

Individuals in larger groups are more successful on spatial discrimination tasks

Ellis J. G. Langley*, Jayden O. van Horik, Mark A. Whiteside, Joah R. Madden

Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter, U.K.

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To understand how natural selection may act on cognitive processes, it is necessary to reliably determine interindividual variation in cognitive abilities. However, an individual's performance in a cognitive test may be influenced by the social environment. The social environment explains variation between species in cognitive performances, with species that live in larger groups purportedly demonstrating more advanced cognitive abilities. It also explains variation in cognitive performances within species, with larger groups more likely to solve novel problems than smaller groups. Surprisingly, an effect of group size on individual variation in cognitive performance has rarely been investigated and much of our knowledge stems from impaired performance of individuals reared in isolation. Using a within-subjects design we assayed individual learning performance of adult female pheasants, *Phasianus colchicus*, while housed in groups of three and five. Individuals experienced the group sizes in a different order, but were presented with two spatial discrimination tasks, each with a distinct cue set, in a fixed order. We found that across both tasks individuals housed in the large groups had higher levels of success than individuals housed in the small groups. Individuals had higher levels of success on their second than their first task, irrespective of group size. We suggest that the expression of individual learning performance is responsive to the current social environment but the mechanisms underpinning this relationship require further investigation. Our study demonstrates that it is important to account for an individual's social environment when attempting to characterize cognitive capacities. It also demonstrates the flexibility of an individual's cognitive performance depending on the social context.

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A compelling and relatively recent approach to understanding the evolution of cognition is to determine the causes and consequences of individual differences in cognitive performance (Thornton & Lukas, 2012). The social environment may be one cause of individual variation in cognitive performance as this governs individuals' access to resources (Wilson, 1975), the stress they experience (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008) and their predation risk (Pulliam, 1973). Although living in a social group can bring benefits, it may also impose a cognitive demand in terms of monitoring and maintaining social relationships. Indeed, brain size and cognitive abilities may have evolved in response to the social environment (the social intelligence hypothesis, Byrne & Whiten, 1988; Call, 2001; Cheney, Seyfarth, & Smuts, 1986; Dunbar, 1998; Humphrey, 1976; Seyfarth & Cheney, 2002; Taborsky &

Oliveira, 2012). Group size is often used to quantify the social environment. Larger groups are likely to have greater fluctuations in composition, as subgroups develop and dissipate and/or there are changes in individual motivations and social status. To cope with this unpredictability, species that live in larger groups are reported as having greater levels of behavioural flexibility (corvids, Bond, Kamil, & Balda, 2007; primates, Amici, Aureli, & Call, 2008) and are more competent on social cognition tasks (lemurs, MacLean et al., 2013), relative to sister taxa that live in smaller groups.

In contrast to our knowledge of how sociality is related to cognition across species, little is known about how the social environment affects individual cognitive performance within species. Within a species, larger groups are more likely than smaller groups to solve novel problems (great tits, *Parus major* and blue tits, *Cyanistes caeruleus*, Morand-Ferron & Quinn, 2011; house sparrows, *Passer domesticus*, Liker & Bókony, 2009). This may simply be because more individuals are present to solve a problem and/or larger groups are more likely to contain individuals with the required skills to solve it (Liker & Bókony, 2009; Morand-Ferron &

* Correspondence: E.J.G. Langley, Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter EX4 4QG, U.K.

E-mail address: ejgl201@exeter.ac.uk (E. J. G. Langley).

Quinn, 2011). Alternatively, different rates of problem solving between group sizes could be related to the costs and benefits of group living. Reduced predation risk in larger groups may allow individuals to invest more time (because of less vigilance, Beauchamp, 2015; Elgar, 1989; Roberts, 1995) and therefore energy in acquiring and processing novel information. It could also be that increased competition, associated with larger group sizes, causes individuals to adopt alternative behavioural strategies, such as innovation, to acquire necessary resources (Reader & Laland, 2002; Thornton & Samson, 2012).

