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RELATIONSHIP BETWEEN RANGING BEHAVIOR AND SPATIAL MEMORY OF FREE-RANGE CHICKENS

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ABSTRACT

Different personalities may lead to different ways of processing environmental information; however, the relationship between personality and cognition is not fully understood as studies on diverse species present contrasting results. As there is great within-flock variability of outdoor ranging behavior in free-range broiler chickens, we tested whether and how ranging behavior impacts on individual spatial memory abilities. The experiment was conducted on one flock (n=200) reared in the same conditions throughout the study, to simulate on-farm situations. As the ranging behavior was stable over time, we compared two distinct groups of male chickens: one that visited the range more (High rangers) and one that was more prone to staying in the poultry house (Low rangers). To test the spatial memory, individuals (n=30) went through two main phases in an arena with 8 cups. For the familiarization phase, individuals were submitted to one trial per day, for seven days, to a situation where all eight cups were baited with mealworms. Animals had to reach a criterion of 5 cups visited out of 8 to advance to the next phase. For the spatial test, only four cups were baited and systematically placed at the same location. This last phase comprised two trials per individual per day, for nine days. During these two phases, latency to visit cups and the number of visits and revisits of all cups were recorded. Low ranger chickens took less time to attain the pre-established threshold of visiting 5 cups out of 8, over the familiarization phase. During the spatial test, the latency to visit four cups decreased between the within-day trials for low ranger chickens and increased for high ranger chickens. Moreover, in the within-day trial analysis, low ranger chickens exhibited an improvement on spatial memory and better spatial memory compared to high ranger chickens. Different speed-accuracy trade-offs may explain these differences between low and high ranger chickens and the way individuals interact and solve the task. Our study strengthens the scientific evidence relating consistent individual differences in behavior, with the ranging behavior of free-range chickens, and cognitive performance during a spatial memory task.

Keywords: birds; broiler; free-range chicken; cognition; personality.

1. INTRODUCTION

In the last decades, the interdisciplinary approach of individual consistent differences in behavior is flourishing among the scientific community as scientists realize that **such** behavioral differences are ubiquitous in the animal kingdom (Gosling, 2001). The fact that a group of animals shows between-individual variation and within-individual consistency that persist through time and different situations (i.e. animal personality) brings theoretical and practical inquiries, since individuals from the same group or population will interact with their social and physical environment in different ways (Dall et al., 2004; Réale et al., 2007; Sih et al., 2004).

Empirical research has highlighted a link between learning performance and personality focusing on diverse personality and behavioral traits, however, the relationship between these traits and cognition is not fully understood, as studies on diverse species present contrasting results (Dougherty et al., 2018). An important animal personality trait believed to influence cognition is known as Exploration-Avoidance. As proposed by Réale et al. (2007) this trait can be seen when the individual interacts with new situations (unknown conspecifics, new habitat, new food, new objects). For cognitive scientists, the link between exploration and cognition (learning performances, mainly) is expected since more explorative individuals are more prone to be in contact with what is to be learned (Carere and Locurto, 2011; Sih and Del Giudice, 2012). For example, individual black-capped chickadees (*Parus atricapillus*) entering a novel arena more quickly had a better performance during an acoustic discrimination task than slower individuals (Guillette et al., 2009). However, for other species, such as the red junglefowl, this relationship is age and task-dependent: more explorative chicks and less explorative adult females were faster to learn a reversal task (Zidar et al., 2018). Pheasants (*Phasianus colchicus*), on the contrary, show a different pattern with slow explorers (when chicks) being slow reversers (when adults) (Madden et al., 2018).

A recent meta-analysis by Dougherty et al. (2018) showed that the direction of the personality/cognition relationship is highly variable and the current hypothesis that exploration is consistently linked to cognitive performance was not supported. Therefore, even if a link between

different personality traits, such as exploration, and cognition may exist for a given species or population, assumptions of the direction and dynamics of this relationship need to be reassessed through further work and made cautiously.

Free-range domestic chickens, the contemporary of the junglefowl, show great variability in range use, when the outdoor range access is finally available (Chielo et al., 2016). Extrinsic factors such as indoor/outdoor stocking density (Campbell et al., 2017a), position of pop-holes (Rault and Taylor, 2017), the access and placement of the poultry house, the availability of shelters and trees (Dawkins et al., 2003), and the internal roosting location (Pettersson et al., 2018) were all potential candidates for explaining this inconsistency at the group-level. Intrinsic factors such as sex, age or the breed/strain (Hegelund et al., 2005; Mahboub et al., 2004; Nielsen et al., 2003; Stadig et al., 2017) are also important variables to take into account when studying the interactions between chicken groups and range use.

A less studied feature of chickens and range interactions is that individual chickens have different personality profiles (Garnham and Løvlie, 2018), and these profiles may, in turn, be related to important cognitive processes. For juvenile and adult red junglefowl, for example, personality, mainly high shyness/fearfulness and low exploration, impacts positively how fast the individuals learned a reversal task (Zidar et al., 2018).

A similar personality/cognition interaction dynamic may be impacting individual chickens in their spatial learning and memory when using the range (Campbell et al., 2018). When foraging or exploring a new environment, animals, such as mammals and birds, use their spatial memory, also called reference memory (White and McDonald, 2002), based on the formation of a complex spatial map that includes cues present in the surrounding environment as well as their relationships (Packard & Cahill, 1995; White & McDonald, 2002). Free-range chickens can be a suitable animal model for the integration of personality and cognition studies as individuals within the same flock vary in visiting the range or not. This potentially exposes birds to different levels of environmental complexity and different ways to navigate this environment. On the one hand, some individuals may require more spatial information processing, since their interaction with the surrounding environment is higher (Campbell et al., 2018). On the other hand, as suggested by Guillette et al. (2017), some individuals

may be slower when processing environmental information, resulting in less exploratory individuals that are not prone to switch between different and potentially new environments, until acquiring sufficient information on one particular area.

In the current work, we studied the relationship between ranging behavior and spatial memory of free-range chickens. We aimed to verify two main predictions. The first one was that individuals could be characterized based on their ranging behavior, to corroborate findings of consistent ranging behavior on laying hens and broilers chickens (Campbell et al., 2017b; Hartcher et al., 2015; Larsen et al., 2017; Pettersson et al., 2018; Taylor et al., 2017). The second prediction was that ranging behavior is linked to different spatial cognitive performances, based on the recent literature and findings of red junglefowl personality and cognition (Zidar et al., 2018, 2017), we hypothesized that low ranger chickens would perform better than high ranger ones. To test behavioral consistency within-individuals, we initially checked for the stability of individual range visits. Then, according to their placement in the number of range visits continuum, the chickens on the extremes were selected: the highest rangers and the lowest rangers to undergo a spatial cognitive test. To test whether the level of ranging behavior is related to changes in processing spatial information, mainly reference memory, we used a cohort of individuals that were trained to find the constant location of four rewarded black cups among 8 identical black cups.

2. METHODS

This study was conducted at the experimental unit UE 1206 EASM of INRA, France, from February to May 2015. All applicable international, national and/or institutional guidelines for the care and the use of animals followed the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Animal care and experimental treatments complied with the guidelines of the French Ministry of Agriculture for animal experimentation and European regulations on animal experimentation (86/609/EEC).

2.1. SUBJECTS

For this experiment, the free-range system consisted of a poultry house (4 m x 5 m) giving access to an outdoor range (27 m x 27 m) through one pop-hole. A flock of 200 *naked neck* broiler chicks (S757N, males and females mixed) was placed at day-old in the poultry house, all chicks being identified one week later with a wing tag. Birds had indoor *ad libitum* access to feed and water. During the first three days from placement, artificial lighting was provided continuously, then from day 4 to day 14 it was gradually decreased, until total use of natural lighting. The indoor ambient temperature was maintained at 28°C during the first week and decreased 1°C each week, until reaching 23° at the age of 38 days.

