ORIGINAL ARTICLE

Group size and associative learning in the Australian magpie (*Cracticus tibicen dorsalis*)

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Abstract Group living can present unique challenges that may require individuals to possess cognitive skills, such as the ability to recognise group members and maintain relationships with specific individuals. These skills may be particularly important for animals that live in large groups, because the intricacies of social life may become more complex when more individuals are involved. Previous research has found that species with regular social interactions tend to show elevated cognitive performance relative to those that rarely interact, yet intraspecific variation in performance among individuals in social groups of varying size is rarely explored. We investigated the relationship between the ability to solve an associative learning task and group size among individuals of a free-living, social bird, the Australian magpie (*Cracticus tibicen dorsalis*). Individuals varied in their likelihood of interacting with and solving the task. Individuals from larger groups were more likely to approach the associative learning task, suggesting that group size influences individual propensity to attempt a novel task. However, group size did not influence the likelihood that individuals solved the task. Rather, age had an important effect; adults were more likely to solve the association task than juveniles. Our finding that free-living individuals occurring in large social groups were more likely to interact with a novel task suggests that group size may affect differences in performance at a cognitive task within a species.

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Significance statement Research suggests that there is considerable variation in cognitive ability among species from different social settings, yet variation among individuals that differ in sociality is yet to be sufficiently explored. We investigated variation in associative learning among individuals in social groups of varying size in a wild population of magpies, a cooperative bird species. Presenting a colour association foraging task to individuals revealed that individuals from larger groups were more likely to attempt to solve the task. Additionally, older individuals were more successful at solving the task, suggesting that both social and individual differences contribute to associative learning ability. These findings present a significant contribution to understanding cognitive variation among individuals, because social differences, in particular group size, may determine the opportunity that an individual has to acquire the skills and behaviours necessary for overcoming social and ecological challenges.

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Animals that live in stable social groups may face significant cognitive demands. For example, individuals may benefit from recognising suitable cooperative partners, monitoring other group members, responding to the behaviour of others and assigning value to specific relationships in order to maximise the benefits of group living (Dunbar 1998; Melis et al. 2006; Croney and Newberry 2007; Silk 2007; Brosnan et al. 2010). Cognition refers to the storage and organisation of information and its application in learning, memory, decision-making and problem-solving and may therefore provide individuals with the ability to overcome social challenges (Croney and Newberry 2007; Shettleworth 2009; Rowe and Healy 2014). Research with highly social animals has revealed corresponding increases in cognitive ability with increased levels of sociality. For example, highly social birds

have been shown to consistently outperform their relatively non-social sister taxa in cognitive tests set to reflect the ability to monitor and assess social relationships (Dunbar 1998; Bond et al. 2003). Thus, the degree of phylogenetic relatedness or similarity in niche occupation among species does not necessarily determine individual performance in a cognitive task, but the demands of a social lifestyle might (Bond et al. 2003).

Evidence for a possible relationship between cognition and sociality is apparent throughout the literature (Drea 1998; Bond et al. 2003; Sol et al. 2008; Morand-Ferron and Quinn 2011; Sallet et al. 2011), yet studies investigating the potential causes of *individual* variation in cognition in wild animals are lacking (Thornton et al. 2014; Thornton and McAuliffe 2015). However, a recent study demonstrated that captive macaques (*Macaca mulatta*) that were raised in larger groups had a larger brain size showed greater neuronal development and maintained more harmonious relationships as adults than those from smaller groups, indicating a possible effect of group size on the cognitive development of individuals (Sallet et al. 2011). Similarly, a study on zebra finches (*Taeniopygia guttata*) demonstrated a positive association between sociality and neuronal architecture, such that highly social individuals had more new neurons compared to less social individuals (Lipkind et al. 2002; Barnea et al. 2006; Adar et al. 2008). Individuals from stable, social groups may be more likely to establish and maintain hierarchies, have a greater need to distinguish cooperators from cheats and identify kin (Croney and Newberry 2007; Weib and Scheiber 2013). Group-living individuals may therefore develop sophisticated cognitive skills in order to effectively interpret and communicate information in complex social situations such as group navigation, territory defence and group foraging (Scace et al. 2006; Boeckle and Bugnyar 2012; Thornton and Samson 2012). These processes are likely to become more difficult in larger groups comprising more individuals, and thus, individuals in larger groups may be more likely to exhibit enhanced and more robust cognitive skills due to their complex social environment (van Schaik et al. 2012). Thus, an increased demand for the ability to solve social problems may translate to heightened cognitive skills in a non-social domain; however, evidence for this specific link is lacking.

