that may differ from other classes, creating a conflict of self v.s. group. I predict that when a group member faces a trade-off that limits their available foraging time, for example egg incubation, their contributions to cooperative activities will decrease. During these trade-off periods, I expect other members of the group to increase their individual contributions to counterbalance the reduction.

P284 Kin recognition in *Drosophila*: the importance of ecology and gut microbiota

Anne Lize, University Of Liverpool
Raegan McKay, Zenobia Lewis

The development of spatial proximity loggers, such as Sirtrack® radio collars, allows social associations among individuals to be recorded continuously over time. Such data enables the construction of high-resolution temporal networks which can be used to test questions that would require levels of observation otherwise impractical to achieve.

However, following field testing, we have found that these loggers have highly variable performances, which computer-based simulations and analytical models have demonstrated would have serious ramifications to any network we might seek to produce using these devices. Some collars oversample and some under-sample, which will produce data that could be misinterpreted as differences in sociality. Further, the internal clocks on these collars are often not synchronised to each other. The combination of the different sampling strengths and misalignment of the internal clocks for any two given collars produce large amount of “nuisance” interactions where only one collar, often the more powerful, recognises the other. We propose a protocol and associated software that addresses these problems to correct for these sampling biases and misalignment of the clocks to generate reliable data that can be used to explore the temporal dynamics of social networks.

P285 Traditional behavioural assays and aggressiveness in a very social avian species (*Estrilda astrild*)

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Ana V. Leiteo, Andre C. Ferreira, Paulo G. Mota, Gonzalo C. Cardoso

In many birds species a variety of behavioural assays have been shown to correlate with aggressiveness. In social species, however, assays using isolated individuals may be poor predictors of behaviour within groups. We measured aggressiveness directly in groups of a very social species, the common waxbill (*Estrilda astrild*), and performed 5 traditional behavioural assays on the same individuals: tonic immobility, mirror test, novel object test, open-field test, and a variant of the latter in an enriched environment. We found that larger males were more aggressive, that differences in aggressiveness were repeatable, but that none of the traditional behavioural tests predicted aggressiveness, even controlling for body size. These results suggest that novel experimental designs more akin to the ecology of social species may be needed to assay avian aggressiveness in some species.

P286 Measuring flocking responses of humans interacting with a computer simulation

Alexandre Campo, Université Libre De Bruxelles
Andrea Perna

Flocks of starlings and schools of fish are impressive examples of collective animal behaviour in which hundreds or thousands of individuals move together in perfect synchrony. Collective robotics has long been interested in reproducing this behavior for exploration and monitoring of hostile environments.

Simulation models can reproduce different aspects of the collective motion of birds and fish by assimilating them to particles that can be repelled by, attracted to, and aligned with other individuals within one or more different zones. One major limitation of these models is that they make assumptions about individual cognitive capabilities and give few clues concerning the perception of individuals and the actions elicited in response.

To gain better understanding of the individual behavior that leads to collective motion, we propose to let a human subject take the role of one individual in a simulated swarm. The human subject receives information from the point of view of the individual and controls it with a joystick. He is instructed to seamlessly integrate and move with the swarm.

By recording the responses of the subjects together with the corresponding external stimuli, we can obtain detailed information about the cognitive mechanisms used to achieve collective motion.

P287 The contribution of microclimate to spatial structuring and territory choice by the Colombian Payasita poison frog *Oophaga histrionica*

Adolfo Amézquita, Universidad De Los Andes
Diana Maria Galindo Uribe

The reduced dispersal capacities of most anuran species may increase the potential for neutral or deterministic processes in promoting phenotypic and genotypic divergence. Neotropical poison frogs of the genus *Oophaga* are highly philopatric, exhibit homing abilities and strongly defend their territories against conspecific male intruders. In *Oophaga pumilio*, the use of olfactory cues, and the availability of mates and reproductive resources have been recognized as mechanisms and contributing factors in the choice of territories. However the role of environmental cues remains poorly understood, and may well affect the survival and performance of ectotherms organisms as amphibians. We studied the contribution of microclimate heterogeneity to the spatial distribution in a population of *Oophaga histrionica* from the Colombian Choco region. We measured the abundance of individuals related to

temperature, relative humidity, light intensity conditions, the number on bromeliads, as an essential resource for reproduction, slope and altitude. We found that this population is distributed in a patchy way, with a great number of individuals in sites of higher elevation with more stable conditions of temperature and relative humidity during daytime. In order to understand the potential consequences of these factors on genetic divergence processes, we are collecting microsatellite data within this population.

P288 Stickleback males increase red colouration and courtship behaviours in the presence of an attractive rival

Sin-Yeon Kim, Universidade De Vigo
Alberto Velando

In species where females preferentially select the most colourful males, males may strategically invest in colouration according to the presence of rivals. In this experimental study, we tested this in the three-spined stickleback (*Gasterosteus aculeatus*) in which mature males exhibit carotenoid-based red colouration to attract mates and defend their territories against male competitors. We challenged experimental males with an attractive (red-ornamented) dummy male whereas control males were presented with a dull (non-ornamented) dummy five minutes per day during six days. We found that at the end of treatment the males presented with an attractive rival showed a significantly larger area of red colouration than the control males. The experimental males also exhibited more frequent courtship behaviours (i.e. fanning and gluing) to females than the control males during the second half of the treatment period. Our findings suggest that male sticklebacks regulate mating effort according to the presence of competitive rivals by increasing their investment in costly signals when successful mating and territory defence is at risk.

P289 Do primates like babies? : Preference for infantile physical features in nonhuman primates

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Recent neuroimaging studies empirically showed that baby faces as well as infantile physical images were spontaneously perceived by humans as cute and attractive and elicited strong motivation for

caretaking (*M. L. Glocker et al. 2008*). Endocrine factors influence cuteness perception in humans as perceived cuteness of baby faces varied with hormonal levels (*R. Sprengelmeyer et al. 2009*). These results are empirical findings supporting the baby schema hypothesis proposed by the ethologist Konrad Lorenz (1943). Whether the baby schema also influences cuteness perception in nonhuman primates remains an open question as literature on preference for infantile physical features is still scarce in animals. Here, we experimentally tested the preference for infantile images by using visual paired comparison (VPC) tasks in two old world monkey species, i.e., Japanese macaques and Campbell's monkeys. We found that both species preferred to look at infantile images over adult images at the intra- and the inter-specific levels. This is the first empirical demonstration showing the attractiveness of baby infantile physical features in nonhuman primates, raising the question of the evolutionary origins of the instinctive human perception of baby schema.

P290 To See Or Not To See: Visual Contact, A Primary Need For Social Animals?

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Laurence Henry, Marion Coulon, Hugo Cousillas, Martine Hausberger, Isabelle George

One characteristic of sociality is the active seeking of proximity by conspecifics. Although active interactions and physical contacts can be involved, in many cases, visual contact at least plays an important role. In the present study, we investigated whether this motivation for visual contact is strong enough to become a "primary reinforcer". Thus, we used an operant conditioning procedure to test whether isolated adult European starlings, a social species of birds, would actively trigger social or non-social stimuli presented as 2D pictures. The results show that true conditioning with no training and no other reward than the pictures is possible. Moreover, starlings expressed a preference for pictures of conspecifics over pictures of (1) landscapes and (2) monkeys. A mere picture can therefore act as a "primary reinforcer" in an operant conditioning procedure.

P291 Understanding enrichment induced agonism in rats through network analyses and motivational profiles

Becca Franks, Columbia University
James P. Curley

Aggression—agonism more generally—represents a substantial cost of group living both in the wild and in captivity. Though environmental enrichment can be effective at reducing aggressive behavior, it can also induce agonism as animals compete with each other to gain access to a limited resource. To understand this dynamic further, we used network analyses to test our hypothesis that in the presence of a limited resource, a pair of rats with similar motivational profiles will be more likely to engage in agonistic interactions than a pair with dissimilar motivational profiles. We group housed 12 female rats in a complex environment and measured all agonistic interactions directly after enrichment provisioning as well as one hour later. Two months later, we gathered data on an individual's motivation to obtain treats and maintain safety and thus calculated each pair's motivational similarity. Modeling these data as a network, we found the predicted increase in agonism directly after enrichment vs. an hour later ($p < .001$) and that motivational similarity was associated with significantly greater agonism ($p < .01$). These results suggest an important role of motivation and demonstrate that studying environmental enrichment may provide broad insights into the dynamic causes of agonistic behavior.

P292 Social behaviour in horse groups- a comparison.

Hrefna Sigurjonsdottir, University Of Iceland

Since 1996 social behaviour of horses kept in pastures have been studied in many groups in Iceland where the Icelandic horse has been the only breed since the country was settled 100 years ago. Here results from 21 such studies are used for comparison. Most groups were studied for more than 75 hours. The group types vary from small (6) single sex- groups of 1year olds to large mixed groups. The largest was a semi-feral herd (130 horses) with four stallions and their harems kept in a 215ha pasture. Some groups were temporary while others were stable. The results showed interesting differences between different group types. For instance, both negative and positive interactions were significantly more frequent in unstable groups and also in groups without stallions. Aggression was negatively correlated (significantly) with mean age. The higher the ratio of subadult to adults the higher the rate of aggression, play and allogrooming. Thus, the relevance for management is clear. Dominance hierarchies were significantly linear in all non- stallion groups but not so in all harems. The results can help us interpret the nature of the social system/sociograms in horse

groups with respect to dominance hierarchies and bonding.

P293 Are horses sensitive to humans' emotional state during a leading task?

Vanessa Andre, Université De Rennes 1
Anne Sophie Vallet, Séverine Henry, Martine Hausberger

Both humans and animals appear to be sensitive to cues displayed by each other while interacting and adapt their behaviours accordingly. However, very little is still known about the relevant elements that have to be considered when humans interact with horses. Here we investigated whether humans' emotional state had an impact on horses' heart rate and level of obedience in a simple leading task. Professionals (6 women, 2 men) and non-professionals (3 women, 3 men) were asked to lead a horse along a given path. Experiment 1 was performed on 8 professionals and 3 horses; experiment 2 on 6 non-professionals and 13 horses. Humans' and horses' heart rates were recorded during the interaction. People also reported *a posteriori* on their positive and negative emotional states (questionnaire). Non-professionals had lower heart rates and expressed less negative feelings than professionals ($p < 0.05$). Alongside, horses showed higher heart rates with non-professionals ($p < 0.001$). These results suggest that horses are able to perceive humans' emotional states. The results reinforce the idea that knowledge of factors which might impact on humans' emotions should be promoted, as appropriated emotions might be key elements to prevent accidents.