At day 31, 120 chickens were chosen randomly and equipped around the neck with a plastic poncho labelled with a unique acronym for easy identification. From day 38, when feathering was complete, birds were allowed free access to the outdoor range (meadow-like, open space with vegetal cover, without trees or shelters available), day and night. The initial stocking density in the poultry house was 10 chickens/ m², and 3.7 m²/chicken in the outdoor range. Birds' sex was determined at 65 days of age.

2.2. RANGING BEHAVIOR

The chickens carrying a poncho were observed by scan sampling. Six interspaced scans per day at four different ages (D44, D49, D57, and D64) were performed. The experimenter, using binoculars, counted the marked birds from a high chair placed outside the range, to minimize disturbance. For each scan, the location of each chicken was noted on one of the 16 range zones, previously delimited with small wood stakes, or inside the poultry house (Figure 1). As some animals preferred to stay close to the building's edges, Zones A to C were gradually longer, except for zone D (A = 4m, B = 9m, C = 14m, and D = 2m). This range division allowed us to have a more

heterogeneous distribution of the individuals and differentiate chickens who ranged near the poultry house from those who went further on the range.

Figure 1 about here

These observations made it possible to determine the number of times the chickens were seen on the range (number of range visits) and to calculate an individual distance index. When an animal was seen in a given zone, we considered it walked the equivalent of **the** half-length of this zone plus the total length of already crossed zones, in **the** case of zones B, C or D. For example, when a given individual was seen in zone B, we considered it walked the 4 meters of zone A plus 4.5 m (half-length) of zone B. The distance index was then calculated as follows:

Individual distance index = number of times seen in zone A*2 + number of times seen in zone B*8,5 + number of times seen in zone C*19 + number of times seen in zone D*26

The distance index integrated the ‘number of range visits’ with the distance that individuals moved away from the poultry house, adapted to incorporate the size of the range zones. A high distance index corresponded with a high level of ranging behavior.

The 120 birds were classified according to their total number of range visits and their individual distance index. Those placed at the extremities of this continuum were called *low rangers* or *high rangers*, the former meaning an individual with a low number of range visits, and the latter an individual with a high number of range visits. When individuals presented the same number of range visits, those presenting a higher distance index, in the case of high rangers, or a lower distance index, in the case of low rangers, were chosen for testing in a spatial memory task.

2.3. SPATIAL MEMORY TASK

From 66 to 88 days of age, 30 chickens underwent a series of cognitive tests. These individuals were selected among the 120 animals, according to two criteria: sex (only males were selected in order to control for sex influences on cognition - [Bushby et al., 2018](#)) and ranging behavior level 'high rangers'/'low rangers' (after group observations on the range).

Following classification of ranging behavior, 15 healthy individuals from either extreme, i.e. the 15 highest rangers and the 15 lowest rangers, were selected for the spatial memory task. The group was then divided in two subgroups, equally balanced in the number of high rangers and low rangers chickens, to be tested throughout the day (morning and afternoon). The first subgroup was caught in the morning and kept in crates without food placed in the test room for at least 1 hour before the beginning of the cognitive task. As soon as all chickens from this subgroup finished the cognitive tests, they were released back into the poultry house. In the afternoon, we proceeded in the same way with the second subgroup. The testing order of the individuals, as well as the testing order of the subgroups, was similar throughout the experiment.

The apparatus used for this task was a wooden square structure (l : 1.6m, w : 1.6, h : 0.7m, Figure 2), with a yellow plastic floor and illuminated by a linear fluorescent lamp. The walls were opaque, with a curtain **surrounding** the apparatus to both prevent animals from escaping and homogenize all the sides of the arena. Black visual cues of different shapes were placed on each wall of the apparatus and on the surrounding curtain. Eight identical cups were placed at equidistance in this structure. Cues on the wall were not associated with specific cups. The height and depth of these cups could be manually adjusted, depending on the task phase. All behavioral data were recorded using a digital video camera recorder.

Figure 2 about here

2.3.1. FAMILIARIZATION

During the first stage of the familiarization (Figure 3), **with the test set up**, pairs of chickens (one low ranger and one high ranger) were placed in the apparatus and were allowed to explore it for

10 minutes. Familiarization in pairs was used to facilitate exploration of the arena and reduce the stress of the social isolation (Fontana et al., 2016; Weldon et al., 2016), the new environment (apparatus structure, cups) and the new food (mealworms). The 8 cups in the apparatus were 10 cm high and 2 cm deep. This setup allowed individuals to easily see the inside of the cup. Each cup was baited with one mealworm. The height and the depth of each cup was chosen in order to motivate exploration and to encourage individuals to put their heads in the cup and eat the mealworm. Each pair of chickens underwent, in this stage, one familiarization trial once a day on four occasions (between D66 and D72). By the end of the 4 days, all birds were actively moving in the arena and eating the mealworms.

For the second stage of the familiarization (Figure 3), all 8 cups (15 cm high and 5 cm deep) were baited with one mealworm. The new dimensions of cups were used to prevent animals from easily seeing the reward in the cup and to motivate them to approach the cups one by one. Each animal was individually introduced into the apparatus and allowed to explore the cups until all mealworms were eaten or up to a maximum trial duration of 10 minutes. Each animal was submitted to one trial per day for 7 days (D73 to D79). At the beginning of each trial, the individual could be placed in one of two possible entrances, randomly chosen and alternated from trial to trial.

We pre-defined a familiarization threshold of 5 cups visited out of the 8. Since the number of baited cups during the next phase (spatial test) was 4, it was important that the animals visited more than 4 cups. Birds that did not meet this criterion did not advance to the next phase. For each trial, the number of cups visited (number of times the chicken placed its head above the cup and ate the mealworm) and the latency to visit at least 5 baited cups was recorded.

Figure 3 about here

2.3.2. SPATIAL TEST

The same apparatus and cup dimensions used during the second stage of the familiarization were used for this learning task but only 4 out of 8 cups were baited (Figure 3). The location of the

baited cups was permanent for all individuals and trials. Thus to solve the test, birds needed to learn the spatial location of the 4 baited cups. Birds were individually introduced in the apparatus and allowed to explore it until all mealworms were eaten or after a maximum time of 5 minutes. Each animal underwent two trials (inter-trial interval of 1h15min) per day for 9 days (D80 to D88). As for the familiarization task, chickens were introduced in the apparatus from two different entrances, from trial to trial. The aim of this alternation was to prevent a stimulus-response behaviour or the use of egocentric strategies, requiring individuals to rely solely on intra and extra-maze cues.

For each trial, the total number of visited cups, the number of visited baited cups (the chicken placed its head above the cup and ate the mealworm) and non-baited cups, the latency to visit all baited cups, the number of revisited baited cups, the total number of revisited cups (baited and not baited) were recorded. Through these data it is possible to calculate an index relating to reference spatial memory:

$$\text{Index to assess spatial reference memory: } \frac{\text{visits and revisits to baited cups}}{\text{visits to all cups}}$$

This reference memory index measures the chicken's ability to discriminate between baited cups and non-baited cups (Nordquist et al., 2011; Tahamtani et al., 2015). The index results are between 0 and 1, with 1 being the best possible score.

3. STATISTICS

3.1. RANGING BEHAVIOR

The stability of the ranging behavior (number of range visits) between 4 days of observations was analyzed by Spearman correlation, due to non-normality of the data. In order to avoid multiple correlations, we combined the data for days 44 and 49 and for days 57 and 64 for each chicken (both

sexes), then the correlation between the two periods (days 44 + 49 and days 57 + 64) for the number of visits were tested.

The variable “number of range visits” and “distance index” were then calculated by adding all visits on the outdoor range for each chicken at the four ages of observations in order to characterize the ranging behavior level of each chicken. The sex effect for these variables was analyzed on the pooled data of four observation ages using a Mann-Whitney test. Of the 120 individuals with a poncho, 113 could be studied throughout the study (n = 62 females, and n = 51 males). The losses were due to predation and/or lost ponchos.