There are a large number of explanations for intraspecific co-variation between problem-solving ability and group size, many of which suggest that individuals in larger groups may be more adept at solving novel problems than those living in smaller groups (Sewall 2015). These explanations include the following: shared vigilance among individuals (Sorato et al. 2012; Ridley et al. 2013) allowing group members to invest more time in problem-solving activities, the 'pool of competence' hypothesis which suggests that larger groups contain more individuals and therefore have a higher chance of containing individuals competent at solving novel tasks (Liker and Bokony 2009; Morand-Ferron and Quinn 2011), and

finally, individuals living in larger groups may demonstrate greater individual problem-solving success due to their inherent cognitive abilities gained from monitoring and/or maintaining more social relationships (Cole et al. 2011). These explanations describe the potential relationship between sociality and individual problem-solving ability and reveal how solving more complex social problems may increase the cognitive domain of an individual to solve non-social problems as well.

However, some aspects of intraspecific variation in cognitive performance may reflect other (i.e. non-cognitive) differences in individual traits and tendencies. This can include differences in sex and age, because these factors may influence an individual's capacity to develop or display behaviours required to solve a novel task (Drea 1998; Thornton and Samson 2012). The influence of some factors, such as age, on cognitive variation has support from empirical research with birds (Cole et al. 2011; Morand-Ferron et al. 2011), fishes (Kelley and Magurran 2003), primates (Blunnel et al. 1980; Reader and Laland 2001; Gunhold et al. 2014) and other mammals (Thornton and Samson 2012). Typically, younger individuals tend to display high innovative tendencies due to their lower competitive abilities, which may drive alternative strategies and behaviours (Kendal et al. 2005). Some of these alternative behaviours may be cognitively demanding and thus enhance their ability to overcome novel problems (Kendal et al. 2005). Furthermore, certain attributes may influence individual fear towards novel stimuli (termed neophobia), for example, limiting the experience of cognitively challenging situations (Benson-Amram and Holekamp 2012). These attributes may even be associated with individual personality, which may play an important role in describing different exploratory behaviours within a population (Cole and Quinn 2012; Thornton and Samson 2012). Differences in individual tendencies and motivation may therefore influence the likelihood of individuals developing enhanced skills and may play a role in describing cognitive variation within a population (Krause et al. 2010; van Schaik et al. 2012; Griffin and Guez 2014).

The target species of our study was the Western Australian magpie (*C. tibicen dorsalis*), a social species where group membership is stable over a number of years. The ability to track and evaluate long-term relationships with conspecifics is essential for brood and territory defence (Jones and Thomas 1999). Magpies have been known to hide, retrieve and manipulate food objects, and these activities may be linked to enhanced cognitive abilities (Kaplan 2004). Previous observations of magpies have described the potential for tool use and problem-solving such as using sticks to enhance foraging success, suggesting that they may display sophisticated levels of cognition similar to corvids or parrots (Kaplan 2004; McCormick 2007; Boeckle and Bugnyar 2012). In an urban habitat, enhanced cognitive skills and innovative behaviours

may be essential for discovering new food sources in changing and novel environments and may be particularly pertinent for urban populations of this species. However, no explicit test of Australian magpie cognition has been performed.

In this study, we investigated the relationship between associative learning performance and group size in an urban population of free-living Western Australian magpies. We tested one cognitive behaviour, associative learning, in magpies by presenting individuals with a novel associative learning task, which required individuals to associate a novel visual cue with a food reward. We anticipated that individuals from larger groups should be more efficient at solving the novel learning task than those from smaller groups. Using established protocols and observational techniques designed for wild-caught birds (Boogert et al. 2011), the task was presented to isolated individuals (to prevent others from socially learning via observation of group members interacting with the task) to determine the following: (i) whether some individuals are more likely to attempt to solve the task than others, (ii) if there is variation among individuals in the ability to solve the task and (iii) whether variation in solving the novel task is related to group size or other parameters, such as age and sex.

