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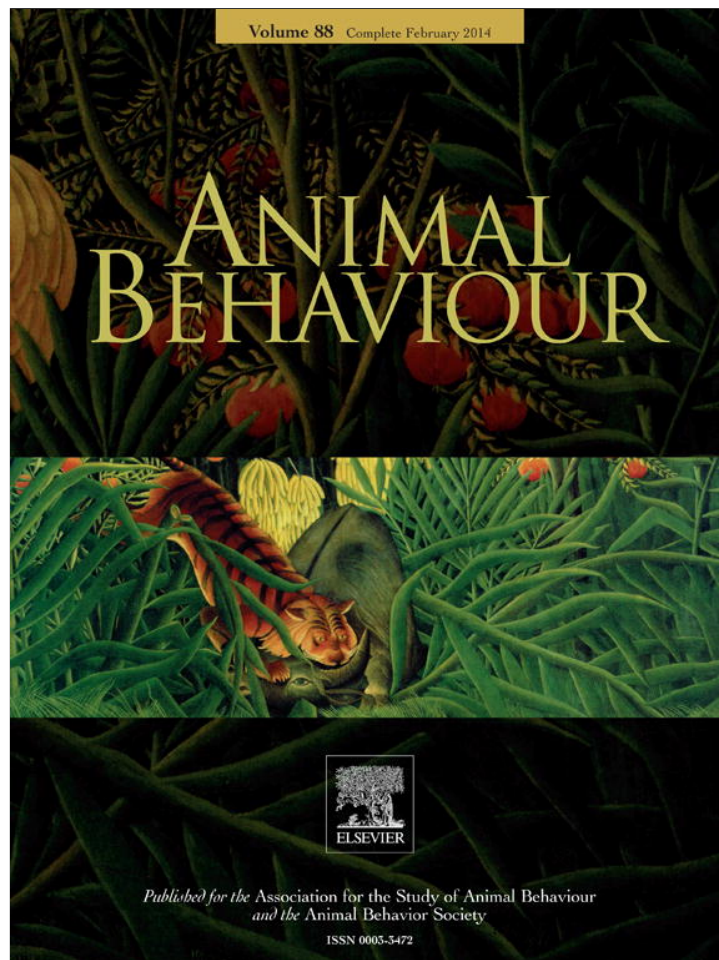
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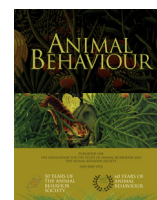
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Commentary

Contaminants as a neglected source of behavioural variation

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Animal behaviour has broad ecological and evolutionary implications. Among other things, it drives social group and population dynamics, affects interspecific interactions and influences how animals cope with environmental changes (Sih, Cote, Evans, Fogarty, & Pruitt, 2012). In addition to the average behaviour of a given species or population, behavioural variation among individuals within populations (i.e. so-called 'animal personality': Réale, Reader, Sol, McDougall, & Dingemans, 2007; Sih, Bell, & Johnson, 2004) has important implications for ecological and evolutionary processes relevant for multiple fields of research, such as community ecology and conservation (McDougall, Réale, Sol, & Reader, 2006; Réale et al., 2007; Sih et al., 2004).

A large amount of effort is currently devoted to identifying the mechanisms responsible for the maintenance of consistent behavioural variation (Dall, Houston, & McNamara, 2004; Réale et al., 2010; Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf, Van Doorn, & Weissing, 2008). A main hypothesis is that consistent behavioural variation can be maintained when the fitness benefits of expressing a certain behaviour differ consistently among individuals as a function of their state, such as their energy balance or energy allocation strategy (Houston & McNamara, 1999). For

example, individuals with a negative energy balance may be consistently bolder than those with a positive energy balance (Rands, Cowlshaw, Pettifor, Rowcliffe, & Johnstone, 2008). Individuals that invest more energy into immediate reproduction than into long-term survival may also be bolder while foraging (Wolf et al., 2007). The behaviour expressed by individuals may further affect their state, leading to a feedback between behaviour and state (Dingemans & Wolf, 2010). For example, individuals with positive energy balance may be better at dealing with predation risk and thus forage more, thereby maintaining a consistently positive energy balance (Luttbegg & Sih, 2010). Depending on the type of relationship between behaviour and state, feedback loops may either amplify or erode behavioural variation over time (Bergmüller & Taborsky, 2010; Luttbegg & Sih, 2010; Fig. 1). Determining the state variables associated with consistent individual differences in behaviour and investigating their potential feedback with behaviour is now a major area of research. There is an urgent need for more empirical work, particularly on how different state variables (e.g. age, size, energy level, residual reproductive value) interact with each other to affect individual behaviour (reviewed in Dingemans & Wolf, 2010).