Despite demonstrable relationships between the social environment and cognitive performances at the species and group level, the effect of the social environment on individual cognitive performance has seldom been explored. Individuals reared in isolation have lower levels of neurogenesis (prairie voles, *Microtus ochrogaster*, Fowler, Liu, Ouimet, & Wang, 2002; mice, Branchi et al., 2006; zebra finches, *Taeniopygia guttata*, Adar, Lotem, & Barnea, 2008; Pravosudov & Omanska, 2005) and are reported to have impaired learning performance in later life (reversal learning in rats, *Rattus norvegicus*, but not acquisition learning or spatial memory, Schrijver, Pallier, Brown, & Würbel, 2004; spatial learning in rats, Holson, 1986; Juraska, Henderson, & Muller, 1984; discrimination learning in rhesus macaques, *Macaca mulatta*, Harlow, Dodsworth, & Harlow, 1965), compared with individuals reared socially (but see for no effect: associative learning in chickens, *Gallus gallus domesticus*, Goerlich, Nätt, Elfving, Macdonald, & Jensen, 2012; spatial learning in skinks, *Egernia striolata*, Riley, Noble, Byrne, & Whiting, 2016). These studies highlight the effects of social stimulation on neural development and function, during which time, however, there may be other ontogenetic factors to consider (Hall, 1998). Outside of critical developmental periods, the social environment may still cause structural changes to the brain (van Praag, Kempermann, & Gage, 2000); young rhesus macaques housed in larger groups were found to have increased grey matter compared with those housed in smaller groups, after approximately 4 months (Sallet et al., 2011). Although such studies demonstrate that an individual's historical social environment may have effects on neural development and cognitive performance, they cannot reveal whether an individual's current social environment influences their cognitive performance. Evidence for this would suggest that the expression of cognitive abilities is subtly adjusted in response to changing social circumstances. Such flexibility would have important implications both for the interpretation of interindividual differences in cognitive performance and for understanding how natural selection may act on such differences depending on the social environment an individual inhabits.

One recent study revealed that an individual's current social group size is related to general cognitive performance. In free-ranging Australian magpies, *Cracticus tibicen dorsalis*, a correlation between cognitive performance, given as a composite score across a battery of four tasks, and group size was seen from early in life through to adulthood (Ashton, Ridley, Edwards, & Thornton, 2018). Ashton et al. (2018) suggested that the challenges of living in larger groups promote cognitive development. However, it is difficult to separate genetic from social explanations for differences in cognitive performances: individual magpies typically live in only one stable group so their flexibility in response to changing social environments is difficult to establish under natural conditions. Manipulations of the social environment are necessary to disentangle these factors.

We explored the effects of the current social environment on learning performance by manipulating the group size of wild-caught captive pheasants, *Phasianus colchicus*, and assessing their learning performances on two spatial discrimination learning tasks.

In the wild, pheasants live in variable group sizes throughout the year, inhabiting large, same-sex groups from September to February with a gradual shift to single-male, multiple-female groups (harems) from March to July for breeding (Robertson, 1997; Whiteside et al., 2018). These harem sizes range from two (one male and one female) to 25 (Robertson, 1997), with an optimal group size of 3.7 for collective predator detection (Whiteside, Langley, & Madden, 2016). If the social environment affects cognitive performance, in a way synonymous with that seen across species and in isolated-rearing experiments, we predict that learning performance will be enhanced in larger groups, compared to smaller groups. Critically, by manipulating the group size of adult female birds, we were able to test causality of the relationship.

METHODS

Study Site, Subjects and Housing

The study was conducted from March to June 2016 at North Wyke Rothamsted Research Farm, Devon, U.K. (50°77'N, 3°9'W). We captured pheasants from the wild using baited funnel traps and housed individuals in one of 10 identical pens (4 × 8 m), in visual but not auditory isolation from each other. All pheasants had access to commercial wheat and water ad libitum and each pen contained elevated perches, branch shelters and two refuge areas (Fig. 1).