Methods

Species and study site

The Western Australian magpie is a large (250–400 g), terrestrially foraging bird that lives in stable social groups where individuals share territory defence, predator detection and, in some cases, chick-rearing duties (Robinson 1956; Hughes and Mather 1991; Edwards 2014). The Australian magpie (*Cracticus tibicen*) is distributed across the Australian continent; however, the Western Australian subspecies (*C.t. dorsalis*) forms particularly large social groups with an average of 15 individuals (range 3–26) defending a territory year-round (Farabaugh et al. 1992; Baker et al. 2000, Edwards et al. 2015). No previous study has found group sizes of Western Australian magpies to change significantly over time (i.e. between seasons or between years; Hughes and Mather 1991; Baker et al. 2000). Magpies are also relatively long-lived, with a life expectancy of up to 25 years, and learning is thought to play a key role in their behavioural development (Kaplan 2004).

The population chosen for this research was located in Guildford, Western Australia. Seven geographically distinct, free-living groups were chosen from this population because many of these individuals were ringed and habituated to human presence (from previous observations conducted by Professors I. Rowley and E. Russell from 1995–1999). Individuals that were not ringed could be distinguished by

their unique plumage markings and colouration; thus, no further ringing or trapping was completed, and the birds were never physically handled during our study. Specifically, females and juveniles had unique scalloped white/grey back and plumage colouration (respectively), which allowed individuals to be distinguished from each other. Birds from these groups were easily observable, allowing their behaviours to be monitored without causing any distress. Individuals were classified as adult male (all dorsal feathers between nape and mid-back white, $n = 12$), adult female (dorsal feathers between nape and mid-back scalloped white and black, $n = 14$) or juvenile (grey or brown belly plumage, $n = 8$) (Robinson 1956; Johnstone and Storr 2004). Typically, magpies are considered adults in their fourth year, as this is when they acquire their full adult plumage and complete their sexual development (Johnstone and Storr 2004). Juveniles could not be sexed because their feather patterns were not yet fully developed, rendering their gender ambiguous (Johnstone and Storr 2004). The number of individuals in each group was recorded during each observational visit as a measure of group size and confirmed that group size was stable, with no significant changes over the duration of the study period.

Experimental procedure

Only individual magpies that were easily identifiable by either rings or distinctive plumage characteristics (this latter method of identification was primarily used for younger birds) were chosen for the experimental task (which was approved by the Animal Ethics Committee, UWA; Approval number RA/100/1272). It was not possible to record data blind because our study involved free-living focal animals in the field. The task required individuals to develop an association between coloured lids and a corresponding food reward. The task consisted of a foraging grid with 30 evenly spaced wells (well dimensions 50 mm × 20 mm) in a polystyrene sheet (sheet size 120 mm × 120 mm × 40 mm) and required individuals to flip square plastic lids from the top of a well to access the food reward underneath. Magpies are subterranean foragers, which involve flipping leaves and bark in search of food (Kaplan 2004). Thus, our particular task effectively mimics natural foraging for this species. Attached to the bottom of each lid was a rubber cap to weigh the lid down loosely within each well. This was required to prevent the lid being blown away by the wind or wells being accidently uncovered while the magpies were walking on the foraging grid. Presentations were conducted from early June to late July 2013 between 6:30 and 11:30 or 14:30 and 18:00, because magpies displayed the highest foraging activity levels during these periods (Mirville 2013) and thus had appropriate motivation to attempt the task.