P294 Who mounts whom and why? Characteristics, causes and consequences of mounting behaviour in finishing pigs

Sara Hintze, University Of Bern
Desiree Scott, Simon Turner, Simone L. Meddle, Richard B. D' Eath

Around 100 million male piglets are castrated annually in the EU, usually without anaesthesia or analgesia. One alternative to castration is entire male pig production. However, entire males perform more mounting behavior than castrates which may be a welfare problem. Eighty entire male and 80 female pigs in single or mixed-sex groups were observed on 24 days during the finishing period. Males mounted about three times as often as females did (total mounting mean $\bar{y} \pm s.e.$: males=18.8 $\bar{y} \pm 2.0$, females=5.7 $\bar{y} \pm 0.9$). Furthermore,

individual differences were stable over time (Kendall's coefficient of concordance: $W=0.33$, $p<0.001$), suggesting that mounting behaviour reflects an individual trait rather than the appearance of random outbreaks. There were no relationships between mounting behaviour and dominance rank in food competition tests or circulating levels of sex hormones at the end of the study. Comparing functionally different forms of mounting revealed that sexual mounting was most common overall (51.6% of all classified mounts) and in males but rare in females. Sexually-motivated mounts lasted longer (Fisher's exact test: $p<0.001$) and induced more distress vocalizations (high-pitched screaming, Fisher's exact test: $p<0.001$) by the recipient compared to other mounting types, indicating a welfare issue. However, the frequency of mounting received did not affect health scores or weight gain.

P295 The behavior of domestic cats (*Felis catus*) changes with their owner's attentional state.

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Toshikazu Hasegawa, Atsuko Saito

The behavior of domestic cats (*Felis catus*) was observed in response to being called by name by their owners, whose attentional state varied. One trial consisted of the owner calling their cat's name once every 3 seconds for 1 minute. The following four conditions were used: (a) the owner looked directly at his/her cat throughout the trials; (b) the owner closed his/her eyes rather than look directly at his/her cat during the trials; (c) the owner read a book or looked at a portable terminal rather than look directly at his/her cat during the trials; (d) the owner turned his/her back to the cat during the trials. In conditions (a) and (d), the cats looked directly at their owners for a longer period of time than in conditions (b) and (c). In addition, the cats exhibited head turning behavior more often when the owners looked directly at their cat or turned their back to their cat (i.e., conditions (a) and (d), respectively) compared to when the owners closed their eyes or read a book or looked at a portable terminal (i.e., conditions (b) and (c), respectively). These results suggest that domestic cats can distinguish their owner's attentional states.

P296 Mamma boys stay aside: The effect of suckling behaviour on the dominance hierarchy within subadult horses

Martina Komárková, Institute Of Animal Science
Jitka Bartoňová, Jana Dubcová

Horses form strong dominance hierarchy within the herd. Top ranked animals profit through higher reproduction and better nutrition. Therefore intergeneration transition of so-called "dominant abilities" can lead to increased fitness. We found earlier that foals of dominant mares suckled longer due to expected higher maternal care and protection. We hypothesised that foals of dominant mothers and foals with longer sucking bout duration should reach higher dominance rank. We investigated suckling behaviour in a group of mares with foals (66 foals up to 4 months of age). Age of the foal ($P<0.01$, general linear model), but not the mother's rank, influenced its dominance rank within a group of herdmates of the same sex 3 years later; older foals reached higher dominance rank. We found marginally significant effect of suckling bout duration on foal's dominance rank ($P=0.09$), but in an opposite way than expected. Foals with shorter suckling bouts tended to reach higher dominance rank as subadults (shorter suckling bouts were not compensated by higher suckling frequency). In conclusion, mother's dominance rank did not predict dominance status in their subadult offspring. Shorter suckling bouts in foals likely reflected higher independency on mothers that led to higher success in dominance encounters in subadulthood.

P297 Dog breed differences in gazing behavior at humans

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Teresa Romero, Toshikazu Hasegawa, Miho Inoue-Murayama

Domestic dogs (*Canis familiaris*) have developed a close relationship with humans through a process of domestication. Eye-contact is a key aspect for initiating and maintaining dog-human interactions. Previous studies have suggested that canine gaze behavior at humans is influenced by domestication history from wolf to dogs, as well as by recent selection for working dogs (Miklosi et al. 2003; Passalacqua et al. 2011). To test the impact of genetic basis on communicative performance in dogs, we examined dog's gaze behavior at humans using two types of behavioral experiments: i.e. the visual contact task (Jakovcovic et al. 2010) and the unsolvable task (Passalacqua et al. 2011). A total of 95 dogs participated in this study. Subjects were classified into five breed groups (i.e. Ancient, Herding, Hunting, Retriever-Mastiff, and Working) based on the genetic relatedness among breeds (vonHoldt et al. 2010). We found significant breed differences of gaze behavior in both behavioral

experiments, with Ancient-type breeds gazing at humans for shorter periods of time than other breed groups. Our findings suggest that dog's spontaneous gaze responses to humans are associated with genetic similarity to wolves, and that cross-specific communicative skills in dogs have been altered by recent selection for modern European breeds.

P298 Gone AWOL. Behavioural management of social distress in ravens (*Corvus corax*)

Alexandru Munteanu, University Of Vienna
Martina Stocker, Mareike Stöwe, Thomas Bugnyar

Acute stress is an adaptive response to environmental changes, but prolonged and elevated levels of stress can be detrimental to health. Social support can act as a buffer, reducing the impact of a stressor on the receiver's homeostasis. However, group life can also promote conflicts and the risk of group members actually intensifying a stress response. We here investigated the interplay between social support and stress in 16 sub-adult captive ravens (7 males, 9 females) that were individually confronted with temporary separations from their two social groups, simulating one aspect of the fission-fusion dynamics reported from the field, where individuals regularly join and leave groups for extended time periods. We predicted that subjects exhibiting high stress during separation (measured via self-directed behaviours and excreted corticosterone metabolites as an indicator for adrenocortical activity) should actively engage in socio-positive behaviours with previously affiliated individuals shortly after reunion, whereas those who showed little stress during separation would avoid interacting with others and/or engage in aggressive interactions with previously non-affiliated individuals. Preliminary results are consistent with these predictions and support the idea that forming and maintaining social bonds affect the valence and intensity of social distress responses in ravens.

P299 Presence of peers reduces agonistic interactions and stress in goats introduced into new groups

Beat Wechsler, Centre For Proper Housing Of Ruminants And Pigs, Federal Veterinary Office FVO, Antonia Patt, Lorenz Gygas, Edna Hillmann, Rupert Palme, Nina Maria Keil

When introduced into a new herd, goats are confronted with unfamiliar animals. Their

behavioural and physiological reactions during this confrontation are likely to differ depending on the presence or absence of familiar conspecifics (peers). To assess these reactions, we confronted 12 goats both alone and with two peers (confrontees) with established groups (n=4) consisting of six goats unfamiliar to the confrontee (unfamiliar goats). Each confrontation lasted for one hour. Agonistic interactions and sniffing behaviour were recorded throughout the confrontations. In addition, concentrations of cortisol metabolites were measured in faecal samples taken before and after the confrontation. Before the start of the experiment, we evaluated the dominance relationships of the involved goats within their respective housing groups. Data were analysed using generalised linear mixed-effects models with the fixed effects presence of peers, rank category and repeated confrontation. Unfamiliar goats directed fewer agonistic interactions and sniffing behaviour towards confrontees when the latter were accompanied by peers compared to when they were alone. Moreover, confrontees with peers had lower concentrations of faecal cortisol metabolites after the introduction. In conclusion, our results indicate that the presence of peers is advantageous for the welfare of goats being introduced into new groups.

P300 The Social Nature of Anointing in Tufted Capuchin Monkeys (*Sapajus sp.*)

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Capuchin monkeys rub a range of strong smelling substances into their fur, such as onions, limes, plants and some chemically defended insects, either alone, 'individually', or in contact with other individuals - 'socially'. Functions for these anointing behaviours could be; insect repellent or treatment of ectoparasites, scent marking, or social bonding. Monkeys may also anoint socially when resources are rare and anoint individually, when resources are in abundance. To address the 'rare-resource hypothesis' we presented two groups of tufted capuchin monkeys with onions in 'rare resource' and 'abundant resource' conditions, and measured the proportions of individual versus social anointing. We used social network analysis to examine changes in the social structure of the groups in response to differing availability of resources. The proportion of individuals anointing socially was higher when resources were rare, but subjects always anointed more socially than individually, even when resources were not limited. When resources were limited, group structure was similar to baseline

group structure. Furthermore, close bonds were strengthened more within groups when resources were rarer than when resources were in abundance. These mixed results suggest that the social nature of anointing may include, but also go beyond, an evolved response to resource availability.

P301 Collective construction in the mound-building mouse

Maria Jose Hurtado, LEEC Université Paris 13
Zsafia Nagy, Peter Szenczi, Vilmos Altbäcker, Renée Féneron, Patrick Gouat

Mound-building mice (*Mus spicilegus*) construct large mounds of soil and plant material in autumn, where juvenile animals overwinter in groups without reproducing. The process includes several successive phases involving 1) the transport and piling up of different kinds of plant materials, 2) covering up the mound with dirt, 3) laying clay tiles on top of the mound, 4) digging a network of tunnels below the mound. Mounds reduced temperature variation of the soil and keep the nest dry during the winter. Mice used mainly seeds and ears of certain plants (*Ambrosia* sp., *Echinochloa* sp., *Chenopodium* spp., and *Setaria* spp.) as building material and the species used differs between mounds. Laboratory studies revealed that within a group of six individuals, two individuals transported most of the material provided for building. When two types of material (cotton as plant material and plaster tiles as clay tiles) were proposed successively, carriers of one material were not the same individuals as the carriers of the second material. This shift in the identity of the carrier according to the material used indicates a specialization for a different transport task.

P302 Are social play and manipulation correlated? A study of a semi-free ranging immature capuchin monkeys in Brazil.