Although all birds were caught from the wild, their origins differed. Of the 30 females included in this study, we had reared eight of the females in the previous year for the first 10 weeks of life. During this period they were subject to a battery of cognitive tasks, before being released into the wild (van Horik, Langley, Whiteside, & Madden, 2016). The other 22 individuals were birds of unknown rearing history; however, it is likely that they were also reared in captivity, released into the wild and migrated to the site from neighbouring commercial shoots. All birds were ≥10 months old, indicated by their body size and the time of year. Individuals were identifiable by numbered patagial wing tags, either attached during rearing, or upon capture if they were not from our released birds.

Group Sizes

Captured birds were randomly assigned to a breeding group. Each group consisted of a single male with either two females

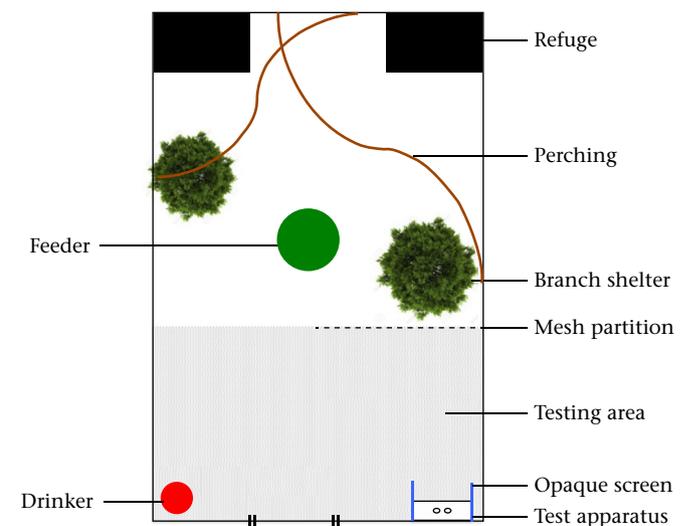


Figure 1. Aerial view of a pen. The mesh partition could be extended to cover the width of the pen to allow testing of individuals without disturbance from conspecifics.

(small group) or four females (large group). There were five replicates of each group size. While housed in these groups, birds were trained to the test procedures. Training lasted 3 weeks (see *Cognitive test apparatus and training*). The task was voluntary and consequently we had a different number of participating females from each group size. For small groups, we tested the cognitive performance of four females, each from a separate pen. For large groups, we tested the cognitive performance of 13 females from all five pens.

We switched all participating females to a pen with the alternate group size after they had completed testing on the first task. Each female was housed with at least one familiar female from her previous group. Because the majority of females that participated in the first task were from large groups, during the second training and test period there were seven pens containing small groups, each with a single participating female and one nonparticipating female; three pens contained large groups (four females), two with two participating females and two nonparticipating females and one with four nonparticipating females. Individuals were left to habituate to their new group composition for 3 nights and 2 days before being tested on the second cognitive task. Four females in a large group came from two pens. The 13 females now in a small group came from seven pens.

Cognitive Test Apparatus and Training

The test apparatus (38 × 14 cm and 4 cm high), located in the test area of the pen (Fig. 1), was situated between two opaque screens so that the apparatus could only be approached and viewed by a bird 'front-on' and prevented conspecifics viewing the box while the focal bird was being tested. Situated on the top of the test apparatus were two identical circular wells (diameter 2.8 cm), 1.2 cm apart, both concealed by a layer of opaque crepe paper. One of the wells contained a mealworm food reward (correct) and the other was blocked with a wooden bung (incorrect).