Initially, the grid was presented opportunistically to isolated individuals in order to encourage the birds to approach the

grid. During these initial presentations, the grid contained equally distributed food rewards and no lids, so that the individual could see the food reward and develop interest and familiarity with the experimental task. In subsequent presentations, the wells were first partially covered and then fully covered with black lids until the birds learned to flip the lids to retrieve the food. This 'step progression method' is a common practice in cognitive tests whereby preparation for the final task involves increasingly difficult presentations of the grid that are only progressed once all members of the group are able to solve the basic function at that particular step (sensu Aplin et al. 2013). In the final presentations of the task, half of the grid's wells were covered with blue lids and half were covered with yellow lids. Removing consecutive lids of the rewarded colour (yellow) and not those of the unrewarded colour (blue) involves successfully associating a lid colour with a reward and thus reflects associative learning (Heyes and Galef 1996; Boogert et al. 2011; Dickinson 2012; Morand-Ferron et al. 2015). A binomial test of 28 individuals interacting with the colour association task for the first time revealed that there was no preference for flipping one colour over another ($p = 0.87$) and thus no evidence for a predisposed preference for flipping the rewarded colour. For every trial, the positions of blue and yellow lids were determined randomly; however, each colour remained representative of its respective reward level. By flipping a correct lid, individuals were able to earn 3 g of polony meat. Polony was chosen as the foraging reward for several reasons: (1) it was highly favoured throughout the training period by all individuals within the population, and (2) it was a 'dead' reward, controlling for the fact that magpies are particularly well adapted to ground foraging with acute hearing to detect subterranean food (Robinson 1956; Kaplan 2004). This reward choice removed the potential confounding effect of individuals using traditional foraging techniques (i.e. hearing and scent) instead of associative learning. Polony was present in all wells at some point during the initial no-lid and black-lid training trials. Additionally, reward wells were chosen randomly and therefore all wells contained polony on a regular basis during the colour trials. Thus, it is unlikely that individuals would exclusively use olfaction to determine reward location within the grid as all wells (rewarded and unrewarded) contained some traces of olfactory cues.

Once an individual was able to perform basic lid-flipping behaviour (as described above), they were presented with the colour association task. Not all individuals performed the basic lid-flipping task over the duration of the study; these individuals were given a score of zero for task interaction and were excluded from analyses related to individual performance in solving a novel task. The foraging grid was baited out of sight of the magpies before being placed on the ground near an isolated individual, which was defined as when the subject was out of sight from other group members *and* at least 15 m away from other foraging individuals. We were confident that other group members were not observing the trial of isolated individuals because magpies quickly recruit to a rich food source that they observe group members feeding on (MOM, personal observation), and we did not have nonfocal magpies recruit to our grid when we trialled our experimental individuals out of sight. Trials were conducted opportunistically and began once an isolated subject had detected the task and began to approach it. Once an individual made first contact with the grid (defined as stepping onto or pecking at the grid from the ground), the time taken to complete the task was measured. The individual was considered not to have interacted with the grid if the individual approached the grid but did not make contact with it during the trial. Trials lasted for a total of 3 min, and if the individual approached but did not directly interact with the task, it was allocated an interaction score of zero. If another individual attempted to interact with the grid while a trial was occurring, the trial was stopped and discounted, and the grid was removed until another trial could be conducted in isolation at a later date. These rules were implemented to minimise the potential for individuals to solve the task because they had the opportunity to observe others attempting the task (i.e. via social learning). We aimed to exclude any effects associated with social learning since this experiment was aimed at exploring variation in individual learning ability. During each trial, the unique identity of the individual was documented and the behavioural responses during the presentation of the grid were captured using a Sony handy cam (XR260VE-HDR).

The video footage was subsequently used to measure the following: the total number of lids that the individual flipped, the total time that the individual spent interacting with the grid during the trial and the colour sequence of flipped lids to indicate success rate (e.g. yellow, blue, yellow, yellow, blue, yellow). An individual was considered to have solved the task if they (a) flipped three or more lids (we chose three as a minimum to control for satiation issues) and (b) flipped at least 80 % correct lids consecutively from the total number of lids that were flipped during a single presentation of the task. For example, if an individual flipped four consecutive correct lids out of a total of five during a single trial, we considered this individual to have learned, and thus solved, the association task. On average, adults and juveniles flipped the same number of lids during a trial (average lid flips adults = 5.05 ± 0.47 SE, juveniles = 4.97 ± 0.25 SE), and therefore, the 80 % pass criterion was deemed acceptable for comparison between ages within the population. Once each 3-min trial was finished, the entire grid, the lids and food rewards were removed and reset out of sight of the magpies. Multiple trials were conducted for each individual to generate individual learning curves for the novel foraging task (maximum one per individual per day, maximum of nine presentations over the entire study period). Thus, the propensity to interact with the task and the ability to flip at least 80 % of correct lids during a single trial were used

to measure variation in associative learning performance across the population.