3.2. SPATIAL MEMORY TASK

3.2.1. FAMILIARIZATION (SECOND STAGE)

A general linear model with repeated measures was performed on the variables “number of cups visited” and “latency to visit 5 cups”. The ranging behavior level (low or high ranger) was included as the between-subject factor and the day (D1 to D7) as the within-subject factor. Greenhouse-Geisser corrections were applied when the assumptions of sphericity were violated. When main effects or interactions were significant, analyses were followed by multiple comparisons corrected by Tukey’s HSD. Ranging behaviour level (low or high ranger) effects on ‘Days to criterion’ variable (number of days to reach the threshold of 5 cups visited out of the 8) was analyzed through a Mann-Whitney test.

At the end of the familiarization period, two individuals (one low ranger and one high ranger) did not meet the criterion for inclusion in the next phase of the task. The total number of chickens for the next phase was n = 28.

3.2.2. SPATIAL TEST

The variables 'latency to visit 4 cups' and the 'reference memory index' were analyzed by a general linear model with repeated measures. The between-subject factor was the ranging behavior level (low or high ranger) and the within-subject factors were the trial (1 or 2) and the day (D1 to D9). Day and trial were included separately in order to verify changes in performance within and between days, since memory within and between-days are mediated by different subregions of the hippocampus and could be potentially different (Kesner et al., 1993; Kesner and Hunsaker, 2010). Greenhouse-Geisser corrections were applied when the assumptions of sphericity were violated. When main effects or interactions were significant, analyses were followed by multiple comparisons corrected by Tukey's HSD.

At the end of the spatial test period, four chickens (one low ranger and three high rangers) were excluded because they did not visit more than 2 cups (with or without mealworms). The number of chickens included in the analyses was $n = 24$.

All statistical analyses were performed using IBM SPSS Statistics 21 and using R version 3.5.3 with the 'R commander' package. Statistical significance was accepted at $p \leq 0.05$, while tendency was considered for $0.05 < p < 0.09$. Data are presented as means or estimated marginal means \pm SD.

4. RESULTS

4.1. RANGING BEHAVIOR

There was a tendency for the total number of range visits to be higher for males than for females (4.33 ± 2.71 and 3.38 ± 2.37 , respectively, $U = 1271$, $p = 0.071$, $\eta_p^2 = 0.02$). Moreover, the distance index was significantly higher for males than for females (24.70 ± 24.77 and 15.16 ± 15.27 , respectively, $U = 1158.5$, $p = 0.015$, $\eta_p^2 = 0.05$).

The number of range visits and the distance index which characterized the groups as low ranger or high ranger are presented in Table 1 for the 113 labelled chickens and the 30 males used for

the tests of cognitive performance. The number of range visits during D44+D49 was positively and significantly correlated with the number of range visits during D57 + D64 ($r_s = 0.307$, 95% CI = 0.13 to 0.47, $p = 0.002$). The total number of range visits was positively and significantly correlated with the distance index ($r_s = 0.795$, 95% CI = 0.70 to 0.87, $p < 0.001$).

Table 1 about here

4.2.SPATIAL MEMORY TASK

4.2.1. FAMILIARIZATION

For the variable ‘number of cups visited’ the interaction of Day x Ranging behavior level was not significant (Greenhouse-Geisser corrected- $F_{3,219, 90.142} = 1.467$, $p = 0.227$, $\eta_p^2 = 0.050$), however there was a significant increase in the number of cups visited by individuals from both groups over the days (effect of day: Greenhouse-Geisser corrected- $F_{3,219, 90.142} = 17.67$, $p < 0.001$, $\eta_p^2 = 0.387$; effect of ranging behavior level: $F_{1, 28} = 3.04$, $p = 0.092$, $\eta_p^2 = 0.098$), which indicated they became habituated to the task.

Similarly, there was no interaction of Day x Ranging behavior level for the latency to visit 5 baited cups (Greenhouse-Geisser corrected- $F_{2,894, 81.020} = 1.033$, $p = 0.381$, $\eta_p^2 = 0.036$). The latency to visit 5 baited cups decreased significantly over days for both groups equally (effect of day: Greenhouse-Geisser corrected- $F_{2,894, 81.020} = 12.68$, $p < 0.001$, $\eta_p^2 = 0.312$; effect of ranging behavior level: $F_{1, 28} = 2.67$, $p = 0.113$, $\eta_p^2 = 0.087$). Low ranger chickens needed, however, significantly fewer days to reach the criterion of 5 visited baited cups among the 8 baited cups than high ranger chickens (1.46 ± 1.26 and 3.06 ± 2.49 , respectively, $U = 64$, $p = 0.023$, $\eta_p^2 = 0.17$).

4.2.2. SPATIAL TEST

For the latency to visit four baited cups there was no Day x Trial x Ranging behavior level interaction (Greenhouse-Geisser corrected- $F_{5.041, 110.911} = 1.085$, $p = 0.373$, $\eta_p^2 = 0.047$). There was a significant interaction of Trial x Ranging behavior level for the latency to visit the 4 baited cups (Greenhouse-Geisser corrected- $F_{1, 22} = 9.89$, $p = 0.005$, $\eta_p^2 = 0.310$). Separated analyses, showed that low ranger chickens took significantly less time between trials to visit the four baited cups ($F_{1, 12} = 6.076$, $p = 0.030$, $\eta_p^2 = 0.336$, Figure 4), while between-trial latency increased significantly from trial 1 to trial 2 for high ranger chickens ($F_{1, 10} = 5.134$, $p = 0.047$, $\eta_p^2 = 0.339$, Figure 4).

The latency decreased significantly over test days in the same way for chickens of both high and low ranging behavior levels (effect of day: Greenhouse-Geisser corrected- $F_{5.173, 113.812} = 3.28$, $p = 0.008$, $\eta_p^2 = 0.130$; effect of trial: $F_{1, 22} = 2.046$, $p = 0.167$, $\eta_p^2 = 0.085$; effect of day x trial: Greenhouse-Geisser corrected- $F_{5.041, 110.911} = 0.690$, $p = 0.700$, $\eta_p^2 = 0.030$; effect of ranging behavior level: $F_{1, 22} = 0.082$, $p = 0.77$, $\eta_p^2 = 0.004$; effect of day x ranging behavior level: Greenhouse-Geisser corrected- $F_{5.173, 113.812} = 0.947$, $p = 0.45$, $\eta_p^2 = 0.041$).

Figure 4 about here

4.2.3. REFERENCE MEMORY INDEX

There was no day x trial x ranging behavior level interaction for the reference memory index ($F_{8, 176} = 1.174$, $p = 0.317$, $\eta_p^2 = 0.051$), however the trial x ranging behavior level interaction was significant ($F_{1, 22} = 13.169$, $p = 0.001$, $\eta_p^2 = 0.374$). The reference memory index increased significantly between the trial 1 and 2 for low ranger chickens (0.732 ± 0.175 and 0.819 ± 0.176 , for low ranger trial 1 and 2, respectively, $p = 0.002$), whereas it was similar between the 2 trials for high ranger chickens. Moreover, the reference index of low ranger chickens for the second trial was

significantly higher when compared to high ranger chickens' two trials (0.745 ± 0.2 , $p = 0.023$ and 0.734 ± 0.209 , $p = 0.005$, for high rangers' trial 1 and 2, respectively, Figure 5).

The reference memory index increased significantly over test days in the same way for chickens of both high and low ranging behavior levels (effect of day: $F_{8, 176} = 3.102$, $p = 0.003$, $\eta_p^2 = 0.124$, Figure 6; effect of day x trial: $F_{8, 176} = 1.076$, $p = 0.382$, $\eta_p^2 = 0.047$; effect of ranging behavior level: $F_{1, 22} = 0.642$, $p = 0.43$, $\eta_p^2 = 0.028$; effect of day x ranging behavior level: $F_{8, 176} = 1.280$, $p = 0.257$, $\eta_p^2 = 0.055$).