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Briseida D. Resende

Perception-Action Theory posits that individuals learn about affordances and physical properties between objects and surfaces when they are motivated to explore the surrounding. We believe that social-bonds are constructed, in part, by the same way: individuals exploring physical and motor affordances of others in social play episodes. Based on these premises, we hypothesize that individuals that manipulate more are also more “social players”. Nineteen infants and juveniles capuchin

monkeys (*Sapajus spp.*) from Tiete Ecological Park (Sao Paulo, Brazil) are the studied subjects. The data were collected using Animal-focal method (20 min per session) from August to December 2011 and we registered 127 hours of work. We verified correlation between manipulation and social play activities only in males, so we might investigate if the increase of these behaviours could favor the arousal of tool-use to crack nuts – activity well known by being more frequent in males in several studies.

P303 Association indices for group-derived animal social networks

Elaine Bettaney, University Of Bath
Darren Croft, Richard James

Social network analysis is a tool used to investigate the social fine structure of animal populations. Observations of associations or interactions between animals are accumulated to build up a network. The structure of the resulting network is then related to the social biology of the system. We focus on group derived data where repeated observations of group membership are used to infer association. Here association indices are used to quantify the strength of network edges between each pair of animals. Using a case study of a wild population of guppies, we investigate potential biases in edge strength originating from the sampling method and suggest modifications to existing association indices which attempt to correct for these biases.

P304 Do cavity nesting bird species prefer social information from con- or heterospecifics?

Tuomo Jaakkonen, University Of Oulu
Sami M Kivelä, Christoph M Meier, Jukka T Forsman

Social information use is a widespread strategy in the animal kingdom and it affects many important behaviors. Cavity nesting birds are excellent model organisms for studying social information use in natural settings. Great and blue tits use conspecific cues in their breeding site choices. Early breeding resident tits are excellent social information sources for migratory collared flycatchers. Flycatchers have been shown to use both con- and heterospecific cues in their breeding site choices in separate studies. Previous research has ignored the multiple sources of social information. In this study wild birds were faced with conflicting social information from con- and heterospecifics. Thus, we were able to assess the relative importance of intra- and

interspecific social information. Our results demonstrate that flycatchers prefer intra- and interspecific cues in different situations when both cues are available. In great tits conspecific copying is frequent in old males. Individuals usually live in multi-species communities amidst a continuous information flow from con- and heterospecifics, thus our results bring social information use research closer to natural conditions.

P305 Redirected aggression reduces the cost for victims among semi-provisioned free-ranging Japanese macaques (*Macaca fuscata fuscata*)

Nahoko Tokuyama, Primate Research Institute, Kyoto University
Takeshi Furuichi

In many social species, soon after a conflict the victim often attacks an uninvolved third individuals. This behavior is called redirection, and its roles remain controversial. We observed semi-provisioned free-ranging Japanese macaques at Iwatayama Monkey Park in Kyoto, Japan, to test three hypotheses concerning the function of redirection: victims perform redirection to (1) indirectly retaliate against the aggressor, (2) reduce post-conflict stress, or (3) reduce post-conflict uncertainty. Our results primarily supported hypothesis (3). Victims received renewed aggression more frequently within 1 min after initial conflict than in the subsequent 9 min. Victims who performed redirection received less aggression from bystanders. Victims might have been able to avoid renewed aggression because they could change their state from victim to aggressor by performing redirection. This effect of redirection did not differ with the victim's rank. However, the lower the victim's rank was, the more frequently he/she received counter aggression from the target of the redirection or its kin. Thus, redirection caused the same magnitude of benefit and a different magnitude of risk according to the victim's rank. Victims may need to judge their situation before performing redirection, which may explain why experienced older monkeys more likely perform redirection.

P306 Kinship or Friendship? What is more important for giraffes (*Giraffa camelopardalis*).

Markéeta Hejzlarová, Czech University Of Life Sciences Prague
Karolina Brandlová

Statements about social relationships of giraffes are currently very different. It was thought that social ties among giraffes are very weak but recent studies documented stronger relationships among individuals. Our research deals mainly with allonursing of captive giraffes (data from 2007 to 2012). Allonursing is the phenomenon when female nurse non-filial young. Giraffes allonursed in 43.8% of all nursing (n=870). The research was made in four zoos (totally 31 females and 49 calves). We assumed that giraffes would choose the non-filial calves according to the coefficient of kinship and prefer the more related calves (kin selection). But this did not affect the frequency of allonursing. Two separated herds were connected before the research. The frequency of allonursing was higher for the animals which had originally lived together. Females favored calves who they knew better. This behavior could be result of the reciprocity and shows stronger social bonds among giraffes. Further research will focus on the social preferences of giraffes in captivity and in the wild by measuring the inter-individual distances. The research was supported by CIGA ZU 20135010 and IGA FTZ 55120/1312/3110.

P307 Transition dynamics in social groups: Testing for generic features of critical transitions in the precocial avian model

Roman Fuchs, University Of Salzburg
Gustav Bernroider

Collective behavior in social organisms may facilitate distributed sensing and cooperations with significant adaptive advantages (e.g. Berdhal et al, Science 339, 2013), culminating in the correlation of group size with brain size in primates. A large number of studies within the ecological and social sciences have been launched more recently to search for generic markers that are typical for the transient behavior of the underlying network dynamics. Here we demonstrate the results of a sequence of studies employing the precocial, juvenile avian model that provides distinct behavioural signatures of social cohesion (e.g. reviewed by Bernroider & Panksepp, Neurosci & Biobehav Rev, 35, 2011). We manipulate social 'connectivity' and 'modularity' by post-natal group-size experience in juvenile quail. We find that most theoretical predictions from complex network dynamics regarding the correlation of modularity and connectivity of groups with changing social conditions (e.g. isolation) are actually met. In particular, response and recovery rates, resistance to stress (resilience) and transitions as measured by isolation calls (DV), seem to follow the generic features of critical transitions in complex systems as

previously suggested by Scheffer (Science, 338, 2012). Our studies also indicate the presence of a post-natal memory for group size in these birds.

P308 Do great tits (*Parus major*) cover eggs in order to hide information from the pied flycatchers (*Ficedula hypoleuca*)?

Olli Loukola, University Of Oulu

Toni Laaksonen, Janne-Tuomas Seppänen, Jukka Forsman

Great tits cover eggs with hair before, but not during incubation. The function of this behavior, however, is still unclear. Pied flycatchers derive fitness benefits from their association with tits while the tits suffer from this. An evolutionary arms race between these species could then result. The options for the tits are to cease providing information, or to attempt hiding the event from flycatchers. Tits should bring more hair to cover the eggs when flycatcher is present compared to situation when only neutral species is present. We conducted playback experiment in Oulu and Turku, Finland. First, we collected all the hair on top of the tit eggs. Second, we tested whether the perceived presence of flycatcher increases the tits egg-covering effort. Our results show that the tits indeed cover eggs more efficiently when flycatcher was present compared to situation when only waxwing (*Bombycilla garrulus*) was present. We also found that the tits in Oulu (over 600 km to the north from Turku) had more hair on top of their eggs in general. This result demonstrates that egg-covering behavior of great tits may have a multifunctional role. It could act as a counter-adaptation against flycatchers and protect eggs from low temperatures.

P309 Weak, stable bonds allow for social stability in an unpredictable world

Christina Stanley, University Of Manchester

Phill Watts, Claudia Mettke-Hofmann, Susanne Shultz

One of the foundations of a socially complex society is the temporal stability of both its social network and its constituent cooperative bonds. This allows for the formation of alliances, societal roles, multi-level social networks and other markers of animal social complexity. In order to achieve temporal stability, a network must be resilient to change yet maintain some degree of flexibility in order to allow individuals to react to changing ecological conditions. We collected long-term data on semi-feral ponies *Equus caballus ferus* and found their

social network to have long-term stability and resilience to major change, whilst maintaining a degree of seasonal flexibility. The weak bonds between unrelated females maintain this stability and allow for stable network positions to be sustained for individuals. We propose that these network properties allow horse populations to persist across a vast ecological gradient and that such benefits may have originally underpinned selection for stable yet flexible networks in modern socially complex species, whilst also promoting cooperative sociality. We also highlight the importance of weak bonds in maintaining the structural integrity of a network.

P310 Aggregation Diptera larvae on homogenous and patchy environment

Julien Boulay, Université De Lille 2 / Université Libre De Bruxelles

Damien Charabidze, Cédric Devigne, Jean-Louis Deneubourg, Valéry Hédouin

Necrophagous Diptera larvae form large maggot-masses on decomposing cadavers. Such aggregates can gather thousands of larvae. No experimentation has investigated the aggregation mechanism in necrophagous larvae.

Forty larvae of *Lucilia sericata* were placed in a dish with a homogeneous diet for 5 times. Results indicate that aggregation took place quickly and was reinforced with time. This experiment demonstrated for the first time under controlled conditions the active aggregation of *L. sericata* larvae.

To highlight inter-attraction between larvae, forty larvae were randomly placed in a circular arena with 2 identical food-patches and video-followed.

Experiments were performed on 2 Calliphoridae species: *L. sericata* and *Calliphora vomitoria*.

For the 2 species, a choice did occur: larvae aggregates on a single food-patch (winner spot).

Aggregation on winner spot took place quickly (<30min) and was stable in time. However, an important number of individuals were observed outside food-patches (15 larvae in average).

Monitoring of one individual over time showed that larvae did not stay in aggregate but moved out and came back. Larva explores the environment all around the winner spot but returned in contact with congeners.

Results of these experiments and conclusion will be discussed in the context of self-organization and gregariousness.

P311 Burrowing bedfellows: how conspecifics affect behaviour in the southern hairy-nosed wombat.

Kris Descovich, University Of QLD & University Of Stirling

Allan Lisle, Stephen Johnston, Clive Phillips

The southern hairy-nosed wombat (*Lasiorhinus latifrons*) is a large fossorial marsupial that acts as an important research model for both conservation and animal welfare. In order to determine the behavioural effects of living in different group sizes, wild-born, adult wombats were organized into large (1B&, 3@&), medium (1B&, 2@&) and small (1B&, 1@&) groups and monitored in a captive, naturalistic environment that allowed both above and below-ground behavioural monitoring. While most activity remained unchanged by the groupings, vigilance behaviour (scanning, air-smelling and object-smelling) was significantly affected, with wombats demonstrating less vigilance while in larger groups. Subsequent analysis showed that vigilance also increased as nearest neighbour distance increased, and distance from the burrow decreased. Vigilance within burrows was similarly affected by social influences, with solitary wombats significantly more vigilant than those denning with a conspecific. These results suggest that *L. latifrons* recognize a protective advantage from the presence of familiar conspecifics, and that vigilance-group size effects are not limited to above-ground activity.