Statistical analyses

Analyses were performed to determine (1) the likelihood of an individual interacting with the grid, (2) the proportion of correct lids that each individual flipped and (3) the ability of an individual to solve the colour association task. All analyses were performed in SPSS Statistics (Version 22.0.0.0, IBM Corporation 2013) and involved a model selection process to determine the effect of each measured variable on the data. The response variables for (1) and (3) were fitted with binary response terms that represented whether the individual did (score = 1) or did not (score = 0) interact with or solve the task. For (2), the response variable was the number of correct lids flipped during the trial, with the total number of lids flipped in that trial set as the binomial denominator. On average, an individual flipped five lids during a single trial. The analysis describing the likelihood of task interaction (1) included data from seven groups, 34 individuals and 147 trials. Analysis of the proportion of correct lids flipped (2) and task completion (3) excluded trials where the individual never interacted with the foraging grid and thus had smaller sample sizes. Analysis (2) included data from six groups, 28 individuals and 97 trials, while analysis (3) comprised 18 individuals (7 juveniles and 11 adults) from four groups with a total of 53 trials (31 conducted on juveniles and 22 on adults).

Multifactorial analyses were conducted using generalised linear mixed models (GLMMs), specifically a series of generalised estimating equations (GEE, a derivation of a GLMM, Hardin and Hilbe 2013), with a binomial distribution and a logit link function. Group and individual identity were included as random effects in all analyses to account for the effect of repeated measures on the distribution of the data. All probable explanatory terms were considered, including sex, age (adult or juvenile), group size, trial number and time spent interacting with the task. However, because sex was confounded with age (all juveniles' sex was classified as 'unknown') and age consistently explained more variance in the data than sex, sex as a predictor term was excluded from all models. The number of trials (number of task presentations that an individual received) and the total time an individual spent interacting with the task (per presentation) were included as predictor variables. These variables and the biologically relevant two-way interactions between them were included in the model selection process (see Supplementary data).

All statistical models represented an a priori biological hypothesis (see Supplementary data) and were ranked in order of their corrected quasi-likelihood under independence model criterion (QICc, see Supplementary material for further information on the use of QICc for data analysis) value, such that lower values were considered to have more statistical

power (Burnham and Anderson 2002). The model with the highest weight (w_i) and the lowest QICc value was considered the most parsimonious, although all models within five QICcs of the best model were taken for further analysis, and represented the 'top model set.' (sensu Grueber et al. 2011; Symonds and Moussalli 2011). From this top model set, predictor weights for all individual terms were calculated using the sum of the QICc weights for each top model that contained that variable (Symonds and Moussalli 2011). Thus, more important terms had a value approaching unity and variables from unlikely models would tend towards zero (Symonds and Moussalli 2011). Only terms with a predictor weight greater than 20 % and with confidence intervals that did not intersect zero were considered significant predictors of the data (sensu Grueber et al. 2011).

Results

Among the 34 individuals that were presented with the novel foraging task, a total of six (18 %) did not interact with the task (after approaching it) during the study. Of the 28 birds that did interact with the grid, 10 individuals reached the criterion for associative learning. These ten individuals comprised 29 % of *all* individuals tested in the study, 36 % of the individuals who interacted with the task and 56 % of the individuals that flipped at least three lids.

Interaction with the task

Group size was the most significant factor influencing the likelihood that an individual would approach and interact with the novel task (Table 1). Specifically, magpies living in larger groups were more likely to interact with the task than those living in smaller groups (Fig. 1). Individual age also explained a significant amount of the variation in the data (Table 1) with juveniles more likely to interact with the task than adults (Fig. 2). Other aspects of task interaction, such as trial number, showed no significant effects on the likelihood of an individual interacting with the task (see Supplementary data).