Anthropogenic contaminants (ACs), defined as products typically not found in nature and generated by human activity (e.g. heavy metals, fertilizers, pesticides, residual birth pill compounds: the British Geological Society, 2013) could be a particularly potent factor contributing to consistent behavioural variation within

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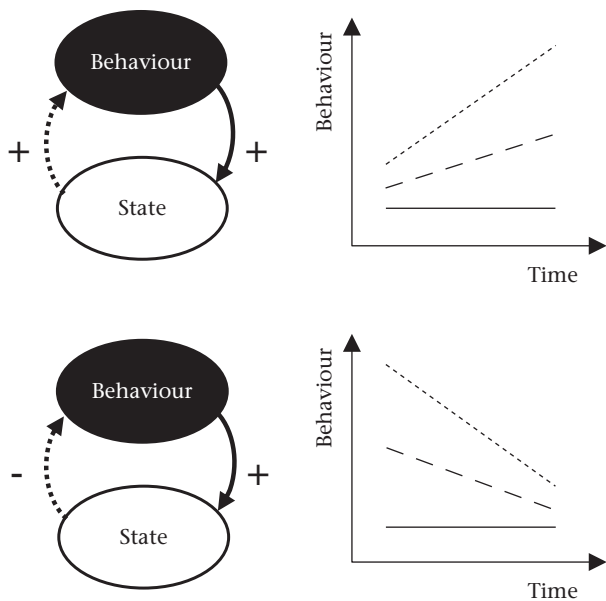


Figure 1. Examples of feedback loops between personality and anthropogenic contaminant (AC) state (left-hand diagrams) and their implication for consistent individual behavioural variation (right-hand graphs). The right-hand graphs present the behaviour of three individuals (solid, dashed and dotted lines) as a function of the time exposed to AC. Note that this axis may be continuous, or discrete (i.e. the behaviour of individuals before and after AC exposure). Upper panel: the behavioural trait value expressed by individuals may increase AC state, which may in turn increase the behavioural trait value of the individual. Such a positive feedback loop may act to exacerbate individual differences in behaviour, thereby increasing repeatability. Lower panel: the behaviour may increase the AC state of individuals, but an increased AC state may decrease the behavioural trait value expressed (e.g. through its toxicity). In such a case, the negative feedback loop will erode or eliminate individual differences in behaviour. Thus, we would expect the repeatability of this behaviour to decrease.

populations (see Bell, 2001, 2004). ACs are ubiquitous in most environments (e.g. Kolpin et al., 2002) and may directly alter the behaviour expressed by individuals (i.e. the level of exposure or contamination would act as a state, hereafter referred to as 'AC state'; Zala & Penn, 2004). Examples of the effects of ACs on behaviour include residual psychiatric drugs present in the water increasing the boldness of fishes (Brodin, Fick, Jonsson, & Klaminder, 2013), brominated flame retardants altering male parental nest guarding (Verboven, Verreault, Letcher, Gabrielsen, & Evans, 2009), sublethal doses of pesticides altering navigation and orientation behaviours (Bortolotti et al., 2003; Colin et al., 2004), heavy metal accumulation decreasing antipredator behaviour or foraging activity (Cheung, Tai, Leung, & Siu, 2002) and exposure to pyrene affecting the probability of winning staged contests in males (Dissanayake, Galloway, & Jones, 2009).

AC state could also interact with other state variables. Hence, the behavioural shifts resulting from AC state could differ among individuals as a function of their life history strategy or energy balance (just as natural hormones do; Lancaster, Hazard, Clobert, & Sinervo, 2008). More importantly, an individual's AC state and behaviour may feedback into each other if behaviour both determines and is affected by AC exposure and accumulation. This is likely to apply in cases where AC exposure and accumulation occur through feeding and affect the behaviours driving food acquisition. For example, individuals with a higher activity level may also incur higher encounter rates with ACs in their environment, which may further affect their activity level. Likewise, individuals with a higher voracity would be likely to consume more (potentially contaminated) prey items, which could affect further their voracity. A vast