Figure 5 about here

Figure 6 about here

5. DISCUSSION

Our study strengthens the scientific evidence relating consistent individual differences in behavior, with the ranging behavior of free-range chickens, and cognitive performance during a spatial memory task. Low ranger chickens took less time to attain the pre-established threshold of visiting 5 cups out of 8, over the familiarization phase. During the spatial task, the latency to visit four cups decreased between the within-day two trials for low ranger chickens and increased for high ranger chickens. Moreover, in the within-day trial analysis, low ranger chickens exhibited an improvement on spatial memory and a better spatial memory index compared to high ranger chickens.

Behaviorally, males and females differed in the number of visits to the range and how far they ranged, with males visiting the range on more occasions and travelling farther from the poultry house. These results support what was evidenced by other studies in domestic chickens: males and females differ in social attachment and social reinstatement patterns, with females being more sociable, and therefore less prone to be in social isolation, than their male counterparts (Vallortigara, 1992; Vallortigara et al., 1990). Males also show weak physiological and behavioral responses during social isolation when compared to females (Weldon et al., 2016). Social isolation may be a common situation

in the range since there is a negative relationship between stocking density (animal/m²) and distance from the poultry house that results in low individual proximity to social partners. (Chielo et al., 2016).

The number of range visits was significantly correlated between the two periods of observations (D44+49 and D57+64), showing a certain stability over time. When looking at the individuals on the extremities of the ranging behavior continuum, high rangers did visit the range more frequently than low ranger chickens, suggesting the existence of personality traits (i.e. between-individual differences and within-individual consistency - (Dall et al., 2004)) even in domestic species as chickens, strongly selected for production (Finkemeier et al., 2018; Richter and Hintze, 2018). These findings support previous studies reporting that chickens can exhibit individual differences in multiple features, such as environmental preferences (Nicol et al., 2009) and fear responses (Campbell et al., 2016). Moreover, chickens' movement patterns (Rufener et al., 2018) and range use (Campbell et al., 2017b; Hartcher et al., 2015; Larsen et al., 2017; Taylor et al., 2017) were already demonstrated to vary consistently between individuals.

During the familiarization phase of the spatial memory task, low ranger individuals were faster to attain our familiarization threshold (five cups visited) when compared to high rangers. Moreover, during the spatial test, low ranger chickens exhibited an improvement on spatial memory index and a decrease in the latency to reach the four baited cups between trials compared to high ranger chickens. Campbell et al. (2018), using a similar framework, compared the relationship between spatial cognition and range use in free-range laying hens. However, contrary to our results, the authors found that individuals presenting more visits to the range were faster to reach the learning criterion and find a food reward in one arm of a T-maze. These conflicting results may be linked to that, even if aiming to study spatial cognition, the tasks proposed presented different levels of complexity, the T-maze being simpler when compared to our arena with multiple cups. As Campbell et al. (2018) tested only females and, in our study, we tested only males, an alternative explanation is that cognitive abilities are linked to sex. For example, male Vanajara chickens cognitively tested on Y and T mazes had a better overall performance than females, however from day 84 of age, both sexes performed equally (Panigrahy et al., 2017). On the contrary, females chicks of the red junglefowl learned a reversal task faster than males (Zidar et al., 2018). Sex influences on cognitive abilities have also been seen in other species

such as guppies (Lucon-Xiccato and Bisazza, 2017) and lizards (Carazo et al., 2014). For great tits (*Parus major*), for example, personality and learning performance interacts in a sex-dependent way: fast-exploring males outperform slow males, but slow-exploring females outperform fast females (Titulaer et al., 2012).

Our results are, however, in line with the coping styles literature (Coppens et al., 2010; Koolhaas et al., 1999) where slow-exploring, reactive animals perform better under variable and unpredictable situations than fast-exploring, proactive individuals. Reactive juvenile red junglefowl, more fearful in a tonic immobility test, were quicker to explore a new color cue in response to an alteration of rewarded stimulus, showing high behavioral flexibility (Zidar et al., 2017).

The latency to visit the cups during the spatial test (four rewarded cups out of eight) showed no differences over days between groups, however, high ranger and low ranger chickens exhibited different patterns in the between-trial analysis, with low ranger chickens decreasing and high ranger chickens increasing their time to reach the rewarded cups. High ranger chickens may be faster during their first trials due to internal motivation to explore the test arena, however these individuals seem to be more oblivious to their surroundings. On the other hand, low ranger chickens may be more accurate and, in turn, take more time to create an effective spatial map. These results agree with White et al. (2017) and their study of individual differences in brook trout (*Salvelinus fontinalis*) spatial learning ability: bold fish are less attentive to environmental cues and explore their environment randomly, which in turn results in more time to execute the task. Fast-exploring mallard ducks (*Anas platyrhynchos*) were slower than slow-exploring individuals to reach the final compartment when in a maze, possibly because they engaged in other activities, such as foraging, and therefore paid less attention to spatial cues (Bousquet et al., 2015).

In the spatial test, low ranger individuals also showed an improvement of reference memory index between trials within the same day, and not between different days when compared to high ranger individuals. As this occurred within trials of the same day, on an interval of approximately 1h15min, it may suggest that a short-term memory was being improved over long-term memory (i.e. reference memory). Nordquist et al. (2011), in the first work using a holeboard task in chickens,

suggest that long and short term memories are not fully independent in chickens, mainly during acquisition phases, and this may be the case for the chickens in our study.

From an ecological point of view, [Sih and Del Giudice \(2012\)](#) suggest that there is a trade-off between speed and accuracy, with fast-explorers animals favoring short-term gains and therefore being more inaccurate in their decision process. Contrarily, slow-exploring individuals prefer to gather more environmental information and take time to make a decision ([Chittka et al., 2009](#)). This speed-accuracy hypothesis is further supported by our result showing that the main difference between our high ranger and low ranger chickens within the spatial test phase can be seen through analyses of the reference memory index between trials, with low ranger chickens showing a better performance when compared to high ranger chickens.

Currently, when providing a range to chickens, the individual variability is rarely considered. However, through this work, we have shown there is not only high variability in terms of ranging behavior, but also that the ranging behavior level can impact individuals' abilities during a spatial memory task, therefore free-range chicken cognition. The variation in the individual x environment interaction could be the source of different cognitive abilities, as is the case for juvenile Atlantic salmon (*Salmo salar*) exposed to enriched conditions and presenting improved neural plasticity in the forebrain and better learning ability assessed in a spatial task ([Salvanes et al., 2013](#)). The same was observed in laying hens exposed to different housing conditions (battery cages, littered pens or free range) as they exhibit distinct brain morphologies, probably linked to the contrasting spatial complexity of these systems ([Patzke et al., 2009](#)).

6. CONCLUSION

To further improve our knowledge of the impact of ranging behavior and cognitive performances in free-range chickens, it is necessary to bear in mind two main points: the first one is that memory is not a single faculty and the relationships between ranging behavior and cognitive performances may be dependent on the memory system (short vs long term) considered.

The second point is that our measure of ranging behavior was based on a **single** variable (number of range visits). Range use can potentially be a part of three of the five major animal personality traits proposed by Réale et al. (2007), which can be also applied to free-range chickens: shyness-boldness, exploration-avoidance or activity, however, it was outside of the scope of the present study to present a convergent validity and include ranging behavior as a part of one of these three major personality traits through multiple tests. Nonetheless, it is important to note that our variable did show time repeatability between different ages, **an important step to be considered as a component of a major personality trait** (Bell et al., 2009).

From an interdisciplinary perspective, all that information can provide a better knowledge about animals' inner perceptions and their own interactions with the physical (e.g., food source, predation) and social environment (Réale et al., 2007), contributing to improvements of their quality of life, mainly for those under human care, such as wild captive animals and livestock (Boissy and Lee, 2014).