Learning the colour association task

Adult magpies were significantly more successful at flipping correct lids during the task than juveniles (Table 2), but there was a strong correlation between age and the time spent solving the task. Thus, adults were generally more efficient at producing successful lid-flipping sequences compared to juveniles, although with increasing time, this success declined, a trend not apparent in juveniles (Fig. 3). Adults were also significantly more likely to reach the criterion for learning the colour-reward association in comparison to juveniles (Table 3, Fig. 4). In

Table 1 Top model set of the terms affecting the likelihood that individuals interacted with the task

Model	QICc	Δ QICc	w_i
Group size + age	160.12	0	0.52
Group size × age	161.25	1.13	0.29
Group size	162.12	2	0.19
Basic intercept	190.49	30.371	
Predictor	Sum of Akaike weights	Effect ± SE	CI
Group size	1.00	0.5, 0.28	0.173, 0.608
Age	0.81	Adult −1.32, −2.54	0.735, 3.12
		Juvenile 0, 0	

Only models within 5 QICc units of the top model are included. The analysis was conducted on 34 individuals from seven groups and involved a total of 147 trials. Individual and group identity were included as random terms

addition, the time that an individual spent interacting with the task also explained individual task performance, as more time spent with the task led to a higher likelihood that an individual would solve it (Fig. 5). No other terms were informative in describing the differences in learning performance among individuals.

Discussion

One of the most important aims of cognitive research is to reveal the selective pressures driving the evolution of cognition (Thornton and Lukas 2012) and the factors that contribute to inter-individual variation in cognitive behaviours. Our findings suggest that performance in a novel colour association task was influenced both by social group size and an individual's age. Learning ability was not directly affected by group

size, but magpies were more willing to approach and interact with the novel task if they belonged to a larger group. Thus, our hypothesis that individuals in larger groups would be more successful at solving the associative learning task was not fully supported. Group membership may play an important role in exploratory behaviours; however, it is not essential for the ability to solve novel challenges. Similar studies on wild spotted hyenas (*Crocuta crocuta*, Benson-Amram and Holekamp 2012) and vervet monkeys (*Chlorocebus aethiops*, van de Waal and Bshary 2010) revealed that higher social dexterity was not linked to enhanced ability to solve novel problems and thus raises the question of the transferability of skills from the social to the non-social domain. Although we found that adults were more adept at learning the colour association task, they were less likely to approach and interact with the task than juveniles. Our findings suggest that group membership, as well as developmental factors and/ or individual experience, may play an important role in exploratory behaviours and the ability to solve novel challenges.