array of behaviours shown to be affected by AC exposure are associated with resource acquisition by animals (Clotfelter, Bell, & Levering, 2004), and so this first scenario is likely to be ubiquitous among animal study systems. ACs could also feedback with behaviour by affecting how much energy individuals allocate to various fitness functions such as growth, reproduction and body maintenance (i.e. ACs affect the resource allocation pattern of animals). For example, AC state could decrease the survival of animals or increase their reproductive effort (Massarin et al., 2011), which could lead them to express a more risk-prone behaviour (i.e. individuals would become bolder; Réale et al., 2010), leading to a further increase in AC state (e.g. Brodin et al., 2013). Interestingly, most behaviours currently investigated for their consistent variation among individuals within populations (i.e. so-called 'personality traits': Réale et al., 2007) are tightly associated with the life history strategy of individuals, regulating how resources are allocated to growth, reproduction and maintenance (Réale et al., 2010). Determining the interactions between behaviour and AC state is thus paramount to understanding how consistent variation in behaviour within animal populations is maintained and why the extent of such variation differs among study systems (Sih et al., 2004; Dingemans & Wolf, 2010).

Since behaviour and ACs may interact through multiple pathways, we believe that investigating the relationship between behaviour and AC state requires a mechanistic approach, analysing the interactions between behaviour, AC state, resource acquisition and resource allocation patterns. Note that to be considered mechanistic, such a model need not directly analyse the proximate aspects of AC–behaviour interactions. Our objective is to provide such a conceptual framework that accounts for the interactions between ACs and consistent behavioural variation. We first discuss how ACs can act as a state variable and affect behaviour. Second, we outline how individual behaviour may mediate differences in exposure to and accumulation of ACs. Third, we suggest an experimental and mechanistic approach to study the feedbacks between ACs and behavioural variation. Finally, we present two case studies and show how the interaction between ACs and behavioural variation may be studied in these systems.

Anthropogenic Contaminants Contribute to State-dependent Behavioural Variation

Behavioural expression is sensitive to contaminants, and exposure to contaminants is increasingly regarded as a source of behavioural variation that must be taken into account (reviewed in Clotfelter et al., 2004; see also Dissanayake et al., 2009; Egea-Serrano, Tejado, & Torralva, 2011; Henry et al., 2012). AC exposure or accumulation rates often act as state variables, affecting the expression of behaviour. For example, ethinyl oestradiol (derived from birth control pills and postmenopausal hormone replacement therapies) occurs in most freshwater streams and decreases aggressiveness of individuals (Bell, 2001). Other endocrine-disrupting chemicals also affect boldness under various risky situations (Eroschenko, Amstislavsky, Schwabel, & Ingermann, 2002; Schantz & Widholm, 2001). Nitrogenous compounds originating from farming and fossil fuel combustion decrease activity in many amphibians both during larval and adult stages (Egea-Serrano et al., 2011; Miaud, Oromí, Guerrero, Navarro, & Sanuy, 2011). By modifying particular behaviours, ACs may thus alter existing correlations between behavioural traits, or generate new ones (Brodin et al., 2013). Hence, exposure to contaminants may explain the occurrence of particular behavioural associations in the same way that exposure to predation (Bell, 2005) or parasitism does (Barber & Dingemans, 2010).

Table 1
Studies currently available on the relationships between anthropogenic contaminants (ACs) and behavioural individual variation