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9. BIBLIOGRAPHY

Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis.

521 Anim. Behav. 77, 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
 522 Boissy, a, Lee, C., 2014. How assessing relationships between emotions and cognition can improve
 523 farm animal welfare. Rev. Sci. Tech. 33, 103–110.
 524 Bousquet, C.A.H., Petit, O., Arrivé, M., Robin, J.P., Sueur, C., 2015. Personality tests predict
 525 responses to a spatial-learning task in mallards, *Anas platyrhynchos*. Anim. Behav. 110, 145–
 526 154. <https://doi.org/10.1016/j.anbehav.2015.09.024>
 527 Bushby, E.V., Friel, M., Goold, C., Gray, H., Smith, L., Collins, L.M., 2018. Factors influencing
 528 individual variation in farm animal cognition and how to account for these statistically. Front.
 529 Vet. Sci. 5, 193. <https://doi.org/10.3389/FVETS.2018.00193>
 530 Campbell, D.L.M., Hinch, G.N., Downing, J.A., Lee, C., 2017a. Outdoor stocking density in free-
 531 range laying hens: effects on behaviour and welfare. Animal 11, 1036–1045.
 532 <https://doi.org/10.1017/S1751731116002342>
 533 Campbell, D.L.M., Hinch, G.N., Downing, J.A., Lee, C., 2016. Fear and coping styles of outdoor-
 534 preferring, moderate-outdoor and indoor-preferring free-range laying hens. Appl. Anim. Behav.
 535 Sci. 185, 73–77. <https://doi.org/10.1016/j.applanim.2016.09.004>
 536 Campbell, D.L.M., Hinch, G.N., Dyall, T.R., Warin, L., Little, B.A., Lee, C., 2017b. Outdoor stocking
 537 density in free-range laying hens: radio-frequency identification of impacts on range use. animal
 538 11, 121–130. <https://doi.org/10.1017/S1751731116001154>
 539 Campbell, D.L.M., Talk, A.C., Loh, Z.A., Dyall, T.R., Lee, C., 2018. Spatial Cognition and Range use
 540 in Free-Range Laying Hens. Animals 8. <https://doi.org/10.3390/ani8020026>
 541 Carazo, P., Noble, D.W.A., Chandrasoma, D., Whiting, M.J., 2014. Sex and boldness explain
 542 individual differences in spatial learning in a lizard. Proc. R. Soc. B Biol. Sci. 281, 20133275–
 543 20133275. <https://doi.org/10.1098/rspb.2013.3275>
 544 Carere, C., Locurto, C., 2011. Interaction between animal personality and animal cognition. Curr.
 545 Zool. 57, 491–498.
 546 Chielo, L.I., Pike, T., Cooper, J., 2016. Ranging behaviour of commercial free-range laying hens.
 547 Animals 6. <https://doi.org/10.3390/ani6050028>
 548 Chittka, L., Skorupski, P., Raine, N.E., 2009. Speed-accuracy tradeoffs in animal decision making.

549 Trends Ecol. Evol. 24, 400–407. <https://doi.org/10.1016/j.tree.2009.02.010>

550 Coppens, C.M., de Boer, S.F., Koolhaas, J.M., 2010. Coping styles and behavioural flexibility:
551 towards underlying mechanisms. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 4021–4028.
552 <https://doi.org/10.1098/rstb.2010.0217>

553 Dall, S.R.X., Houston, A.I., McNamara, J.M., 2004. The behavioural ecology of personality:
554 consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734–739.
555 <https://doi.org/10.1111/j.1461-0248.2004.00618.x>

556 Dawkins, M.S., Cook, P. a, Whittingham, M.J., Mansell, K. a, Harper, A.E., 2003. What makes free-
557 range broiler chickens range? In situ measurement of habitat preference. *Anim. Behav.* 66, 151–
558 160. <https://doi.org/http://dx.doi.org/10.1006/anbe.2003.2172>

559 Dougherty, L.R., Guillette, L.M., Guillette, L.M., 2018. Linking personality and cognition: a meta-
560 analysis. *Philos. Trans. R. Soc. B Biol. Sci.* <https://doi.org/10.1098/rstb.2017.0282>

561 Finkemeier, M.-A., Langbein, J., Puppe, B., 2018. Personality research in mammalian farm animals:
562 Concepts, measures, and relationship to welfare. *Front. Vet. Sci.* 5, 131.
563 <https://doi.org/10.3389/FVETS.2018.00131>

564 Fontana, I., Tullo, E., Scrase, A., Butterworth, A., 2016. Vocalisation sound pattern identification in
565 young broiler chickens. *Animal* 10, 1567–1574. <https://doi.org/10.1017/S1751731115001408>

566 Garnham, L., Løvlie, H., 2018. Sophisticated Fowl: The Complex Behaviour and Cognitive Skills of
567 Chickens and Red Junglefowl. *Behav. Sci. (Basel)*. 8, 13. <https://doi.org/10.3390/bs8010013>

568 Gosling, S.D., 2001. From mice to men: what can we learn about personality from animal research?
569 *Psychol. Bull.* 127, 45–86. <https://doi.org/10.1037/0033-2909.127.1.45>

570 Guillette, L.M., Baron, D.M., Sturdy, C.B., Spetch, M.L., 2017. Fast- and slow-exploring pigeons
571 differ in how they use previously learned rules. *Behav. Processes* 134, 54–62.
572 <https://doi.org/10.1016/j.beproc.2016.07.006>

573 Guillette, L.M., Reddon, A.R., Hurd, P.L., Sturdy, C.B., 2009. Exploration of a novel space is
574 associated with individual differences in learning speed in black-capped chickadees, *Parus atricapillus*. *Behav. Processes* 82, 265–270. <https://doi.org/10.1016/j.beproc.2009.07.005>

575 Hartcher, K.M., Hickey, K.A., Hemsworth, P.H., Cronin, G.M., Wilkinson, S.J., Singh, M., 2015.

Relationships between range access as monitored by radio frequency identification technology, fearfulness, and plumage damage in free-range laying hens. *Animal* 1–7.
<https://doi.org/10.1017/S1751731115002463>

Hegelund, L., Sørensen, J.T., Kjær, J.B., Kristensen, I.S., 2005. Use of the range area in organic egg production systems: Effect of climatic factors, flock size, age and artificial cover. *Br. Poult. Sci.* 46, 1–8. <https://doi.org/10.1080/00071660400023813>

Kesner, R.P., Dakis, M., Bolland, B.L., 1993. Phencyclidine disrupts long- but not short-term memory within a spatial learning task. *Psychopharmacology (Berl)*. 111, 85–90.
<https://doi.org/10.1007/BF02257411>

Kesner, R.P., Hunsaker, M.R., 2010. The temporal attributes of episodic memory. *Behav. Brain Res.* 215, 299–309. <https://doi.org/10.1016/j.bbr.2009.12.029>

Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M. a W., Blokhuis, H.J., 1999. Coping styles in animals: Current status in behavior and stress- physiology. *Neurosci. Biobehav. Rev.* 23, 925–935.
[https://doi.org/10.1016/S0149-7634\(99\)00026-3](https://doi.org/10.1016/S0149-7634(99)00026-3)

Larsen, H., Cronin, G.M., Gebhardt-Henrich, S.G., Smith, C.L., Hemsworth, P.H., Rault, J.L., 2017. Individual ranging behaviour patterns in commercial free-range layers as observed through RFID tracking. *Animals* 7. <https://doi.org/10.3390/ani7030021>

Lucon-Xiccato, T., Bisazza, A., 2017. Sex differences in spatial abilities and cognitive flexibility in the guppy. *Anim. Behav.* 123, 53–60. <https://doi.org/10.1016/j.anbehav.2016.10.026>

Madden, J., Langley, E., Whiteside, M., Beardsworth, C., van Horik, J., 2018. The quick are the dead: Pheasants that are slow to reverse a learned association survive for longer in the wild. *Philos. Trans. R. Soc. B Biol. Sci (This Issue)*. <https://doi.org/10.1098/rstb.2017.0297>

Mahboub, H.D.H., Müller, J., Von Borell, E., 2004. Outdoor use, tonic immobility, heterophil/lymphocyte ratio and feather condition in free-range laying hens of different genotype. *Br. Poult. Sci.* 45, 738–744. <https://doi.org/10.1080/00071660400014267>

Nicol, C.J., Caplen, G., Edgar, J., Browne, W.J., 2009. Associations between welfare indicators and environmental choice in laying hens. *Anim. Behav.* 78, 413–424.