Factors influencing interaction with a novel foraging task

Magpies living in small groups were less likely to interact with the task than those living in large groups, which is similar to
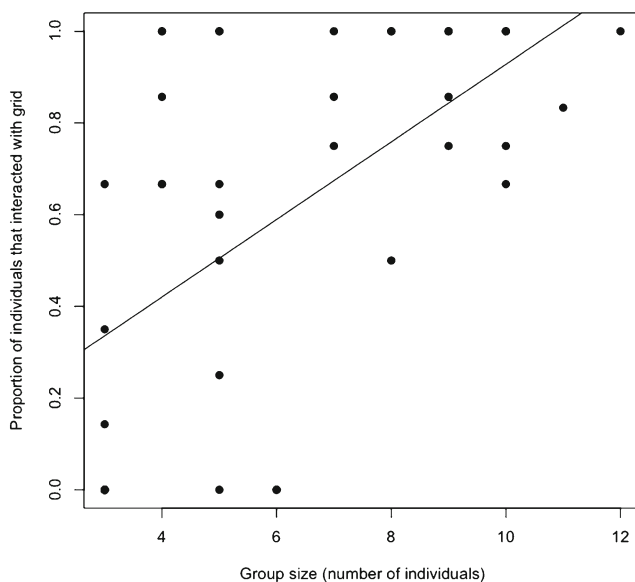
Fig. 1 The effect of group size on the proportion of individuals that interacted with the novel foraging task (each data point represents a different trial date). The *trend line* was generated from the predictions of the model of greatest parsimony presented in Table 1, from 147 presentations of a novel task to 34 individuals from seven different groups
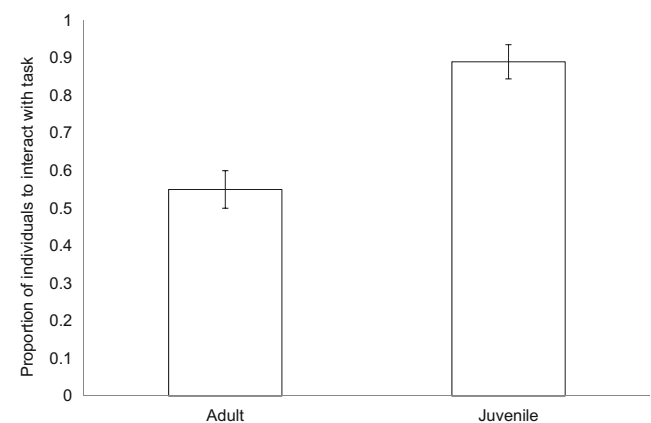
Fig. 2 The effect of age on the mean (±SE) frequency of individuals interacting with a novel foraging task. Data includes 147 presentations of a novel task to 34 individuals from seven different groups

Table 2 Top model set of the terms affecting individual flipping success (number of wells that contained a food reward)

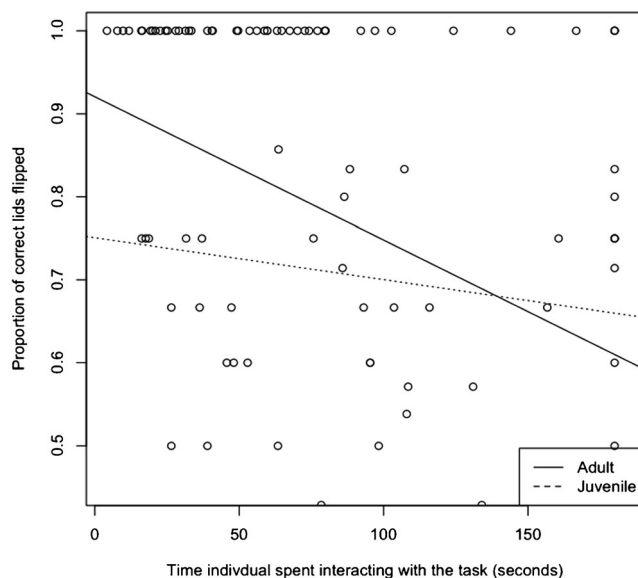| Model	QICc	Δ QICc	w_i
Trial + age × time	311.78	0	0.57
Group size + age	313.43	1.65	0.25
Age × trial	314.05	2.27	0.18
Basic	333.56	21.78	
Predictor	Sum of Akaike weights	Effect ± SE	CI
Age × time interacting with task	0.57	Adult −0.00, −0.02	−0.02, −0.00
		Juvenile 0, 0	

The response variable used was the proportion of correct lids flipped. Only models within 5 QICc units of the top model are included. The analysis was conducted on 28 individuals from six groups involved in a total of 97 trials. Individual and group identity were included as random terms

previous work on house sparrows (*Passer domesticus*), where birds from larger groups were more likely to approach, and consequently solve, a novel foraging problem than those from smaller groups (Liker and Bokony 2009). Our findings support the idea that individuals from larger groups are less likely to demonstrate neophobic behaviours than those from small groups, with individuals who are less fearful of novelty and therefore more likely to interact with a novel task because of their specific social environment (Morand-Ferron and Quinn 2011; Overington et al. 2011). Moreover, if the opportunity to socially interact and learn from others varies with group size, individuals may also differ in their ability to display cognitive skills and behaviours that are only acquired through interaction with others (Croney and Newberry 2007; Liker and Bokony 2009; Krause et al. 2010; Morand-Ferron and Quinn 2011; van Schaik et al. 2012).