Contaminant	Contaminant class	Organism	Class/Order	Exposure type	Behaviour(s) affected	Behaviour affects AC state	Individual variation in AC state	Individual variation in behaviour	Repeated behavioural measures	Source
Ethinyl oestradiol	Endocrine disrupter	Threespine stickleback	Fish	Passive absorption	Aggression and courtship				X	Bell (2001)
Benzodiazepine	Anxiolytic drug	European perch	Fish	Passive absorption	Activity, boldness, feeding rate and sociality			X	X	Brodin et al. (2013)
Fipronil and imidacloprid	Neurotoxic insecticide	Honey bee	Insects	Ingestion	Foraging				X	Colin et al., (2004)
Carbaryl	Neurotoxic insecticide	Fence lizard	Reptiles	Ingestion	Feeding				X	Durant et al. (2007)
Nitrogenous compounds	Fertilizer	Iberian waterfrog	Amphibians	Passive absorption	Activity				X	Egea-Serrano et al. (2011)
Methoxychlor	Endocrine disrupter	Salamander	Amphibians	Passive absorption	Startle response				X	Eroschenko et al. (2002)
Cd, Cu, Pb, Mn, and Fe	Heavy metals	Barn owl	Birds	Ingestion	Diet type	X	X	X		Esselink et al. (1995)
Thiamethoxam	Neurotoxic insecticide	Honeybee	Insects	Ingestion	Foraging				X	Henry et al. (2012)
Heavy metals	Heavy metal	Fathead minnow	Fish	Contact with contaminated sediments	Activity			X	X	Kolok, Plaisance, and Abdelghani (1998)
Uranium	Heavy metal	Daphnia	Crustaceans	Passive absorption	Foraging				X	Massarin et al. (2010)
Uranium	Heavy metal	Daphnia	Crustaceans	Passive absorption	Growth and reproduction				X	Massarin et al. (2011) *
Organochlorines	Endocrine disrupter	American dipper	Birds	Ingestion	Diet type	X	X	X		Morrissey et al. (2004)
Imidacloprid	Neurotoxic insecticide	Gammarus	Amphipods	Passive absorption	Foraging				X	Nyman et al. (2013)
Persistent organic pollutant	Endocrine disrupter	Loggerhead sea turtle	Reptiles	Ingestion	Diet type or migration	X	X	X		Ragland et al. (2011)
Hydrocarbons	Air pollutant	Human	Mammals	Passive absorption	Activity and space use	X	X	X		Schlink et al. (2010) *
Persistent organic pollutants	Endocrine disrupter	Glaucus gull	Birds	Ingestion	Parental behaviour			X	X	Verboven et al. (2009)

* Studies that used a modelling approach.

Mechanistic models of the effects of ACs on organisms suggest that exposure to contaminants may affect behaviour through their effects on state variables associated with energy acquisition. Such modifications may in turn alter the cost and benefits of behavioural expression (Dingemans & Wolf, 2010). For example, exposure to heavy metals may result in heightened metabolic costs and negative energy balance (Massarin et al., 2010; Massarin et al., 2011), leading to increased expression of behaviours associated with resource acquisition. In the lizard *Sceloporus occidentalis*, individuals cope with higher maintenance costs associated with ACs by decreasing their activity while increasing their feeding rate (Durant, Hopkins, & Talent, 2007). Alternatively, ACs may also alter how the energy is allocated to competing functions such as growth, reproduction or survival. For example, organochlorines (used as pesticides) also cause shifts in energy allocation patterns and life histories tactics (e.g. Congdon, Dunham, Hopkins, Rowe, & Hinton, 2001), which may eventually affect consistent behavioural variation (Dingemans & Wolf, 2010; Réale et al., 2010).

Variation in AC exposure could also affect behavioural variation if it affects individuals differently. For example, the repeatability (a measure of how much individuals differ consistently from each other) of critical swimming speed in subadult male fathead minnows, *Pimephales promelas*, decreased after a standardized exposure to sediments contaminated with heavy metals (Kolok, Plaisance, & Abdelghani, 1998). Exposure to heavy metals did not affect the average swimming speed of the population, but it affected the relative rank of individual swimming speed. Thus,

some individuals were affected differently by exposure to a given level of AC. To our knowledge, no other studies have yet applied an individual approach to assess the effects of contaminants on behaviour. We believe much insight could be gained by using this approach on available data sets (e.g. Brodin et al., 2013).

Individual Behaviour Mediates Anthropogenic Contaminant Exposure and Accumulation

Exposure and accumulation of ACs can occur by contact (Ragland, Arendt, Kucklick, & Keller, 2011) or direct ingestion of contaminated food items (Esselink et al., 1995) while animals move within their habitat to forage or find other resources. Several behaviours associated with resource acquisition, such as activity, exploration or voracity, show important variation within populations. For example, individual great tits, *Parus major*, differ in their dispersal tendencies (Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009), and individual spiders (*Agelenopsis aperta*) differ in their willingness to kill and ingest prey (Riechert & Hedrick, 1993). To date, most empirical evidence for behavioural mediation of contaminant exposure comes from studies comparing discrete categories of foraging behaviour (e.g. resident versus migrants) or diet preferences (Table 1). Ragland et al., (2011) showed that migratory male loggerhead sea turtles, *Caretta caretta*, are more prone to accumulate persistent organic pollutants than are resident males. Resident American dippers, *Cinclus mexicanus*, accumulate more organochlorines than do temporary migrants

(Morrissey, Bendell-Young, & Elliott, 2004). Esselink et al. (1995) showed that barn owl, *Tyto alba guttata*, populations feeding at different trophic levels show different rates of heavy metal accumulation.