605 <https://doi.org/10.1016/j.anbehav.2009.05.016>
 606 Nielsen, B.L., Thomsen, M.G., Sørensen, P., Young, J.F., 2003. Feed and strain effects on the use of
 607 outdoor areas by broilers. *Br. Poult. Sci.* 44, 161–169.
 608 <https://doi.org/10.1080/0007166031000088389>
 609 Nordquist, R.E., Heerkens, J.L.T., Rodenburg, T.B., Boks, S., Ellen, E.D., van der Staay, F.J., 2011.
 610 Laying hens selected for low mortality: Behaviour in tests of fearfulness, anxiety and cognition.
 611 *Appl. Anim. Behav. Sci.* 131, 110–122. <https://doi.org/10.1016/j.applanim.2011.02.008>
 612 Packard, M.G., 1995. Modulation of Multiple Memory Systems. *Test* 752–756.
 613 Panigrahy, K.K., Behera, K., Mandal, A.K., Sethy, K., Panda, S., 2017. Effect of age and sex in
 614 determining cognitive ability in Vanaraja chickens. *Br. Poult. Sci.* 58, 605–609.
 615 <https://doi.org/10.1080/00071668.2017.1373388>
 616 Patzke, N., Ocklenburg, S., van der Staay, F.J., Güntürkün, O., Manns, M., 2009. Consequences of
 617 different housing conditions on brain morphology in laying hens. *J. Chem. Neuroanat.* 37, 141–
 618 148. <https://doi.org/10.1016/j.jchemneu.2008.12.005>
 619 Pettersson, I.C., Weeks, C.A., Norman, K.I., Knowles, T.G., Nicol, C.J., 2018. Internal roosting
 620 location is associated with differential use of the outdoor range by free-range laying hens. *Br.*
 621 *Poult. Sci.* 59, 135–140. <https://doi.org/10.1080/00071668.2017.1404007>
 622 Rault, J.L., Taylor, P.S., 2017. Indoor side fidelity and outdoor ranging in commercial free-range
 623 chickens in single- or double-sided sheds. *Appl. Anim. Behav. Sci.* 194, 48–53.
 624 <https://doi.org/10.1016/j.applanim.2017.05.010>
 625 Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal
 626 temperament within ecology and evolution. *Biol. Rev.* 82, 291–318.
 627 <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
 628 Richter, S.H., Hintze, S., 2018. From the individual to the population – and back again? Emphasising
 629 the role of the individual in animal welfare science. *Appl. Anim. Behav. Sci.*
 630 <https://doi.org/10.1016/j.applanim.2018.12.012>
 631 Rufener, C., Berezowski, J., Maximiano Sousa, F., Abreu, Y., Asher, L., Toscano, M.J., 2018. Finding
 632 hens in a haystack: Consistency of movement patterns within and across individual laying hens

633 maintained in large groups. *Sci. Rep.* 8, 12303. <https://doi.org/10.1038/s41598-018-29962-x>
 634 Salvanes, A.G.V., Moberg, O., Ebbesson, L.O.E., Nilsen, T.O., Jensen, K.H., Braithwaite, V. a, 2013.
 635 Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proc. R. Soc.*
 636 280, 20131331. <https://doi.org/10.1098/rspb.2013.1331>
 637 Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: An ecological and evolutionary
 638 overview. *Trends Ecol. Evol.* 19, 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
 639 Sih, A., Del Giudice, M., 2012. Linking behavioural syndromes and cognition: A behavioural ecology
 640 perspective. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2762–2772.
 641 <https://doi.org/10.1098/rstb.2012.0216>
 642 Stadig, L.M., Rodenburg, T.B., Ampe, B., Reubens, B., Tuytens, F.A.M., 2017. Effects of shelter
 643 type, early environmental enrichment and weather conditions on free-range behaviour of slow-
 644 growing broiler chickens. *Animal* 11, 1046–1053. <https://doi.org/10.1017/S1751731116002172>
 645 Tahamtani, F.M., Nordgreen, J., Nordquist, R.E., Janczak, A.M., 2015. Early Life in a Barren
 646 Environment Adversely Affects Spatial Cognition in Laying Hens (*Gallus gallus domesticus*).
 647 *Front. Vet. Sci.* 2, 1–12. <https://doi.org/10.3389/fvets.2015.00003>
 648 Taylor, P., Hemsworth, P., Groves, P., Rault, J.-L., 2017. Ranging Behaviour of Commercial Free-
 649 Range Broiler Chickens 2: Individual Variation. *Animals* 7, 55.
 650 <https://doi.org/10.3390/ani7070055>
 651 Titulaer, M., van Oers, K., Naguib, M., 2012. Personality affects learning performance in difficult
 652 tasks in a sex-dependent way. *Anim. Behav.* 83, 723–730.
 653 <https://doi.org/10.1016/j.anbehav.2011.12.020>
 654 Vallortigara, G., 1992. Affiliation and aggression as related to gender in domestic chicks (*Gallus*
 655 *gallus*). *J. Comp. Psychol.* 106, 53–57. <https://doi.org/10.1037/0735-7036.106.1.53>
 656 Vallortigara, G., Cailotto, M., Zanforlin, M., 1990. Sex differences in social reinstatement motivation
 657 of the domestic chick (*Gallus gallus*) revealed by runway tests with social and nonsocial
 658 reinforcement. *J. Comp. Psychol.* 104, 361–367. <https://doi.org/10.1037/0735-7036.104.4.361>
 659 Weldon, K.B., Fanson, K. V., Smith, C.L., 2016. Effects of Isolation on Stress Responses to Novel
 660 Stimuli in Subadult Chickens (*Gallus gallus*). *Ethology* 122, 818–827.

661 <https://doi.org/10.1111/eth.12529>

662 White, N.M., McDonald, R.J., 2002. Multiple Parallel Memory Systems in the Brain of the Rat.

663 *Neurobiol. Learn. Mem.* 77, 125–184. <https://doi.org/10.1006/nlme.2001.4008>

664 White, S.L., Wagner, T., Gowan, C., Braithwaite, V.A., 2017. Can personality predict individual

665 differences in brook trout spatial learning ability ? *Behav. Processes* 141, 220–228.

666 <https://doi.org/10.1016/j.beproc.2016.08.009>

667 Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., Løvlie, H., 2017. A comparison of animal

668 personality and coping styles in the red junglefowl. *Anim. Behav.* 130, 209–220.

