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Individuals in larger groups are more successful on spatial discrimination tasks

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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.

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 &

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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, Elfwing, 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

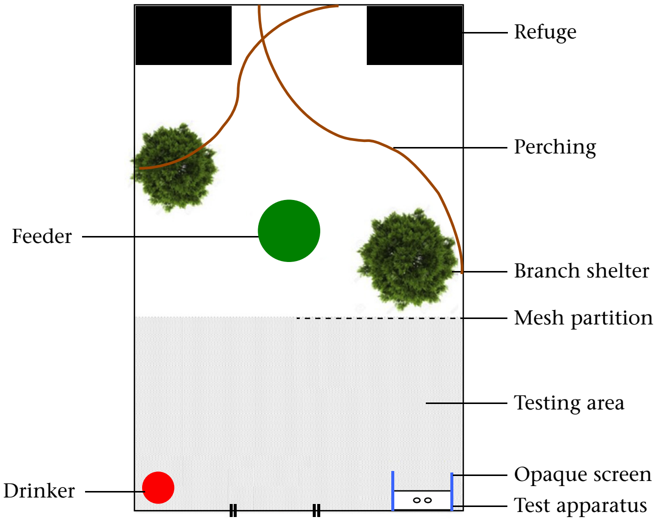

Figure 1. Aerial view of a pen. The mesh partition could be extended to cover the width of the pen to allow testing of individuals without disturbance from conspecifics.