In contrast to such studies focusing on discrete behavioural categories, there are no empirical studies that investigate the links between continuous behavioural variation and the probability of being exposed to or accumulating ACs. Schlink et al. (2010), however, did provide a theoretical approach. They tested different algorithms of human movement patterns on exposure to air contaminants passively absorbed by breathing, and they found that differences in exposure can arise from individual differences in movement patterns. Such theoretical findings await confirmation from empirical investigations. We believe that investigating how ACs affect consistent behavioural variation calls for a more mechanistic approach than what is usually employed in current toxicological–behavioural assays (Clotfelter et al., 2004).

How to Study the Interaction between Behavioural Variation and Anthropogenic Contaminants

A mechanistic approach

Dynamic interactions between individual behaviour, physiology and AC states may be approached through 'process-based' or mechanistic models, derived from dynamic energy budget (DEB) theory (Kooijman, 1993). Such models explicitly consider resource acquisition and allocation to various functions such as structural maintenance and growth (see Fig. 2, grey flowchart) and thus offer an avenue to incorporate interactions between factors affecting both acquisition and allocation of resources. Extensions of this theory already incorporate the toxic effects of some contaminants on energy allocation (DEBtox: Jager, Heugens, & Kooijman, 2006) and provide a framework for modelling various physiological alterations caused by AC exposure. We suggest that behaviour can be integrated within such a model, as a determinant of resource acquisition. Resource acquisition can then be associated with AC exposure and accumulation. Indeed, behaviour mediates how individuals acquire resources (Fig. 2, black circle) and, consequently, their level of exposure to ACs and the amount of ACs they accumulate (Fig. 2, white circle). For example, the foraging behaviour of an individual could determine the type and abundance of potentially contaminated food items ingested (see Fig. 2, relationship 1) and how much AC it is likely to assimilate in the body (Fig. 2, relationship 2). Note that individual behaviour could lead to differences in AC accumulation or exposure even when the contaminant is diluted in the environment and passively absorbed (e.g. Brodin et al., 2013; Schlink et al., 2010). Moreover, individual differences in metabolism or physiology, often linked to individual behavioural differences, may mediate such variation in AC state in homogeneously contaminated environments. In turn, AC state may have a direct impact on behaviour (depicted as relationship 3 in Fig. 2; reviewed in Zala & Penn, 2004). AC state may also alter how an animal allocates its energy to structural maintenance as opposed to reproduction. For example, *Daphnia* exposed to uranium toxicity display increased allocation of energy to maintenance, probably as a result of the toxic effects of the ACs on the digestive tract (Fig. 2, relationship 4; Massarin et al., 2011). The energy balance and allocation patterns are known to affect an individuals' behaviour and to drive consistent differences in behaviour within populations (reviewed in Dingemans & Wolf, 2010). For example, animals with heightened metabolism may need to forage more or on different prey (Fig. 2, relationship 5; Oliviera, Taborsky, & Brockman, 2008; Réale et al., 2010).

Investigating the interactions between behaviour and ACs may take multiple pathways, potentially leading to feedback