P312 Learn to beat an identity cheat

William Feeney, The Australian National University
Naomi Langmore

Arms races between brood parasites and their hosts provide model systems for studying the evolutionary repercussions of species interactions. However, how hosts identify brood parasites as threats, and how they prevent parasitism from occurring remains poorly studied, despite its ecological and evolutionary significance. In this talk I discuss this 'frontline' of the arms race between brood parasitic Horsfield's bronze-cuckoos, *Chalcites basalis*, and their primary host, the superb fairy-wren, *Malurus cyaneus*, in Australia. More specifically, I will discuss whether: 1) superb fairy-wrens identify cuckoos as unique threats, 2) recognition of cuckoos is learned or innate, and 3) whether cooperative breeding facilitates nest defence.

P313 Urban house sparrows (*Passer domesticus*) show resilience to the experimental removal of high-ranking individuals

Robin Kubitzka, University Of Turku

Jukka Suhonen, Timo Vuorisalo

House sparrows (*Passer domesticus*) form gregarious flocks characterised by fluctuating group composition and social dominance. It was shown recently that targeted removals of high-ranking individuals reduce overall group stability by increasing intra-group aggression. However, how social dominance affects group performance and stability in a fission-fusion like society remains largely unknown. Here, we determined dominance-related social interaction patterns in an aviary population of N=17 wild-caught urban house sparrows after (i) experimentally removing three high-ranking individuals and (ii) reintroducing them into the group after one week. Implementing social network theory, we constructed three distinct networks (agonistic, non-aggressive joining, supplanting at feeder) for each of three treatments (baseline, removal, reintroduction).

We did not observe differences in agonistic interaction frequencies between treatments; neither did males and females differ in initiating social interactions. However, males supplanted less often following targeted removals and joined conspecifics more often during reintroduction than in the baseline and removal treatments.

We conclude that urban sparrows show resilience to the removal of high-ranking individuals since agonistic interaction levels remained unaffected.

Males but not females increasingly used non-aggressive over aggressive scrounging tactics following targeted removals which may be a sex-specific change in social foraging tactics as a response to perturbation in their social environment.

P314 Always together: mate defense or predation risk avoidance in mesites?

Anna Gamero, University Of Göttingen

Peter Kappeler

Being a member of a cohesive group has fitness benefits such as decreased predation risk, increased feeding efficiency and access to social information and mates. However, feeding competition and the risk of parasite transmission exert centrifugal forces on group-living animals. Thus, the degree of cohesion is expected to vary as a function of social and ecological factors.

White-breasted mesites (*Mesitornis variegata*) are medium-size birds endemic to Madagascar which live in highly cohesive breeding pairs or small groups. Breeding adults mate monogamously and cooperate in the care of offspring and territory defense. They forage on the ground and form associations with other bird species that act as sentinels as they give alarm calls from the canopy. We investigated the effect of predation risk and mate defense on mesite group cohesion by analyzing inter-individual distances as a function of group size, the presence of sentinels and mating status.

Mating status had no influence on the cohesion of breeding partners but individuals tended to be further from each other with increasing group size and when sentinels were present. Thus, the high predation risk associated with a terrestrial life-style is primarily responsible for the unusually high cohesion exhibited within social units of this species.

P315 Effects of costly partner switching on cooperative behavior in human social network

Peter Bednarik, CRC Evolution Of Social Behavior, University Of Göttingen
Dirk Semmann

Various explanations have been put forward to explain the vast amount of cooperation among humans. Recent theoretical models find that certain network structures can favor the evolution of cooperation, yet experimental evidence suggests that static networks do not enhance cooperation in humans. However, when players are allowed to change their social ties to partners, cooperation is found to be significantly higher. Here, links to defectors are broken with a much higher probability than to cooperative partners which leads to a self-organization into clusters of cooperators. Existing studies assumed that relationships can be established without any cost. We have conducted an experiment with varying costs for building new relationships. As predicted, individuals were much less likely to break and form social ties. Surprisingly, the cooperation levels are not affected by the introduction of costs despite of the vastly reduced dynamics. Especially when costs are high, very few social ties were broken. Even though the network was almost static, the achieved cooperation was much higher compared to a static network setting. We find that the potential choice to quit collaboration, even if very costly, is sufficient to significantly increase cooperation among humans.

P316 Determining the Effects of Competition on Territory Size of the Dusky Damselfish *Stegastes adustus* off Bocas del Toro Archipelago: a Density-dependent Scenario

Todd Cline, The Pennsylvania State University
Lais Chaves, Micah Marty, Carlos Ormund

The dusky damselfish, *Stegastes adustus*, is a Caribbean reef fish, which displays a very aggressive territorial behavior. Within their territories they are known to "farm" fast-growing filamentous algae, a valuable resource for herbivorous fish. However, little research had been done to examine what effects conspecific abundance has on the competition interactions and mean territory size of *S. adustus*. The areas of interest were Lime Point (LM), a shallow and wave exposed reef, and Pete's Reef (PT), a shallow and wave protected reef. Both are fringing reefs close to the shoreline off Isla Colon in the Bocas Del Toro archipelago in Panama. This experiment addressed the question: Will individual territory size and competitive interactions differ between Pete's Reef and Lime Point according to conspecific abundances? This was tested using the following hypothesis: Given that there was a higher density of *S. adustus* at LM, there would be greater intraspecific competition in that habitat. Overall, it was expected that individuals would therefore possess smaller territories at LM and also higher number of agonistic interactions with conspecifics. Data on damselfish abundance were obtained by a previous study using visual census technique within 20m² transects. Abundances were significantly higher at LM (t-test; $p=0.000000$), showing at least a fourfold increase on this exposed reef (Mean±SE; $4.4±0.78$ individuals per 20m² at PT and $17.81±1.11$ at LM). Individual territories sizes were obtained in this study during free dives using marked weights to lay out an observed territorial perimeter, which was then measured using a measuring tape. These measurements were used later on to determine the area of each territory. Once the territory was determined, a three minute observation was performed using the focal animal methodology in order to observe the number of competitive interactions and record any additional behavioral data on a dive slate. If the fish retreated out of direct sight, the timer was stopped as not to skew the behavioral data. The difference in mean territory sizes between reefs were statistically significant ($p=0.0001494$), with the larger territories being found at PT where there were far less conspecifics. Mean total number of attacks did not differ significantly between reefs ($p=0.6066$), suggesting that overall number of attacks has no effects on territory size. However, the mean overall number of conspecific attacks on territories

although also not significant ($p=0.1787$), presented a greater frequency of occurrence at Lime Point. Conspecific attacks accounted for 30% of competitive interactions at LM, whereas only 4% were observed at PT, being parrotfish and wrasses the species at which the dusky damselfish elicited most of the attacks at both reefs. We believe that territory size is driven by a density-dependent process, whereby keeping smaller territories ensures lower energetic costs in efficiently defending against conspecifics when compared to defending a larger territory against a larger amount of conspecifics.

P317 Higher aggression towards closer relatives by soldier larvae in a polyembryonic wasp

Johanna Dunn, University Of Nottingham
Derek W. Dunn, Michael R. Strand, Ian C. W. Hardy

In the polyembryonic wasp *Copidosoma floridanum* females commonly lay one male and one female egg in a lepidopteran host. Both sexes proliferate clonally within the growing host larvae. Distinct larval castes develop from each wasp egg: the majority being 'reproductives' plus some 'soldiers' which sacrifice reproduction and attack competitors. Maturing mixed sex broods are usually female biased, as expected when intra-brood mating is common. Pre-mating dispersal followed by outbreeding is expected to increase sexual conflict over brood sex ratios and result in greater soldier attack rates. Due to sexually asymmetric relatedness, intra-brood conflicts are expected to be resolved primarily via female soldier attack. We observed soldier behaviour *in vitro* to test whether lower intra-brood relatedness (manipulated by whether or not the father was from the maternal population) increased inter-sexual aggression by female as well as male soldiers. As found in prior studies, females were more aggressive than males but, contrary to expectations, soldiers of both sexes showed more aggression towards more closely related embryos. We speculate that lower intra-brood relatedness indicates maternal outbreeding and may suggest a rarity of mating opportunities for reproductives maturing from the current brood, which may thus enhance the value of opposite sex brood-mates.

P318 Completing the Circle? Cooperation & Imitation in Adult Humans

Cara Evans, University St Andrews
Rachel Kendal, Kevin Laland, Michal Arbiloy, Camille Troisi

Objective: Experimental evidence supports long-held notions that humans involuntarily imitate (or mimic) each other's behavioural mannerisms, and that this serves to enhance cooperative interactions and social group cohesion. A circular relationship between mimicry and cooperation has been suggested, yet to date there is no empirical evidence of a direct relationship leading from cooperation to mimicry. We investigated whether cooperation in a joint-goal, joint-payoff task leads to a subsequent increase in behavioural mimicry.

Methods: 80 subjects were randomly allocated to either a cooperation or control condition. Subjects cooperated with a confederate on a novel, joint-payoff coordination task (a 'buzz wire'), while control subjects undertook the same task alone. Subsequently, all subjects undertook a communication exercise with the confederate, during which a measure of behavioural mimicry (face touching) was ascertained.

Results and Conclusions: Subjects who cooperated with the confederate demonstrated a decrease in mimicry relative to control subjects. However, an interaction effect between experimental condition and performance on the coordination task suggested a positive relationship between cooperative task performance and mimicry. The implications of subject perceptions of cooperative outcomes on mimicry will be discussed.

P319 Costs and benefits of provisioning behaviour in a subsocial burrower bug

Lisa Filippi, Hofstra University
Maiko Wakiyama, Hiroko Kuroiwa, Hiromi Mukai

Progressively provisioning offspring represents one of the most extended types of parental care. When dependent young have little capacity to feed by themselves, the provisioning behaviour benefits the parents greatly. While benefits may be clear, theory predicts that the evolution of provisioning also depends on costs to future reproduction. However, detection of costs of provisioning has rarely been identified, at least in insects. In this study, we attempted to quantify the costs and benefits of care under laboratory conditions in a subsocial burrower bug, *Adomerus rotundus*, females of which display complex maternal care, including egg-mass guarding and progressively provisioning nymphs. Experiments involved removing the egg-mass from mothers just prior to hatch, or removing mothers from newly hatched broods, after allowing them to feed on post-hatch trophic eggs, but before the mothers could provision. Mothers who had their egg-mass removed increased the size of the next brood, and

nymphs without mothers to provision them showed decreased weight compared with controls. These results indicated that the provisioning by mothers actually generates current nymphal benefits and future reproductive costs to the female, probably suggesting that the effect of the benefits to nymphs might be enhanced more than the costs under natural conditions.