We trained individuals to voluntarily approach the test apparatus when a visual cue (black and white swirl pattern) was displayed on the wall of the pen accompanied by the experimenter tapping and scratching the apparatus to attract a bird. The experimenter was located behind a screen and not visible to the focal individual while it was interacting with the apparatus. Females that reliably interacted with the apparatus were trained to peck 'open' the crepe paper that covered the wells. Habituation to our presence, the test apparatus and the procedures is a time-consuming process with wild birds. To 'speed up' this process we reduced handling by only moving the birds upon capture from the wild and for the change in group size, thus improving their likelihood of participating. Participating individuals were given equal exposure to the apparatus during training.

Cognitive Testing

Individuals were tested on two distinct spatial tasks that differed only in the positions of the wells. The two tasks exactly matched, in layout and affordances, those that we had presented to chicks in the previous year. For Task 1, the top–bottom discrimination, the wells were arranged vertically and the top well was rewarded. For Task 2, the left–right discrimination, the wells were arranged horizontally and the left well was rewarded. Testing began at 0830 hours from Monday to Friday and we chose at random which pen to begin testing each day. The order in which individuals were tested was dictated by the birds' motivation to interact with the apparatus. Testing only proceeded if an individual was alone at the apparatus, as we wanted to avoid any effects of social learning. The opaque screens helped to mitigate this but if

another individual came within 2 m of the focal individual while at the test apparatus, the visual cue and apparatus were removed, and testing ceased. Testing was resumed once this individual was alone. On four occasions it proved difficult to test the focal individual of a large group because multiple individuals were motivated to participate at the same time. In these instances, we ushered the focal individual into the test area of the pen and put up a temporary mesh partition that covered the width of the pen. This allowed the focal individual to be tested without being disturbed by conspecifics and individuals were allowed as much time as necessary to complete the task. As this rarely occurred, we did not include this variable in the analyses; however, the use of the temporary partition did not affect the behaviour of the focal bird, as motivation to participate in the task remained high. It was not necessary to food deprive birds prior to testing as mealworms are a highly valued food reward that individuals were motivated to retrieve.

For each task, each individual received a single test session per day, consisting of 20 presentations of a pair of wells, over 5 days, producing 100 trials per task. Individuals were only allowed to make one choice per pair of wells. When an individual chose the incorrect well first, indicated by pecking at the crepe paper of the well, the wells were removed and a new binary choice was revealed. When an individual chose correctly we allowed the focal individual to consume the food reward before revealing a new binary choice. Therefore, the costs of choosing incorrectly constituted pecking at a blocked well and not retrieving a mealworm reward for that trial. On day 1 of testing, we checked whether an individual's first 20 trials revealed a pre-existing 'position bias' (Mackintosh, 1974) to a particular well. For Task 1, two females (both in a large group) had biases (>80%) for the top well (furthest from the bird), so these were tested with a rewarded bottom well later that day and for the remainder of testing. For the remaining females, the top well was rewarded for the rest of testing and this remained consistent with our chick cognitive testing (as part of a separate experiment). For Task 2, a single female (within a small group) had a bias for the left well; therefore, she was tested with a rewarded right well later that day and for the remainder of testing. The remaining females were tested with the left well rewarded for the rest of testing because this maintained consistency with our chick cognitive testing. All other birds showed no strong pre-existing biases (<75%) on either task. The first 20 trials that revealed a bias for three individuals were excluded from further analysis. On subsequent days, both biased and unbiased birds all received 20 trials per day. Task presentation was not counter-balanced and hence individuals received tasks in the same order.