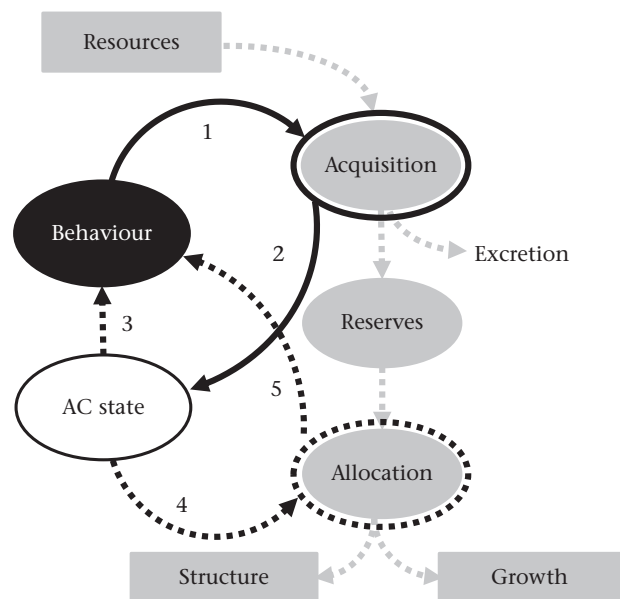


Figure 2. A mechanistic model inspired by the dynamic energy budget (grey boxes and dashed arrows) including the interactions between individual behaviour (black circle, solid arrows) and anthropogenic contaminant (AC) exposure or accumulation levels (white circle, dashed arrows). Individuals acquire resources from their environment. Some of these resources are excreted, and the remaining part is considered to accumulate in a 'reserve' compartment. Reserves may then be allocated to functions such as growth (which includes reproduction in dynamic energy budget (DEB) models) or structural maintenance, depending on the animal's allocation pattern or strategy. The behaviour of an individual, for example activity level or aggressiveness, is often associated with resources acquisition, such as food (1). Individuals may be exposed to AC by moving around in their environment or consuming contaminated prey (2). Behaviour, through resource acquisition, would affect an individual's level of exposure to ACs or the amount of ACs it accumulates over time. AC state may affect behaviours associated with resource acquisition and consequently AC levels (3). Alternatively, AC may modify the individual's allocation pattern (4). For example, it may alter metabolism or life history traits such as growth. The physiological state and life history trajectory of an individual may then modify its behaviour (5).

interactions. Hence, mechanistic models, explicitly analysing the direction (negative or positive), temporal dynamic and relative importance of such pathways are necessary to understand the links between behaviour and contaminants. As we suggest above, models derived from the DEBtox would provide valuable tools for this challenge. The framework we outline here also allows us to investigate how ACs may maintain or erode consistent behavioural variation within populations by generating knowledge on the potential interactions and feedbacks between the pathways we described. For example, exposure to ACs may maintain variation in behaviour if ACs increase the expression of a given behaviour and this behaviour increases AC exposure or accumulation. In this way, individuals expressing a behaviour with a higher intensity experience a larger increase in AC state, which consequently increases behaviour expression (Fig. 1, upper panel). Conversely, if a behaviour is inhibited by an increase in AC exposure, we expect ACs to erode or attenuate individual variation in that behaviour over time (Fig. 1, lower panel). This is expected because individuals expressing a behaviour with a high intensity will experience larger doses of AC, thus decreasing expression of behaviour to a larger extent (Fig. 1, lower panel). This may be the case in systems where individual activity level increases AC state (Schlink et al., 2010) and ACs decrease the activity level of individuals (e.g. Nyman, Hintermeister, Schirmer, & Ashauer, 2013). The toxic effects of ACs would lead us to consider negative feedback loops eroding behavioural variation as more frequent among animal populations. However, we also emphasize scenarios where ACs could increase

consistent behavioural variation among individuals (see the two case studies we describe below).

Longitudinal data

A first step in determining the effects of ACs on individual behavioural variation is to establish how ACs affect behaviours associated with resource acquisition or behaviours that are associated with resource allocation patterns. This can be done using repeated observations conducted at the individual level over time, with special attention paid to the temporal dynamics of individual variation in AC state (Fig. 3a). For this approach to be truly mechanistic, one needs to first assess the relationship between a given behaviour and resource acquisition or allocation strategy and then how resource acquisition/allocation affects AC state. This can be achieved by manipulating behaviour and resource acquisition/allocation. Data on how behaviour affects AC state could then be coupled with repeated assessments of each individual's behaviour for different levels of AC state to investigate how each individual responds to ACs (see Fig. 3b). Note that individuals may react differently to an increase in AC state (i.e. they may show a different relationship between behaviour and AC state). This approach would be complementary to the more conventional one, which compares the average behavioural shift among groups of individuals exposed to different levels of ACs (Fig. 3c). The consistency of individual behavioural and AC state variation can be estimated using repeated measure designs and mixed modelling approaches, partitioning the behavioural and AC state variation into different components such as between- and within-individual variance (Dingemans, Kazem, Réale, & Wright, 2010; Nakagawa & Schielzeth, 2010). This approach is now widely used in behavioural studies, to quantify the extent of consistent behavioural variation among individuals in a population (reviewed in Bell, Hankison, & Laskowski, 2009). Surprisingly, data on AC state effects on individual behavioural variation is extremely rare. In fact, we found only two studies reporting AC effects on individual variation (Brodin et al., 2013; Kolok et al., 1998; Table 1). Implementing such an approach would be very valuable for many reasons. First, it would provide a stronger predictive framework to forecast the effects of contaminant exposure on wild animal populations that are hard to study in laboratory settings. Consistent behavioural variation and allocation patterns are likely to affect many population-level processes like space use as well as interspecific interactions through its effects on diet (Brodin et al., 2013; see also Sih et al., 2012 for a review of this topic). Second, additional knowledge of the multiple paths of effects we describe here would also increase considerably our ability to assess the consequence of ACs by focusing on their effects at doses below thresholds at which they cause death or major health issues in animals. Since ACs are found in most ecosystems, our framework would also be an additional step towards understanding consistent behavioural variation in animals. Of course the relative importance of the paths of effects we described and in particular the importance of their interactions remain to be assessed.