P320 Choice of resting partners in a dynamic dairy cow herd analysed using social network analysis

Anke Kristina Gutmann, University Of Natural Resources And Life Sciences

Anna Herzog, Christoph Winckler

Repeated regrouping of dairy cows leads to an unstable social environment for the animals. A better understanding of social relationships and measures thereof might help to improve animal welfare. Social network analysis was used to investigate whether familiarity (timespan since integration-TSI) and experience (lactation-Lac) can explain synchronicity(S)- and lying-neighbour(Nb)-networks in a cubicle-housed dynamic herd (n=45). For a total of n=220 scans from video recordings (10 days every 30 minutes from 0730-1930) all lying animals and their neighbours were noted to calculate S as the percentage of scans where both animals were lying (mean±SD=50.8±13.8), and Nb as the percentage of being neighbours within this data set (mean±SD=5.20±5.65). Multiple Regression via Double-Dekker Semi-Partialling for S and Nb in Ucinet® showed a weak, but non-random relationship between Nb and difference in TSI at a pairwise-level (r=-0.12, p=0.003). Multivariate ANOVA at the individual level with TSI and Lac as explanatory variables revealed significant effects on mean age (F=8.83, p<0.001) and mean TSI (F=10.5, p<0.001) of synchronous animals, and on mean TSI (F=4.13, p=0.001) of neighbours. Results indicate that more familiar cows were more synchronous and lied in neighbourhood more often. Younger cows were more synchronous with and lied more often next to older cows.

P321 Leaders follow leaders to reunite the colony: relocation dynamics of an Indian queenless ant in its natural habitat

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K Anoop, Annagiri Sumana

Several factors cause animals to relocate. Ant species are unique in that they not only have to

relocate adults, but they must also move their brood while maintaining colony cohesion. We explored the colony relocation dynamics of the ponerine ant *Diacamma indicum* in its natural habitat. Irrespective of whether ants relocated from their original nest in their natural habitat or from a nestbox in an unfamiliar but natural habitat, colonies experienced fission and multiple fragmentations. However, this fission was transient, and the colonies eventually unified at a single site. Tandem running, a behaviour in which one ant leads a follower ant from one site to another, was used to relocate about 96% of the colony members. The evacuation phase was significantly shorter than the reunification phase, and this may be an adaptive response to a disturbance in the ant's dwelling. Unlike other ants, the leaders were sighted at most of the temporary sites and thus, in principle, had the opportunity to compare the conditions of alternative sites directly. Most leaders discovered the final site by following other leaders; leaders following leaders occurred throughout the relocation process and constituted 30% of the total tandem runs.

P322 Food exchange behavior between multiple founding queens of *Polyrhachis moesta* (Hymenoptera: Formicidae) changes during hibernation

Satoshi Koyama, Tokyo University Of Agriculture And Technology

Ayano Hashimoto, Ken Sasaki, Toshiyuki Satoh

In some ant colonies founded by multiple queens, genetically unrelated queens cooperate to establish the colony. To test whether founding queens differentially adjust the amount of food exchange to nestmate and non-nestmate *Polyrhachis moesta* (Emery) queens before and after hibernation, food exchange in founding queens with different nutritional conditions was investigated. The proportion of non-nestmate queens showing food-begging behavior before hibernation was higher than that of nestmate queens. The number of begging behaviors was greater after hibernation than before hibernation, both between nestmates and between non-nestmates. Weight loss in fed queens performing food exchange with nestmate queens was significantly greater after hibernation than before hibernation. These results suggest that founding queens can discriminate between nestmate and non-nestmate founding queens and change the level of cooperation with founding queens before and after hibernation.

P323 Testing the role of direct, indirect and generalised reciprocity in grooming exchanges of wild Barbary macaques

Sandra Molesti, University Of Lincoln
Bonaventura Majolo

Grooming is thought to be costly for the donor and beneficial for the recipient. Reciprocity assumes that individuals act as the donor and recipient of grooming and switch roles over time to balance the benefits and costs. Three main patterns of reciprocity may follow a grooming given by A to B: (1) direct reciprocity, where B grooms A; (2) indirect reciprocity, where another individual C grooms A; and (3) generalized reciprocity, where B grooms any individual including A. We tested the role of direct, indirect, and generalized reciprocity in explaining grooming exchanges of wild Barbary macaques. We collected the occurrence and latency of the three types of grooming reciprocity during one hour focal session run simultaneously on two partners who just stopped grooming (post-grooming session) or who were in proximity (i.e. within 1.5 meters) without grooming (control session). We ran the analyses on 284 post-grooming and 63 control sessions. Directly reciprocated grooming from B to A was more likely to occur, and occurred earlier when A had previously groomed B than in control sessions. We found no evidence for indirect or generalised reciprocity. Our results indicate that grooming distribution in Barbary macaques is partner-specific and occurs according to direct reciprocity.

P324 Multiplicity of animal interaction in collective behavior

Takayuki Niizato, Tsukuba University

There are many kinds of interactions among individuals to construct animal collective behaviors. However, how do we apply this multiplicity of interactions in collective behaviors when we construct models? Here we propose the multiplicity of interaction in a simple model, which is constructed from three factors, which are asynchronous updating, learning site patterns and agent's anticipations. We found out that the first of two contribute to an efficient searching strategy. Furthermore, adding agent's anticipation enables to show a sign making (avoidance) in heterogeneous environments. Surprisingly, our model suggests that a searching strategy and a boundary making like a territorial behavior, which seems to contradict each other, turns out two aspect of our simple interaction rule. Finally, we discuss the possibility of animal collective cognition when heterogeneous

environments change with time. Our study suggests that the concept of the multiplicity of interaction in asynchronous updating is very important to understand many aspects of the emergence of animal collective behaviors.

P325 Familial cooperation and conflict in a subsocial bug

Shintaro Nomakuchi, Saga University
Lisa Filippi

Trivers (1974) proposed that in animals with parental care of eggs and young, siblings compete for parental resources and attempt to gain more investment than is optimal for parents by begging. However, whether conflict behaviors actually occur among them depends on various constraints, influencing the costs and benefits of the behavior. Important constraints are assumed to be: 1) semelparity or iteroparity, 2) whether or not parental resources can be shared among offspring, and 3) resource exploitation ability of offspring. I present here intra-familial interactions in a subsocial bug, *Parastrachia japonensis*, with semelparity and indivisible food for nymphs. In young nymphs, we could not observe any conflict behaviors, but rather observed aggregating as the simplest cooperating behavior. The aggregating cooperation was particularly prevalent when young nymphs fed on a drupe provided by the mother. As the nymphs developed, however, they tended to feed individually, suggesting the possibility that conflict behavior emerged. This study also demonstrated that cannibalism among nymphs occurred under starving conditions, and the degree of relatedness affected the incidence of cannibalism.

P326 Energetic costs of male-male interactions in murid rodent species with different social organization

Eugene Novikov, Institute Of Systematics And Ecology Of Animals, Siberian Branch Of The Russian Academy Of Sciences
Dmitry Petrovski, Olga Potapova, Dmitry Samsonov, Pavel Zadubrovskiy

Energetic cost of reproduction for males is associated mainly with the expression of secondary sexual traits including those behavioral patterns that provide the access to females. The patterns of social interactions that are responsible for reproductive success obviously vary among the species with different social structure. However there are almost no comparable data of interspecies variability of metabolic costs of male interactions. Here we

presents the data of metabolic rates measured before- and just after dyadic trials of males of four sympatric rodents inhabits semi-arid zone: social subterranean mole vole, solitary promiscuous dwarf hamster, monogamous steppe lemming and narrow-skulled vole. In all of the species metabolic rates increased after the trial in comparison with resting metabolic rate (RMR) measured previously and then gradually dropped to the initial RMR level. The magnitude of such increase differed among tested species being maximal in dwarf hamsters. Minimal rates of increase were detected in steppe lemmings. Generally, dominated males revealed lower metabolic rates after the trial than subordinates. So in studied species of murid rodents metabolic response of males on interaction with conspecific male is determined by the peculiarities of social structure of the species and social rank.

P327 The Role of Projection in the Control of Swarms

Daniel Pearce, Moac
Matthew Turner, George Rowlands

Animals show an impressive variety of organised group behaviour, including shoals of fish, flocks of birds and herds of mammals. These large groups provide many advantages over solitary behaviour, such as protection from predators, increased awareness and group decision making. The underlying "rules" which give rise to this effect have proven hard to identify. We propose a model in which a flock organises its density in order to optimise the visual information available to an individual, subject to the flock remaining fairly compact. This results in a marginally opaque flock, which is at the maximum density that still allows most visual information to pass uninterrupted across the length of the flock. This has the advantage of allowing long-ranged, instantaneous information transfer over the extent of a flock while remaining consistent with the cognitive abilities of the animals. It also constrains the density. We show evidence for marginal opacity within real starling flocks, and propose the Hybrid Projection Model; a Self-Propelled Particle (SPP) model to study this. This model is shown to recreate many features observed within real animal swarms.

P328 The Role of social environment on shoaling preference in fighting fish (*Betta splendens*)

Chantima Piyapong, Burapha University

The Siamese fighting fish (*Betta splendens*) is known for the aggressive behavior. However, its shoaling behavior has been observed when fish is reared together. By using binary choice tests, the role of social environment on shoaling preference of adult *Betta splendens* males and females will be investigated. It predicts that the females and the males of the pale color morphs will show more shoaling preference than the males and the males of the dark color morphs, respectively.

P329 Confusion among counterfeiters: multi-species interactions within an ant-mimicking community

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Ant-like appearance is seen in over 2000 species of arthropods. One of the most spectacular cases of ant mimicry is observed in the spider genus *Myrmarachne*, which, due to its ant-like appearance, gains protection from visually-oriented predators. Here we examine whether *Myrmarachne* deceives other ant mimicking arthropods as well. We investigated the responses of an ant-mimicking praying mantis (*Euantissa* sp.) towards a) an ant (*Oecophylla smaragdina*), b) an ant-mimicking spider (*Myrmarachne plataleoides*), and c) non-mimic jumping spiders. We found that the mantids were frequently attacked and bitten by the ants. Additionally, although the mantids oriented towards the mimic and the non-mimic spiders similarly, they rarely approached, never attacked, and frequently withdrew from the mimics compared to the non-mimetic spiders. The mantids never attacked ants, but discriminated between the model and the mimic by withdrawing from ants significantly more than they withdrew from the mimics. Our preliminary work demonstrates that *Myrmarachne plataleoides* faces reduced aggression from predators that are ant mimics themselves. Mimicry is often studied from the perspective of a single mimic deceiving a specific target audience. However, the dynamic interplay between several mimic, non-mimic, and model species may be asymmetric, and needs further study.