669 <https://doi.org/10.1016/j.anbehav.2017.06.024>

670 Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., Sorato, E., Løvlie, H., 2018. The relationship

671 between learning speed and personality is age- and task-dependent in red junglefowl. *Behav.*

672 *Ecol. Sociobiol.* 72. <https://doi.org/10.1007/s00265-018-2579-2>

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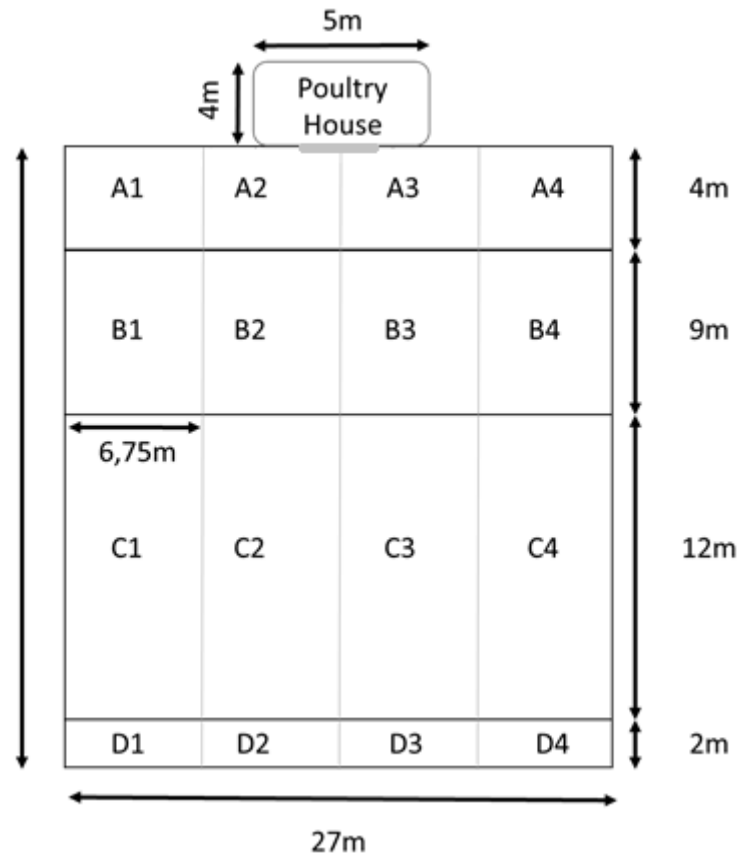


Figure 1 – Schematic figure of the poultry house and the outdoor range divided virtually in 16 different zones. Zones A to C were gradually longer, except for zone D (A = 4m, B = 9m, C = 14m, and D = 2m). This range division allowed a more heterogeneous distribution of the individuals and to differentiate chickens who ranged near the poultry house from those who went further on the range. The pop-hole giving access to the outdoor range is placed between zone A2 and A3 (grey bar).

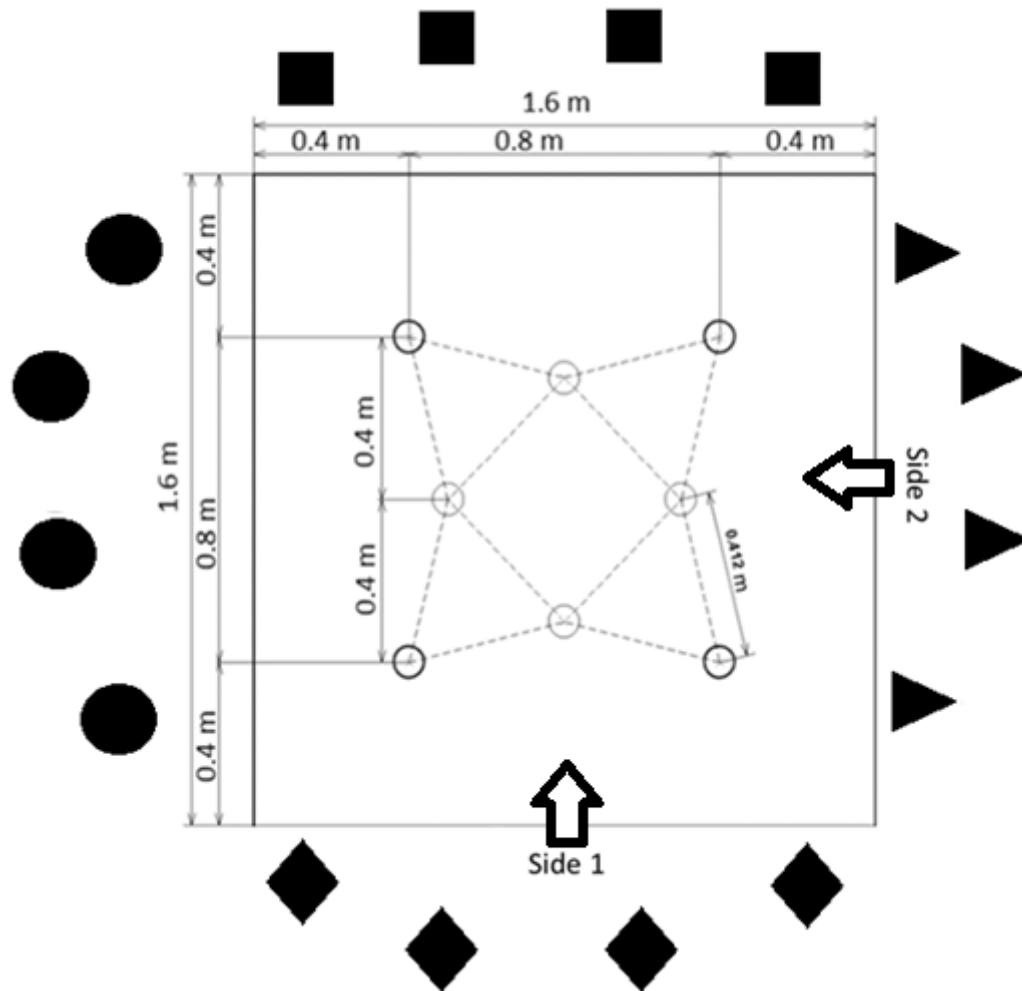


Figure 2 – Schematic figure of the apparatus used to test spatial memory. Circles represent the eight cups within the arena where mealworms were placed as a reward. Chickens could enter the arena from two different sides (dark arrows). Black patterns around the arena walls and on the surrounding curtain were available to chickens to rely on spatial guidance.

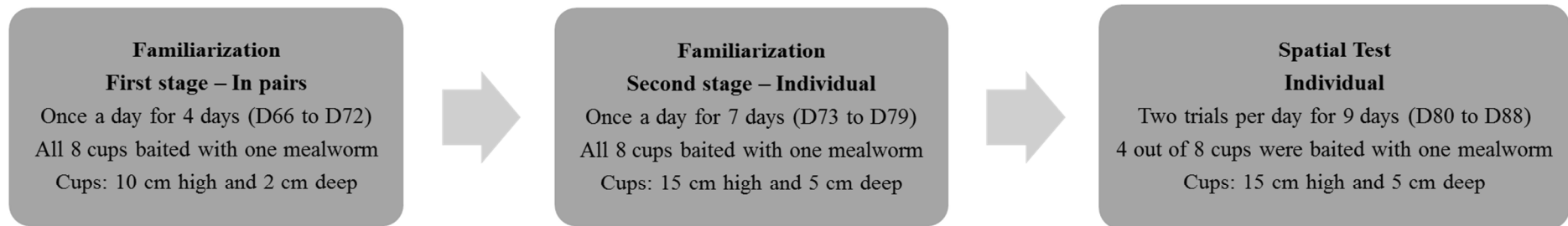


Figure 3 - Summary of the spatial memory task, describing each of the phases, and trials within phases, the birds underwent from familiarization to spatial test.