Candidate study systems

AC state and behavioural variation may be easier to study in systems where a limited number of contaminants are at play. Indeed, different ACs often operate in synergy (i.e. 'cocktail effect': Kortenkamp, 2007). Implementing longitudinal studies where ACs and behavioural variation are monitored at the individual level could also be more feasible with bigger and longer-lived organisms such as birds, mammals and reptiles. Long-lived organisms may accumulate ACs such as brominated flame retardants or organochlorines in fatty tissues that are often amendable for repeated sampling without killing the individuals (Rowe, 2008). In contrast, AC accumulation is hard to establish for short-lived organisms such

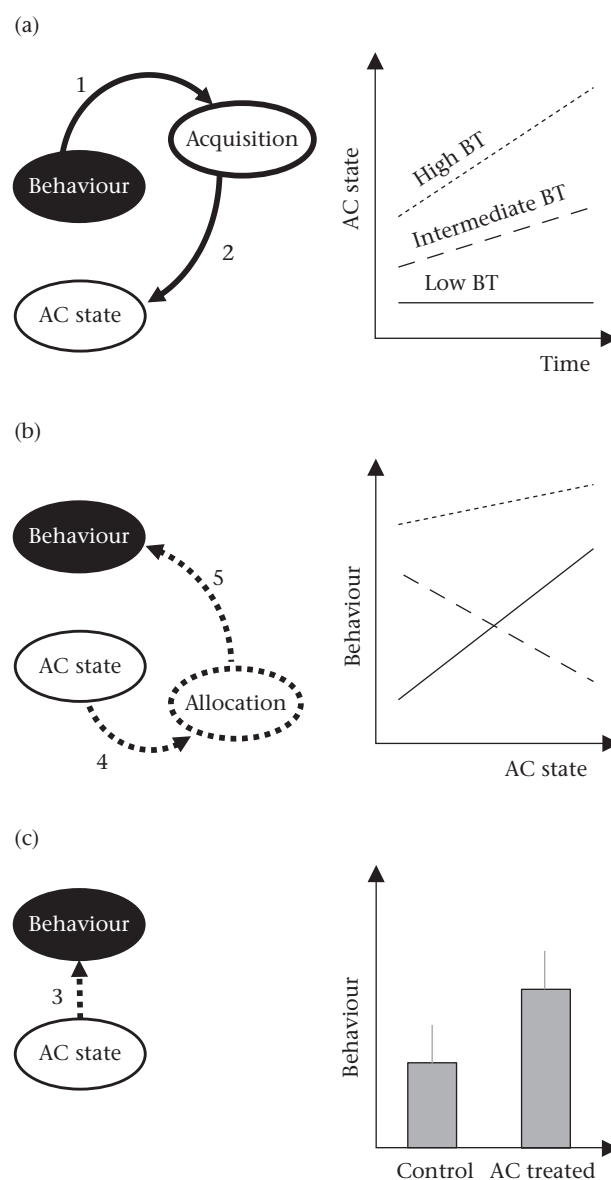


Figure 3. Steps for an empirical investigation of the feedbacks between anthropogenic contaminant (AC) state and behaviour. (a) A first step is to collect repeated measurements of the AC state of individuals with known behavioural differences (each individual's behavioural type is measured prior to the experiment). The effects of these behavioural differences on resource acquisition and AC state also need to be assessed. (b) A second step is to detail how each individual's behaviour changes as a function of a change in AC state. Such relationships require repeated behavioural measurements on individuals subjected to controlled doses or exposure levels of AC. Differences in these relationships among individuals will likely be the result of a change in resource allocation. (c) Steps in (a) and (b), which involve repeated measurements of individuals' AC states and behaviours, would greatly complement the more widely used approach, testing the average effect of ACs on behaviour through standardized bioassays.

as arthropods. They are however easier to maintain under laboratory conditions and can be used for standardized experimental work where AC state and resources can be manipulated. Despite such limitations, we outline briefly two case studies where the dynamics between AC state and behavioural variation is amenable to empirical investigation.