Statistical Analysis

All analyses were conducted in R v.3.1.1 (R Core Team, 2015). We used the lme4 package (Bates, Machler, Bolker, & Walker, 2014) to fit a generalized linear mixed model (GLMM) with a binomial error structure to assess whether learning performance (correct/incorrect) is explained by an individual's group size. Mixed models cope relatively well with unbalanced designs (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The model included 'Trial (11–100)', 'Group size (small/large)', 'Task (1 = top–bottom/2 = left–right)', 'Start performance (percentage correct of first 10 trials)' and 'Origin (known/unknown bird)' as explanatory factors. A two-way interaction between group size and trial was included to assess whether group sizes differed in their 'rate' of learning. We defined rate of learning as the speed at which individuals increase their probability of making a series of correct choices with increasing trial number. A main effect of group size indicates a difference between the group sizes in the 'accuracy' of learning. We defined accuracy as overall performance by the end of the task, inclusive of

performance on all trials. The trial variable consisted of trials 11–100 because the first 10 trials were removed and included in the ‘start performance’ explanatory variable. The latter is the percentage of trials that were correct during the first 10 test trials and this controlled for differences in start performances between individuals, which we felt was important because we did not train to criterion and individuals naturally begin tasks at different levels of inherent preference. We used the percentage of the first 10 trials correct during testing because it allowed us to acquire an informative measure of initial bias to a well location, but it is also a low enough number of trials to allow individuals time to learn the affordances of the task and to avoid having to remove many data from the response variable. The inclusion of Task accounted for the difference in task type and whether it was the first or second task the individual had experienced, as individuals were presented with the two tasks in a fixed order. The inclusion of Origin accounted for whether we had reared the individual and they had previously experienced these cognitive tasks as a chick; seven individuals were reared by us (known), 10 were not (unknown). To facilitate convergence, the trial variable was standardized ($(X - \mu)/\sigma$) which resolved the issue. The model estimates presented are from the model with standardized trial variable. We used a random intercept and random slopes model by nesting trial within bird as a random effect. This allowed individuals to vary in their rate of learning performance. The minimum adequate model was reached by backward stepwise removal of nonsignificant variables, determined using the ‘drop1’ function in the base package. To visualize the data we plotted curves drawn using a binary logistic regression model in the ggplot2 package (Wickham, 2009) for each group size and each task. As the group sizes differed in their starting performances, we conducted a post hoc analysis to test for a difference between the group sizes. We did this for each task using a Wilcoxon rank-sum test due to the unbalanced sample sizes.

Ethical Note

During capture, traps were checked at least three times a day. All captive bird husbandry adhered to the DEFRA Code of Practice (DEFRA, 2009). Birds were subject to minimal handling. Participation in cognitive tests was voluntary and experimenters were concealed from view of the birds, keeping stress to a minimum. Birds were held in captivity for 3 months, after which they were released back onto the site. All work was approved by the University of Exeter Psychology Ethics Committee and the work was conducted under Home Office licence number PPL 30/3204 to J.R.M.

RESULTS

Individuals differed in the accuracy of their learning performances according to the size of group they were tested in (GLMM: $X^2_1 = 10.475$, $P < 0.002$), with individuals in larger groups more likely to choose correctly than individuals in smaller groups (Table 1, Figs. 2 and 3). There was a significant effect of trial (GLMM: $X^2_1 = 50.138$, $P < 0.001$), indicating learning (Table 1, Fig. 3), but no interaction between trial and group size, indicating no difference between the group sizes in learning rate (GLMM: $X^2_1 = 0.267$, $P = 0.605$). There was a significant effect of task (GLMM: $X^2_1 = 53.871$, $P < 0.001$; Table 1, Fig. 2), with higher levels of performance on Task 2 (left–right task) than Task 1 (top–bottom task; Table 1, Fig. 2). We controlled for variation in starting performances and found this was also a significant predictor of learning performance (GLMM: $X^2_1 = 18.726$, $P < 0.001$), with individuals that made more correct choices in their first 10 trials, having a higher level of performance for the remainder of the task. The birds’ origin (known/unknown) was not related to their learning performance

Table 1

Minimum adequate model of a generalized linear mixed model (random slopes and random intercepts) on factors affecting learning performance (Correct 1 yes/0 no) on spatial discrimination tasks for females while housed in two different group sizes

Variable	Estimate	SE	95% Confidence interval		Odds ratio
Intercept	0.234	0.141			
Group size					
Large	0.386	0.121	0.130	0.643	1.471
Task					
2 = left–right	0.888	0.124	0.625	1.151	2.430
Trial	0.797	0.050	0.691	0.903	2.219
Start performance	1.142	0.141	0.843	1.441	3.133

The analysis included 17 individuals that performed 100 trials on each task. The model was fitted with a log-link function.