P330 Age superiority, more than body weight, determines dominance at the dyadic level in a beef cattle herd

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Marek Špinka, Ilona Stahulová, Francisco Ceacero, Marie Āime Anková, Radim Kotrba

Body weight (a phenotype-related cue) and age (a “conventional” cue) are two major determinants of dominance in dyads of social animals. We investigated the influence of these determinants on dyadic dominance in female beef cattle. We recorded agonistic interactions ($n=11226$) in a female beef cattle herd for 10 years (29-39 cows/year in the herd). We ascertained 43%-84% of dyadic relationships in each year. 82-96% of these relationships were stable between subsequent years and the hierarchies were extremely transitive. We used generalised linear model to investigate whether the direction of dominance in a dyad was affected by the quantitative differences in age and in body weight. The probability of being dominant increased strongly with age superiority of the focal animal ($F_{1,1382}=161.1$, $P<0.001$). Moreover, this dependence was at steepest between -1 and 1 age difference, increasing by a full 66%. The body weight advantage of the focal cow in a dyad also increased her probability of being dominant, but the effect was weaker ($F_{1,1382}=122.8$, $P<0.01$) than the effect of age. In conclusion, the “conventional” and stable cue of age superiority influenced dyadic dominance more than the changing phenotypic cue of body weight difference, leading to a strongly linear and stable dominance structure.

P331 Do dogs discriminate between pro-social and anti-social human behavior?

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The aim of this study was to examine whether dogs discriminate between egoistic and altruistic human behaviors. The experiment was conducted on 32 dogs of both sexes. Each dog observed three persons who were dressed identically and were seated in a row, 5 meters away from the dog, 1 meter away from each other. Each person was holding a bowl containing food. Their gaze was directed towards the floor to avoid eye-contact with the dog. Each person was asked to behave in a certain consistent manner towards the fourth person who was approaching each of them soliciting food. One person always shared food (the altruist), the second person responded randomly (ambivalent) and the third person always refused (the egoist). The begging person approached each of the three sitting persons three times and then left the room. The handler released the dog which could then approach any of the three seated persons.

For each dog, such trials were performed three times, so that the seated persons would relocate to sit in a different order. Results revealed that dogs attempted to solicit food from the egoist significantly less frequently than from the other two persons, as examined both for the results of the dogs' first choice ($\chi^2=8.31$, $df=2$, $p=0.016$) and for all three decisions ($\chi^2=9.929$, $df=2$, $p=0.07$). There was no difference in the preference for altruists or persons behaving in the ambivalent way. This result indicates that dogs tend to remember egoists, while the predictability of pro-social behavior is not of major importance to them.

P332 Characterisation of the social grooming network within a large group of semi-captive Japanese macaques (*Macaca fuscata*)

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Japanese macaque groups are composed of related females, organised in matriline, and unrelated males which are the dispersing sex. Grooming in this despotic species is preferentially exchanged within matriline, but also observed between remote kin and unrelated individuals. Less is known about the distribution of grooming among males. We investigated the social grooming network of a group of Japanese macaques ($N=134$) and applied scan sampling over a three months period. Social network analysis revealed a significantly higher *degree*, reflecting the number of grooming partners, in females than in males, in adults than in subadults, and in higher than in lower ranking individuals. The same was true with respect to central positioning, i.e. the *eigenvector centrality*. Within the male grooming network, neither age nor rank proved to influence *degree* and *eigenvector centrality*. Within the female grooming network, however, the *eigenvector centrality* differed significantly between matriline. Females developed a more tightly knit grooming network (density: 0.023 vs. 0.01) with a larger mean cluster size (7.6 vs. 6.3) compared to males. Thus, grooming networks differ considerably between the sexes but group cohesion is largely determined by females.

P333 Effects of previous losses and the individual identification during male-male contest in the hermit crab *Pagurus middendorffii*

Chiaki Yasuda, Hokkaido University
Satoshi Wada

Males of *Pagurus middendorffii* show precopulatory guarding behaviour, and male-male contests often occur between a guarding male and an intruder. Intruders often give up the contest without physical combat based on self-assessment, and they use mutual-assessment when the contest escalates. Males also seem able to identify specific females when they often encounter each other. Intruders might use information about opponents and/or guarded females learned in past contests to determine their behaviour during subsequent contests since this could reduce fighting costs. To examine this hypothesis, we observed male-male contests during two consecutive periods. When intruders lost the first contest, we used them in a second contest where the guarding pairs were (1) the same guarding pair, (2) the same opponents guarding a female that the intruder has never encountered, or (3) a guarding pair including a male and female that the intruder has never encountered. In the presentation, we will discuss the effects of previous losses and the familiarity of opponents on the behavioural decision of intruders.

P334 Effects of maternal allostatics and intrauterine position on social behavior in the caviomorph rodent *Octodon degus*: Consequences of masculinized female phenotypes on group dynamics.

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M.J. Frugone, M. Soto-Gamboa

Sex allocation theory predicts that the parental investment in male and female offspring is equitable; however intrinsic and extrinsic factors may affect the resource/care allocation between sexes in the same litter. Stress may be important proximate mechanisms underlying variation in mammalian litter features, and female pup phenotypical masculinization. In addition, Intrauterine position (IUP) affect in similar direction female phenotypes. A potential consequence of female masculinization is increased social stress, which possibly influences group stability and the phenotypes of females in the next generation. We studied the effect of maternal stress and intrauterine position effects on litter sex allocation and in the offspring female phenotypes, using the social caviomorph rodent, *Octodon degus*. Results suggest that maternal allostatics affect mostly litter size, while IUP affects the litter sex ratio. In addition, both mechanisms affect the proportion of masculinized females produced in the litters. Female masculinized phenotypes were aggressive and affect

the social group dynamics in laboratory conditions. In conclusion, both mechanism have effects on litter traits and have significant consequence on social structure.

P335 Visual exposure to non-specific point-light animation induces a predisposition for biological motion in early hatched domestic chicks.

Momoko Miura, Hokkaido University
Toshiya Matsushima

A motion picture composed of a set of moving points of light creates a vivid perception of living organism, a phenomena known as Johansson's biological motion (BM). We investigated the effects of early visual experiences on preference for BM. Groups of chicks were exposed to a point-light animation depicting a walking hen (W-hen, a BM stimulus) or one of the following non-BM point light animations, i.e., rotating hen (R-hen, a non-BM), pendulum, random motion and stationary pattern. If exposed to animations, males showed a strong preference for W-hen to R-hen at the tests, whether they were exposed to BM or non-BM. Stronger preference appeared when chicks approached the stimuli more actively, similarly to imprinting. If exposed to stationary pattern, males showed no preference in spite of similarly high number of approach. In females, only those chicks exposed to W-hen showed obvious preference to W-hen. Of those females exposed to animation, there seemed to be no correlation between the number of approach and the BM preference. It is suggested that the BM preference is an innate nature, but the preference should be permissively induced for functional expression in early post-hatch period particularly in males.

P336 Preliminary investigation of the representation of visual proportions in 4-day-old domestic chicks (*Gallus gallus*)

Lucia Regolin, University Of Padua
Elena Biscaro, Rosa Rugani, Giorgio Vallortigara

Many studies have shown that nonhuman animals can choose the larger of two discrete quantities of items. Less emphasis has been given to the investigation of discrimination of continuous quantities, which was the aim of the present study. During training, three-day-old chicks were presented with two stimuli, each characterized by different and complementary proportions of red/green areas (ýý vs. ýý in an overall area of 16 cm²). Food could be found in proximity of only one

of the two stimuli: Half chicks were trained to respond to the $\gamma\gamma$ green area and the other half to the $\gamma\gamma$ red area. The test was conducted on Day 4. Chicks (N=20) approached the proportion associated with food, even if at test the spatial disposition of the two areas was novel with respect to what experienced at training (Experiment 1). In Experiment 2, chicks (N=10) generalized to test stimuli of enlarged dimension, that created a conflict between the absolute positive area experienced during training and the correct relative proportion between the two areas. Chicks responded on the basis of the proportion, ignoring the absolute values. These findings support the hypothesis that proportions are information that can be processed by very young animals.

P337 The effect of visual environment on female mate choice decision-making

Malcolm Rosenthal, University Of Nebraska-Lincoln
Eileen Hebets

In the wolf spider *Schizocosa floridana*, males attract mates via a complex seismic call. Generally, courtship effort (number of leg taps per minute) is an excellent predictor of copulation likelihood. However, female mating preferences are also affected by light environment, with females preferring high-quantity diet males to low-quantity diet males in the dark, but not in the light. Additionally, latency to copulation is significantly longer in the dark, suggesting that females may be assessing courtship longer, potentially due to lowered predation risk. We hypothesize that through increased assessment in the dark, females are increasing their fitness (females lay larger egg sacs in the dark) either by choosing higher quality males, or by allocating more resources to the mating. We ran courtship trials with field-captured spiders in both light and dark environments and recorded the male's courtship. We raised the offspring and measured offspring number, percentage of eggs fertilized, offspring mass, and growth rate. We then assessed the relationship of male courtship to copulation likelihood and offspring measurements for both light and dark treatments. Results will be discussed.

P338 The use of two different informations in human face recognition

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Yukio-Pegio Gunji

It is well known that human beings has highly accurate face-recognition ability. We are able to identify the faces of our family, friends and one of oneself easily and instantly. It is indicating that this ability is highly sophisticated and has fundamental importance for human beings. However, the mechanism of how we can recognize faces and distinguish them is not obvious. What is at issue is which type of information, detailed figuration of individual parts or whole configuration of parts, has a central role in identification of faces.

We conducted simple experimental tests. Examinees were given a binary image of the face that the outlines and skin textures were deleted. They memorized it. After that, the face images that have the same parts and gradually-changed configuration was presented for examinees and they compare these faces to the memory of the originally-provided face. The results of experience indicate that humans use different type of face information depending on the cases. We tend to use the characteristic of parts when we recognize well-known own face and use the configuration when we cognize stranger's faces.