Psychiatric drugs in fish populations. Psychiatric drugs, such as anxiolytics, are found in urban waste water (Kolpin et al., 2002; Verlicchi, Al Aukidy, Galletti, Petrovic, & Barceló, 2012). Such

drugs are usually found in highly diluted concentrations in rivers, but may be accumulated by aquatic organisms (Meredith-Williams et al., 2012). Individual perch (*Perca fluviatilis*) with a higher burden of accumulated anxiolytics in their body express increased activity and boldness but reduced sociality (Brodin et al., 2013). Individuals exposed to higher doses of anxiolytics also increase their foraging on zooplankton, a prey item that is typically found in the water column, and potentially carrying a higher dose of accumulated anxiolytics. Other studies previously showed that individuals with higher boldness and reduced sociality use the water column more frequently (Magnhagen & Staffan, 2004). It is currently unknown whether this change in diet affects individual AC state. However, we suggest that a chain of effect may link individual differences in foraging behaviour to the level of AC exposure and accumulation. If bolder individuals feed at a higher trophic level than shy ones (i.e. on zooplankton) and if feeding at higher trophic levels leads to increased AC exposure, this chain of effect would become a positive feedback loop, resulting in increased differences in boldness among individuals over time. Unfortunately, the study by Brodin et al., (2013), while using a longitudinal approach, focused on the average effect of ACs on personality traits. A similar experimental design, assessing the repeatability of behavioural traits through time during an extended AC exposure event would provide much insight on the feedback loop we describe, hence building a better knowledge of the interactions of ACs with consistent behavioural variation. Such knowledge should increase our ability to predict the effect of contaminants in other perch populations and related study systems. For example, populations of perch with a mixture of behavioural types could be vulnerable to a different extent to the effects of psychiatric drugs. Considering that ACs are found in all environments assayed to date, we suggest they may be seen as an integral part of the consistent behavioural variation we observe in animal populations.

Neurotoxic insecticides and honeybees. Honeybee, *Apis mellifera*, workers feed on nectar and pollen sources contaminated with neurotoxic insecticides over a wide foraging range (Rortais, Arnold, Halm, & Touffet-Briens, 2005). Returning foragers also expose other bees and larvae within the colony to contaminated food sources (Krupke, Hunt, Eitzer, Andino, & Given, 2012). Depending on their social role within the hive, individuals may be exposed to different doses of insecticides (Fig. 2, relationship 1). Neurotoxic insecticides disrupt synaptic transmission and have been shown to impair foraging activity, navigation skills, olfactory memory and learning skills (Bortolotti et al., 2003; Colin et al., 2004; Decourtye et al., 2004; Decourtye, Lacassie, & Pham-Delègue, 2003). For example, exposure to thiamethoxam increased the proportion of foragers that failed to return to the colony, up to 30% per day (Henry et al., 2012). Thus, a potential feedback loop may exist between the social role of individuals and their AC state. Even within a particular social role, consistent individual differences have been demonstrated for honeybees. Despite this knowledge, individual behavioural differences have not been incorporated when studying insecticidal effects. It is known, however, that foragers differ consistently along a continuum of speed versus accuracy of flower exploration (Burns & Dyer, 2008). Accurate explorers return more resources (i.e. pollen, nectar) when flower quality is low, whereas fast explorers are more efficient when flower quality is high. One could posit that accurate explorers are less likely to get disoriented but may contribute more to the AC state of the colony by returning more contaminated food sources. Finally, colonies express different average behavioural types (Pinter-Wollman, 2012). Wray, Mattila, and Seeley (2011) showed that defensive responses, foraging activity and undertaking (i.e. the removal of dead workers) are correlated and consistent at the colony level. Colonies with higher

foraging activity and defensive responses could be exposed to ACs more than colonies with lower foraging activity. This could translate into higher AC accumulation for colonies in areas with extensive insecticide use.

CONCLUSION

Behaviour and ACs are likely to share dynamic links and potentially feedback into each other. We presented two scenarios in which such interactions could occur either through the process of resource acquisition, or through modifications of resource allocation patterns. While reviews are already available on the effect of AC exposure and accumulation on the average behaviour of a population, literature investigating how individual behavioural differences interact with differences in exposure and accumulation of ACs is still scarce. Furthermore, studies investigating the relationships between an individual's behaviour and AC state are completely lacking. We encourage an increased use of mechanistic models that integrate longitudinal studies (repeated observations) on individual behaviour and AC state. This new research area is an outstanding opportunity to build bridges between behavioural ecology and ecotoxicology and to integrate behavioural ecological knowledge to the investigation of how animal populations respond to human-induced alterations of their environment.

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