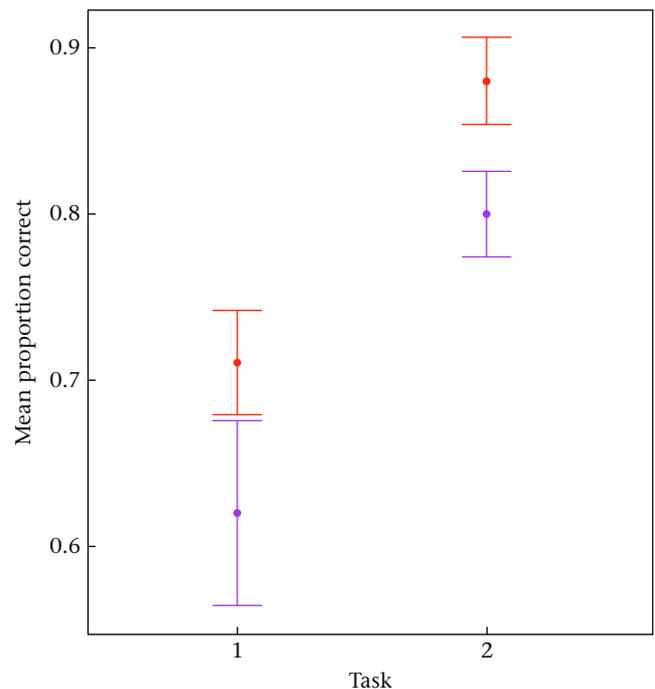


Figure 2. Mean proportion of correct choices made in 90 trials (after first 10 trials removed), by small (purple) and large (red) group sizes on spatial discrimination task 1 (dashed lines) and task 2 (solid lines). Error bars indicate standard errors.

(GLMM: $X^2_1 = 0.741$, $P = 0.389$). The inclusion of this variable also accounts for whether individuals had experienced these tasks as chicks.

Post hoc tests revealed that the group sizes differed significantly in their starting performances and this was found for both Task 1 (Wilcoxon rank-sum test: $W = 289$, $N = 17$, $P < 0.001$) and Task 2 (Wilcoxon rank-sum test: $W = 289$, $N = 17$, $P < 0.001$).

DISCUSSION

We provide the first evidence for a causal effect of the social environment, in terms of group size, on individual cognitive performance. Across two spatial discrimination tasks, individuals housed in large groups performed with higher accuracy than individuals housed in small groups. This was independent of previous experience with the test apparatus during rearing. Generally, individuals improved on the second task irrespective of group size. By exposing the same individuals to two different social environments we have demonstrated that not only is variation in the accuracy of