P339 Visual phenotype matching: cues to paternity are present in rhesus macaque faces

Anahita Kazem, Max-Planck Institute For
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Dana Pfefferle, Anja Widdig

The ability to discriminate between conspecifics based on genetic relatedness is of importance both in acquiring inclusive fitness benefits and to enable optimal inbreeding. In primates, mechanisms allowing recognition of paternal relatives are of particular interest, as in these mating systems patrilineal information is unlikely to be available via social familiarity. We experimentally investigated the potential for phenotype matching based on facial features, in rhesus macaques (*Macaca mulatta*) from a free-ranging population in which genetic relatedness had been well-quantified from pedigrees determined from molecular markers. In a computer-based task, we first demonstrated that human observers are able to detect parent-offspring pairs of all sex combinations from triads of macaque faces. In a further experiment, free-ranging macaques were shown photographs of two unfamiliar conspecifics (unrelated versus paternal half-sibling) in a looking-time task. Individuals biased their inspection time more toward nonkin when the animals pictured were of their own sex (potential threats), relative to when they were of the opposite-sex (potential mates). Our results demonstrate that, as in humans, cues to both paternal and maternal

relatedness exist in macaque faces. Moreover, unfamiliar paternal relatives can be spontaneously discriminated by the animals themselves under natural conditions.

P340 Effects of key contaminants in stormwater on the behavioural responses of the freshwater shrimp, *Paratya australiensis*, to chemical cues.

Lois Oulton, Macquarie University
Grant Hose, Mark Taylor, Culum Brown

Aquatic organisms use chemical cues to gather information from their surroundings in a range of contexts, such as predator avoidance and foraging. A number of studies have shown that chemicals introduced into the aquatic environment, for example heavy metals found in urban stormwater, disrupt chemical cue recognition and consequently the ability of biota to perform ecologically relevant behaviours. The objective of the present study was to investigate the effects of key contaminants found in stormwater wetlands on both antipredator and foraging behaviour in the freshwater shrimp, *Paratya australiensis*. *P. australiensis* is an important component of freshwater ecosystems in south-eastern Australia, and is widely used in acute toxicity tests. Despite this, a scarcity of knowledge concerning toxic impacts on ecologically relevant behaviours exists. The results of this research will enable a more comprehensive understanding of the effects of urban stormwater pollution on aquatic wildlife

P341 Evidence of a universal behavioural unit? Investigating the duration of fixed gazes in free-ranging bighorn sheep.

Petra McDougall, University Of Calgary
Kathreen Ruckstuhl

Research from human subjects suggests a universal behavioural unit of approximately 3 seconds. This 3-second behavioural unit has been demonstrated in human motor movements such as chewing and speaking, as well as social interactions such as embraces. It is further argued that this behavioural unit may be universal across the mammalian order. We are examining the duration of fixed gazes in free-ranging Rocky Mountain bighorn sheep (*Ovis canadensis*) to determine whether these gazes are characterized by 3-second units. Habituated, ear tagged bighorn sheep are video recorded in their natural setting. Videos are played back for frame-by-frame analysis at 30 fps, and individual fixed gaze durations are calculated. Preliminary results lend

support to the universal 3-second hypothesis. Furthermore, a positive correlation is evident between the age of an animal and their mean gaze duration. Further investigation will examine whether gaze durations are normally distributed within individuals of varying ages, or whether skewed distributions may produce this effect. These results compliment previous research on vigilance, as they imply that age differences do not only influence the total proportion of time allocated to vigilance, but also influence the particular qualities of individual gazes within a vigilance bout.

P342 Motion dazzle: an insect's eye view

Roger Santer, Aberystwyth University

'Motion dazzle' describes high-contrast markings that don't camouflage a stationary object, but inhibit an observer's judgement of the object's speed and trajectory when it moves. Possible examples include the zigzag patterns of some snakes, and dazzle camouflage painted on WW1 ships. However, evidence that motion dazzle patterns actually impede motion detection comes only from studies investigating human subjects catching computer-simulated 'prey', and the mechanisms behind the effect are unclear. Therefore, there is a great need to investigate the phenomenon in a broader range of species, and on a mechanistic level. Here I investigate well-characterised motion-detecting neurons in the nervous system of a grasshopper that play an important role in detecting approaching predators and triggering escape responses. Using computer-simulated approaching objects, I investigate whether (and how) motion dazzle markings on a predator can disguise its movements from a prey grasshopper. My results reveal that particular predator patterns can elicit a behaviourally-relevant motion dazzle effect in the visual system of the grasshopper, and propose a mechanistic basis for the phenomenon. Insect visual systems may, therefore, represent an important model system for the further investigation of this poorly understood aspect of animal colouration.

P343 Experiments in Behavioural physiology concerning colour vision in domestic chickens (*Gallus gallus domesticus*)

Juliana Simon, Johannes Gutenberg-University, Mainz, Germany
Christa Neumeyer

Colour vision, especially wavelength discrimination, in domestic chickens was investigated using a behavioural training technique. The experiments were done with hand-reared individuals who were trained to choose between two differently illuminated test fields and show their choice by pecking on them. The data was compared to the characteristics of cones and oil droplets established by Bowmaker (1977, 1997). There are four different cone types in the chicken retina sensitive at 426nm, 474nm, 535nm and between 570nm-605nm. Each type possesses a certain coloured oil droplet in its inner segment. The droplets, named T-type (transparent), C-type (clear), Y-type (yellow), O-type (orange) and R-type (red), are impermeable for shorter wavelengths and therefore act as cut-off filters. Based on their photopigments chickens are supposed to be tetrachromats. Thus their λ_{max} -function should show three locations of best discrimination at the interfaces of the spectrally adjacent cone sensitivity curves. However, in our experiments we found four locations at 453,5nm, 509nm, 545,5nm and between 573,6nm-599,35nm not shown in chickens before! Our results suggest that chickens are pentachromats based on an additional so far unknown combination of photopigment and oil droplet.

P344 A Comparative Analysis of Visuospatial Object Recognition and Language Tests in the Detection of Cognitive Decline in Aging

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Liliane D. D. de Macedo, Alessandra M. Tomás,
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Early memory impairment detection is essential to distinguish normal and pathological aging. To that end it is necessary to select specific and sensitive neuropsychological tests that can be applied successfully in translational research. In the present report we investigated effects of aging on learning, memory and language. To do so, 29 young adult (29.9 ± 1.06 years) and 31 older adults (74.1 ± 1.15 years) were selected. Selected visuo-spatial learning and memory tasks from the Cambridge Neuropsychological Test Automated Battery (CANTAB), and language tests were applied. Cluster and discriminant analysis demonstrated that visuospatial tests distinguished between groups with higher resolution. Neuropsychological tests performances revealed that paired associate learning (PAL), spatial working memory (SWM), and delayed matching to sample (DMS) tests are more sensitive and better discriminate subgroups in both

young adults and aged volunteers than language tests. We selected PAL stage 1 and 2 to investigate spatial memory in *Cebus apella* a New World primate with remarkably cognitive capabilities and the results demonstrate this test is a reliable translational test to investigate visuospatial memory. We conclude that the systematic application of visuospatial memory tests may increase our ability to earlier distinguish normal and pathological aging in both human and primates.

P345 Evolution of migratory strategies in Tyrant Flycatchers: a phylogenetic approach

Valentina Gomez, Universidad De Los Andes
Roberto Marquez

Determining patterns of migratory strategies in a phylogenetic framework is crucial to understanding the evolutionary pathways of complex migratory behaviours. Cyclic migratory movements are present in many bird species expressed in a variety of different patterns and degrees, which range from long-distance continental migrations to short-distance regional ones. Moreover, regional migrations can occur in several forms as well: some species migrate along altitudinal gradients, and others between intra-tropical locations. Furthermore, partial migration occurs when a subset of individuals remain as residents, while the rest migrate, potentially leading to reproductive isolation. The mechanisms behind the expression of these patterns are of particular interest to understanding the evolution of migratory behaviours, since these could shed light on the factors promoting it. Tyrant Flycatchers (Aves: Tyrannidae) exhibit different migratory strategies, which make them a good model to assess the evolutionary dynamics involved in the origin of different migratory patterns. We performed phylogenetic comparative analyses within Tyrannidae, aiming to better understand the evolution of migration, especially focusing on the propensity of convergence in type of migratory behaviour between different lineages, and the plausibility of this behaviour being lost after it has been acquired.

P346 Movement patterns and associations at night roosts in wild non-breeding ravens.

Matthias-Claudio Loretto, Department Of Cognitive Biology, University Of Vienna
Thomas Bugnyar

Non-breeding ravens tend to form groups during foraging and roosting, however, the composition and structure of these flocks is still unclear. In a human influenced landscape, permanent food sources may enhance the formation and stability of these groups. In our field site in the Austrian Alps, ravens (n=40-100, depending on the season) use a local zoo as food source year round. Recent findings showed that not only territorial breeders but also a high proportion of individually marked non-breeders (30%) are constantly present over years, forming a kind of local community. We here investigate the movement patterns of ten local non-breeders using radio telemetry. Results show that these birds spend most of the time in a relatively small area (<10 ha) around the foraging sites. Season affects the spatial distribution, with birds moving out of the valley more often in summer/autumn than in winter/spring. Unexpectedly, the birds use several night roosts in the valley with different regularity; this could be due to previous social interactions with given conspecifics and/or to get information about feeding opportunities. Until now we can exclude ecological factors as well as parameters such as age class, sex or genetic relatedness to be linked with these patterns.

P347 The Homing Frog: Orientation And Homing Behavior In A Territorial Neotropical Frog *Allobates femoralis*

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Matthias-Claudio Loretto, Walter Hörl

Dendrobatidea (dart-poison frogs) exhibit some of the most complex spatial behaviors among amphibians, such as territoriality and tadpole transport from terrestrial clutches to widely distributed deposition sites. Despite this fact, homing ability and orientation mechanisms have not been investigated in dendrobatid frogs. Recent data has shown that *Allobates femoralis*, a dendrobatid frog with paternal extraterritorial tadpole transport, successfully returns to the home territories after experimental translocations of up to 400 m. In the present study, we used telemetry with miniature transponders to obtain homing trajectories. Additionally, we quantified the initial orientation of translocated individuals in an arena assay.