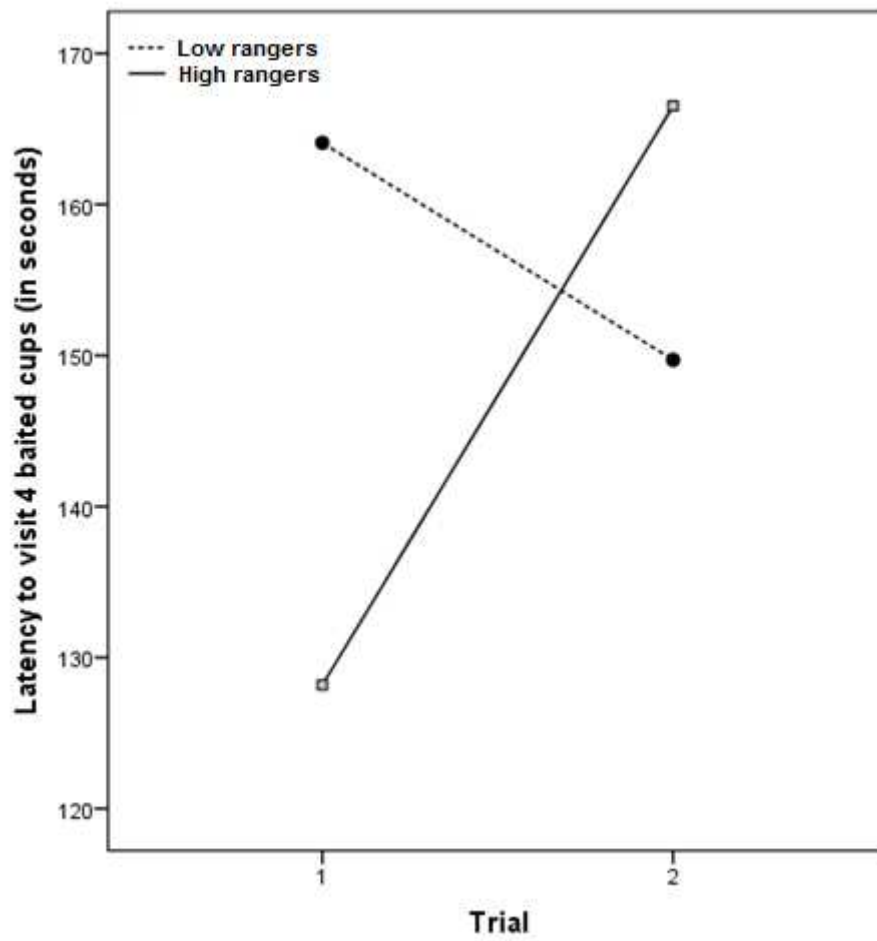


Figure 4 - Latency to visit four baited cups (in seconds) from trial 1 to trial 2 during the spatial training for low ranger (N = 13) and high ranger (N = 11) chickens. The location of the baited cups was permanent for all individuals and trials. Data are presented as estimated marginal means.

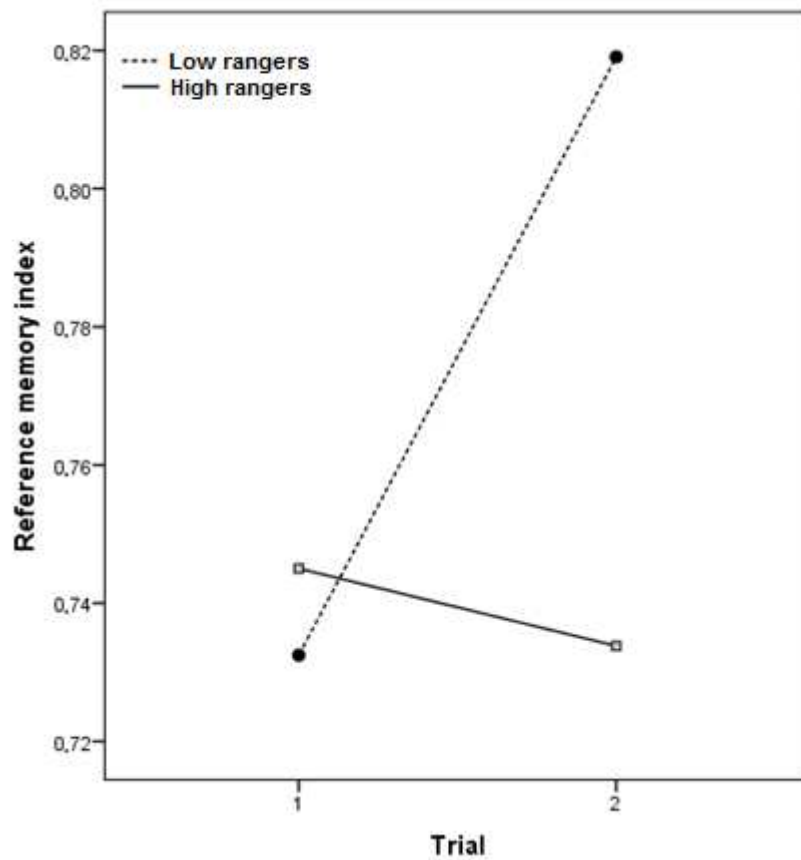


Figure 5 - Reference memory index from trial 1 to trial 2 during the spatial test for low ranger ($n = 13$) and high ranger ($N = 11$) chickens. This reference memory index measures the chicken's ability to discriminate between baited cups and non-baited cups. The index results are between 0 and 1, with 1 being the best possible score. Data are presented as estimated marginal means.

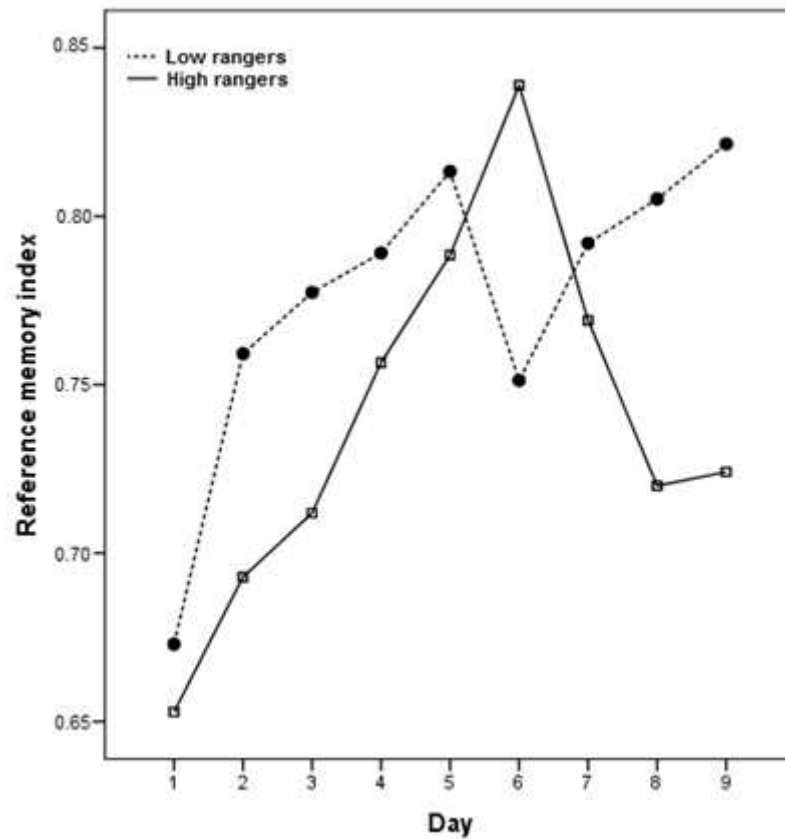


Figure 6 - Reference memory index over days of the spatial training for low ranger (N = 13) and high ranger (N = 11) chickens. This reference memory index measures the chicken's ability to discriminate between baited cups and non-baited cups. The index results are between 0 and 1, with 1 being the best possible score. Data are presented as estimated marginal

Table 1 - Number of range visits and distance index for 113 chickens (males and females) and 30 male chickens who underwent the spatial memory task according to their ranging behavior level: high rangers (n=15) and low rangers (n=15). Data are presented as mean \pm SD.

	Number of range visits	Distance index
Males (n=51)	4.33 \pm 2.71	24.70 \pm 24.77
Females (n=62)	3.38 \pm 2.37	15.16 \pm 15.27
High rangers (n=15)	6.8 \pm 2.30	42.80 \pm 34.49
Low rangers (n=15)	2.8 \pm 0.77	16.68 \pm 8.64