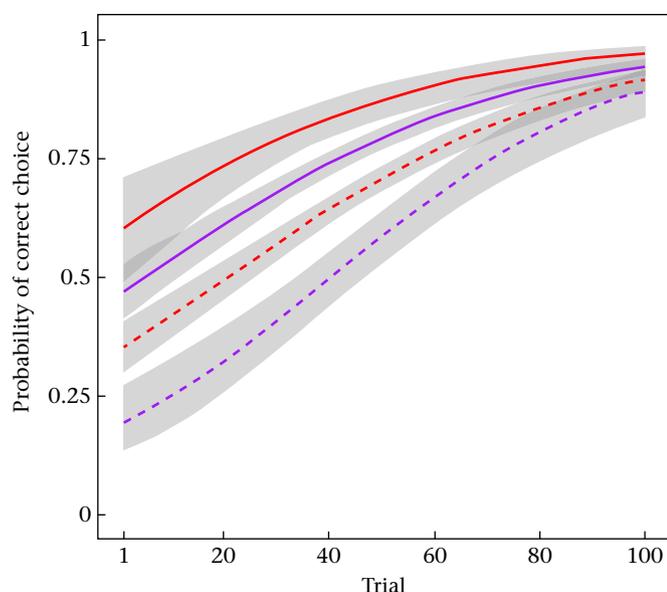


Figure 3. Predicted probability curves drawn using a binary logistic regression model (glm) on performance of females on Task 1 (dashed lines) and Task 2 (solid lines), when in small (purple) and large (red) groups. Grey shaded areas represent 95% confidence intervals.

learning performance predicted by an individual's group size, but also that learning performance is variable and responsive to short-term changes in the social environment.

Individuals housed in smaller groups were more biased towards the incorrect well in their starting performances, with a lower percentage of correct choices in the first 10 trials compared with those in larger groups. This was evident for both tasks. As individuals were randomly assigned to their initial group size and experienced both group sizes, we suspect that these differences are not simply due to individual variation. We propose that the effect of group size on cognitive performances occurs in very early trials and because the group sizes did not differ in their rate of learning, individuals in both group sizes improved at a similar speed; owing to the initial poor performance of small groups, however, the overall accuracy of small groups remained lower than that of large groups by the end of the task. We controlled for this difference in starting biases statistically by including starting performance as an explanatory variable; even so, group size remained a significant predictor of learning performance.

Learning performance was also dependent on the type of task and/or greater experience with the task apparatus. Tasks were presented to individuals in the same order, so we are unable to determine whether learning performance increased during the second task due to generalized learning for the task affordances, or because of the different cues that were used, as perhaps pheasants are better able to distinguish between horizontally positioned than vertically positioned cues. This is an interesting question for future research, but it was not critical for understanding the relationship between group size and learning performance, as large groups performed more accurately overall.

Our results complement findings in Australian magpies, in which group size and a general intelligence factor are correlated (Ashton et al., 2018). Critically, we randomly allocated our pheasants to experimental groups and females were tested in both group sizes, thus demonstrating a direct effect of the social environment on individual variation in cognitive performances. We suggest four (nonexclusive) mechanisms to explain this relationship.

The group size-related differences in learning performance might have been related to differences in the level of attention they could direct at the task. One benefit of group living is collective vigilance, which allows individuals to reduce their own vigilance, in favour of other behaviours that demand their attention (Beauchamp, 2015; Elgar, 1989; Roberts, 1995). We have previously demonstrated that female pheasants in large groups spend a lower proportion of their time being vigilant than females in small groups (Whiteside et al., 2016). Individuals had the opportunity to spend as much time as necessary at the apparatus to complete the task and although we did not record the duration of time spent interacting with the task each day, it is possible that individuals in large groups spent longer at the task apparatus due to less investment in vigilance and this benefited their task performance. Individuals that take longer to complete cognitive tasks perform with higher accuracy (speed–accuracy trade-off, Chittka, Skorupski, & Raine, 2009; Trimmer et al., 2008). Additionally, individuals in the large group may have not only spent longer completing the task but also invested more 'quality' time, paying greater attention to the task due to fewer vigilance bouts. In pipefish, *Syngnathus typhle*, when predator threat was increased, male mate choice discrimination abilities were hindered (Berglund, 1993). This was suggested to be because less attention was paid to the mate choice task, thus resulting in random choices (Guilford & Dawkins, 1987). We speculate that female pheasants in the larger groups may have had fewer 'interruptions' for vigilance bouts and paid more attention to the learning task, thus facilitating their discrimination/learning abilities. Of course, large groups could also provide more sources of distraction involving social interactions between the members which could retard learning performances. The difference between individuals when housed in small and large groups in the overall time taken to complete the task and the number of vigilance 'bouts' and other social interruptions during engagement with the task are interesting avenues to consider for future work.