Tracking experiment revealed that homing trajectories are characterized by long periods of immobility (up to several days) and short periods (several hours) of rapid movement closely fitting a straight line towards home territory. We also found

that translocated *A. femoralis* show significant homeward orientation in the arena assay. Our results demonstrate a highly developed and very precise homing behaviour in male *A. femoralis* while suggesting future directions to test the mechanisms involved.

P348 The utility of Network Analysis in studying aquatic animal movements: an example from two nearshore shark species

Elodie Lédée, Jcu
Colin Simpfendorfer, Michelle Heupel, Andrew Tobin

Understanding how marine species use their environment has become increasingly important in managing and conserving species. Passive acoustic telemetry allows long-term monitoring of the marine animal behaviour and movement via a network of moored listening stations that record the presence of tagged animals. Traditional spatial statistics (e.g. home range) are used to investigate the data. However, these methods provide an incomplete picture of animal movement because the data is manipulated to estimate animal location prior to analysis. Network Analysis is an alternative approach that does not manipulate the data and treats listening stations as network nodes and analyses movement based on flows between nodes. To investigate the utility of Network Analysis in analysing tracking data, the data on sharks' movement was analysed. Results were compared to those from kernel-based home range analysis and showed that both methods provide similar results for identifying core use but were different for general activity use. Both species have similar numbers of path within their core use and general activity areas; including nine common to both species. Average path length showed both species were efficient in moving within their networks. Network Analysis provides new and useful interpretation of tracking data not provided by traditional approaches.

P349 Use of space by cats in an outdoor captive colony

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Thierry Bedossa, Bertrand L. Deputte

Though domestic cats are solitary animals, feral cats may form groups depending on availability and abundance of food resources. Captivity forces individual to live in close proximity. A well designed environment may allow cats to regulate their inter-

individual spacing. The aim of this study was 1- to investigate the use of space in a colony of 33 cats living in a 2101 m² enclosure providing a large number of shelters, feeding places and trees, and 2- to observe their behaviours during an annual cycle. Data were collected 4 times per day, 9 am to 5 pm, 30 days per season, during randomized walks along predetermined trails. Individual home ranges varied between 62 m² and 1567 m², overlapping considerably. While in winter, most of cats remained close to a main shelter, during the summer, they were widely dispersed using all of the available shelters and feeding spots. Interactions, both positive and negative, represented only 1% of the time-budget, though some cats maintain close proximity with others. Our results suggest a lack of territorial behavior in the colony cats, a large interindividual tolerance and a very low level of interactions confirming the solitariness of the cats.

P350 Behavioural Spatio-Temporal distribution on a captive vervet monkey group (*Cercopithecus aethiops pygerythrus*) at Guadalajara Zoo

Gerardo Ortiz, Universidad De Guadalajara
José Claudio Partida

If we assume that functional relationships exist between the organism and its environment, we could expect that a change in the environmental elements (i.e. geophysical, geoecological, and intra-interspecific factors, Ortiz, Correa & Gallardo, 2006) will modify the organism's behavior. In order to analyze the behaviour in captivity regarding the enclosure's ecological characteristics and the presence-absence of visitors, Ortiz, Cañedo & Roosario (2006) studied behaviour's emission and distribution in a captive group of vervet monkeys. In summary, they reported that individuals spent the majority of the time resting, while there was difference between the behaviour's spatial distribution in regard to the presence-absence of visitors.

Recently Guadalajara's Zoo carried out a remodeling which modified the enclosure of the monkeys. Considering the proposal from Ortiz, Correa & Gallardo (2006) and Ortiz & del Toro (in revision), the changes made in the enclosure included the modification of geoecological and interactive elements. Therefore, it may be possible to observe changes in the spatiotemporal emission and distribution of behavior. Thus, the present paper aims to make a comparative analysis of the emission and distribution of behavior of vervet monkeys regarding Ortiz et al. (2006) results.

P351 The relationship between tunnel length and digging rate in leaf-cutter ants.

Andrew Bruce, Monash University
Flavio Roces

Ant nests show a linear relationship between nest size and ant number (Tschinkel 2004; Tschinkel 2005) and it has been hypothesised that this is due to nest volume being adjusted to group size: digging rates being high when the nest is too small and lowered when plenty of space is available (Rasse & Deneubourg 2001). This constitutes a negative feedback mechanism, by which nest volume is tuned to group number. In this study we investigated the relationship between tunnel length, which is an important contributor to nest size, and digging rate. Focusing on tunnel length allowed the presentation of different space conditions while controlling the geometry of the emerging space. We allowed sub-colonies of the leaf-cutter ant *Acromyrmex lundii* to excavate tunnel space in a tube and then removed that space by means of a gate. This showed no significant difference in digging rate in comparison to a control. Further experiments, providing tubes with different initial empty tunnel spaces, also showed no significant differences. Our results suggest that leaf-cutter ants do not adjust their digging rates with respect to available tunnel length.

P352 Humans show greater vertical than horizontal directional accuracy in spatial performance in a large-scale orientation task.

Theresa Burt de Perera, University of Oxford
Lydia Paris, Robert I. Holbrook, Máté Nagy, Tim C. Guilford

Little is known about three-dimensional spatial encoding in humans. Here, we use a multilevel landmark configuration within a seven-storey building as a paradigm to understand human 3D spatial representation. We aimed to determine whether the horizontal or vertical location is encoded more accurately in human subjects by measuring pointing vectors to out-of-view landmarks and plotting them in a spherical coordinate system. We show that the error in vertical encoding of space is smaller than the horizontal error, and consider three potential explanations for this result: 1) the vertical axis is salient because it is polarised by gravity, which might cause spatial relationships in the vertical dimension to be more accurately encoded; 2) accurate vertical encoding might be selected for, since navigational errors made when working against gravity are energetically costly; 3) the

environment shapes the pattern of spatial encoding. We also found that in the horizontal error tended to be towards the direction of the reference vector (i.e. straight ahead). We suggest possible reasons for this horizontal compression bias based on either physical constraints or adaptive explanations such as the need for an acute awareness of what is ahead of us. The ratio between latitudinal and longitudinal geodesic distances did not significantly increase with vertical angle from the horizontal plane, suggesting that overall 3D angular spatial relationships are encoded with similar accuracy away from the horizontal plane. Together, our results show that careful use of spherical coordinate analysis can reveal consistent patterns of bias in human 3D spatial cognition.

Europe more visible to increase their participation in the new European animal welfare projects, such as EUWeINet.

P353 AWARE – farm animal welfare research in an enlarged Europe

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Marek Špinka, Hans Spoolder, Christoph Winckler, Štefan Mihina, Linda Keeling, Vlatko Ilieski, Andrew Butterworth, Marie-Christine Meunier-Salaün

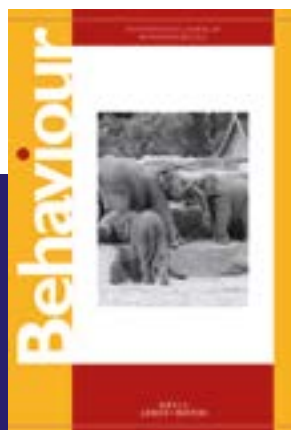
The EU's animal welfare strategy is based on scientific evidence and supported by public awareness about animals as sentient beings, resulting in animal welfare standards that are enforced in all EU countries. However, within Europe, there are geographical differences in the quality and quantity of animal welfare research, education, awareness and implementation. The aim of the FP7 project AWARE (www.aware-welfare.eu; 2011-2014) is to promote integration of European farm animal welfare research, university education, public awareness and implementation across Europe, with special focus on the new, candidate and associated EU countries. AWARE is organized in four Work Packages. WP1 enhances the integration of farm animal welfare research by fostering collaboration through mutual recognition and enhancing networking. WP2 promotes networking in farm animal welfare university education. WP3 focuses on enhancing public awareness and promoting implementation of EU policies. WP4 facilitates mobility of researchers and students. AWARE so far accomplished comparative mapping of farm animal welfare research and university education and organised over 20 road shows, workshops and training sessions for research leaders, young researchers, university lecturers and stakeholders in 12 countries of the East Central Europe, Baltic and East and West Balkan regions with almost 1,000 attendants. It also already succeeded by making partners from this part of

If you have a conference, hire them.

— Pallab Ghosh
*BBC Science
correspondent*

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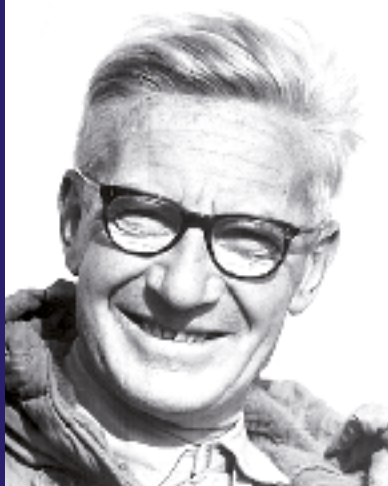
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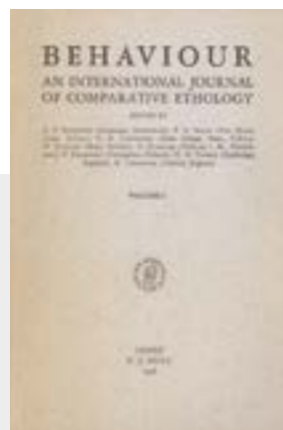
brill.com/beh

Niko Tinbergen, together with W. H. Thorpe, founded *Behaviour* in 1948. Ever since, Brill has developed the journal together with renowned editors like Gerard Baerends and, since 2011, Frans de Waal.

Behaviour has its roots in ethology and behavioral biology (see historical note), in which the emphasis is not so much on how animals compare with humans under strictly controlled conditions (as in comparative psychology), but more on tracing the phylogeny and evolution of natural behavior as shown under naturalistic or natural conditions.



Together with Karl von Frisch and Konrad Lorenz, Niko was awarded the Nobel Prize in Physiology or Medicine 1973 “for their discoveries concerning organization and elicitation of individual and social behaviour patterns”. This is exactly 40 years ago and another reason to celebrate!



In 2013, we celebrate two milestones: *Behaviour* publishes volume 150, in its 65th year, making it one of the oldest still existing journals in its field. Since the journal's inception the field of behavioral biology/ethology has blossomed, because of contributions by Niko and others after him. As a celebration gift, *Behaviour* content from years 2010 – 2012 will be available free from 4 August until 4 October 2013:

You can access *Behaviour* for free until 4 October, using access token BEH150

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