Second, the differences in cognitive performance that we observed may reflect deliberate changes in foraging strategies, manifested in their test performance. Foraging strategies are plastic and readily respond to changes in the level of resources (Belmaker, Motro, Feldman, & Lotem, 2012; Morand-Ferron & Giraldeau, 2010). Group size affects the level of resources available and in a larger group it may be more rewarding to forage independently, that is, be a 'producer' (Barnard & Sibly, 1981). Producers are predicted to have better individual learning performances because their behaviour is reliant on personal information rather than social information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Giraldeau, Valone, & Templeton, 2002). This has been demonstrated in house sparrows: learning performance on a colour discrimination task was positively related to the tendency to forage as a producer while in a group (Katsnelson, Motro, Feldman, & Lotem, 2008). Although learning performance of the sparrows was measured prior to social interactions, Katsnelson et al. (2008) suggested that these two factors (learning performance and tendency to 'produce') may be associated through shared mechanisms. Therefore, when pheasants were housed in the large group, they may have adopted a 'producer' foraging strategy and, by association, demonstrated higher levels of learning performance.

Third, an individual's learning performances may have differed between the group sizes due to differences in stress. In larger groups there is increased within-group competition for resources and this may act as a stressor (Milinski & Parker, 1991). Stress is known to affect performance on cognitive tasks, with a bell-shaped relationship between stress and success often reported (Yerkes–Dodson law; Mendl, 1999). For example, chronic levels of corticosteroids have detrimental effects on performance on spatial learning tasks (kittiwakes, *Rissa tridactyla*, Kitaysky, Kitaiskaia, Piatt,

& Wingfield, 2003), whereas intermediate or short-term levels of stress improve spatial memory performance (Belding's ground squirrels, *Spermophilus beldingi*, Mateo, 2014; rats, Luine, 1996). Although our pheasants had unlimited access to wheat, there may have been increased competition for favourable foraging patches while in the bigger group or other social stressors. Such moderate stresses could have improved their learning performances.

Finally, the individuals may have varied in their learning performances according to their group size due to differences in the levels of social stimulation they experienced. Social stimulation, along with inanimate stimulation, are combined to form environmental enrichment (Rosenzweig, Bennett, Hebert, & Morimoto, 1978), which causes behavioural (Hebb, 1949) and neurological changes (at least in mammals; see van Praag et al., 2000 for a review). Neural mechanisms are associated with learning and memory (Greenough, 1976). We suggest that individuals experience greater social stimulation when housed in the large group due to having more individuals to interact with and this causes alterations to neural structures, which in turn has a positive effect on their individual learning performance. However, it is unknown whether brain plasticity in response to social stimulation can occur over a short period of time, as demonstrated in our study, whether similar neural changes to those that occur in mammals also occur in birds and how long the effects of such social enrichment may last (van Praag et al., 2000).

Conclusion

We have shown that the social environment affects the expression of learning ability, and this reveals an intraindividual flexibility in cognitive performance. This mirrors the correlative patterns we see between and within species, with those living in larger groups outperforming those in smaller groups. However, our manipulation demonstrates that such differences may not be just be fixed strategies, inextricably linked to the mean group size in which the individual lives, but rather a more facultative rapid response to a changing social environment. The potential mechanisms underpinning the higher levels of performance for individuals in the larger group are likely to be related to the benefits and costs of group living, divergences in foraging strategy and/or changes in brain plasticity following increased social interactions. If these processes are present in the wild and female pheasants are more efficient at learning the location of a rewarded stimulus when in a larger harem, compared with when in a smaller group, this could have important implications for the optimal harem size for a female when she chooses which harem to join. We suggest that it is critical to consider an individual's current social environment when characterizing causes of individual variation in cognitive performances and that the effects of their social environment on cognitive performance may be transitory and relatively fast acting.

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