Well-known group-living benefits may also affect individual task interaction, such as risk dilution, where individuals in

Fig. 3 Effect of age on the proportion of correct lids flipped upon the presentation of a novel foraging task and the total time that an individual spent interacting with the task. The *trend lines* were generated from 97 trials with a novel task to 28 individuals from six different groups

larger groups experience lower risk of predation and are overall more exploratory (Sorato et al. 2012; Dardenne et al. 2013). This pattern has been observed in many bird taxa (Elgar 1989) and suggests that predation pressure can influence the time that individuals allocate to novel activities (Marshall et al. 2012; Ridley et al. 2013). For example, studies on cooperatively breeding birds have demonstrated that individuals in larger groups spent less time investing in predator vigilance than those in smaller groups because of their reduced level of predation risk (Farabaugh et al. 1992; Ridley and Raihani 2007; Sorato et al. 2012). This process therefore allows individuals to re-allocate time and resources from vigilance to other behaviours (Sharpe et al. 2010; Ridley et al. 2013). Thus, the number of animals within the group can influence the time that an individual has to allocate to developing problem-solving (and other) behaviours, likely resulting in variation in individual explorative tendencies according to group size. Our findings suggest that initial exploratory behaviour can be influenced by group size, which may have significant implications for individual learning ability, since individuals that are more likely to participate in novel tasks are also more likely to subsequently solve them (Benson-Amram and Holekamp 2012).

Alternatively, individuals in larger groups may experience greater competition for resources, and as a consequence, the less competitive members of a social group may be driven to adopt alternative behavioural strategies (Majolo et al. 2008; Beauchamp 2010; Cheney 2011; Thornton and Samson 2012). This has been demonstrated in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), where individuals choose risky, innovative options more frequently while foraging in a competitive context compared with a neutral context (Rosati and Hare 2012). While variation in the level of competition experienced by individuals may not directly influence learning ability, competitive pressures may drive individuals to adopt risky or innovative behaviours that may subsequently result in learning, which is more likely to occur in larger groups (Reader and Laland 2001; Morand-Ferron et al. 2011; Rosati and Hare 2012; Thornton and Samson 2012).

Table 3 Top model set of the terms affecting the probability of solving a novel foraging problem

| Model	QICc	Δ QICc	w_i
Age × time	130.04	0	0.20
Trial + age × time	130.40	0.36	0.16
Age + time	130.57	0.53	0.15
Group size + time	131.32	1.28	0.10
Age + trial	131.76	1.72	0.08
Age	131.92	1.88	0.08
Group size + age	132.69	2.65	0.05
Group size × time	133.32	3.28	0.04
Time	133.50	3.46	0.68
Age × trial	133.51	3.47	0.03
Group size	133.53	3.49	0.24
Age × group size	134.60	0.10	0.02
Basic	137.69	7.65	
Predictor	Sum of Akaike weights	Effect ± SE	CI
Age	0.76	Adult −10.02, −10.88 Juvenile 0, 0	−1.90, −0.20
Time interacting with task	0.68	0.00, 0.01	0.00, 0.02

Only models within 5 QICc units of the top model are included. The analysis was conducted on 18 individuals from six groups and involved a total of 53 trials. Individual and group identity were included as random terms

Our results also demonstrated that juveniles were more likely to interact with the task than adults. In social species, such as the Western Australian magpie, tasks such as predator vigilance are roles that are often shared among adult group members only (Farabaugh et al. 1992; Ridley et al. 2010; Sorato et al. 2012; Ridley et al. 2013). Thus, adults may have less time to interact with novel tasks than juveniles. Alternatively, juvenile magpies may have demonstrated a higher propensity to interact with the task than older individuals due to lower neophobia or elevated exploratory tendencies. This possibility is well supported in the literature and suggests that differences in age may contribute to the likelihood that an individual will attempt to solve a novel problem (Kendal et al. 2005; Greenberg 2003; Biondi et al. 2010;

Thornton and Samson 2012). For example, juvenile meerkats are more likely to interact with novel tasks than adults, which is likely due to their low fear in exploring new objects and situations (Thornton and Samson 2012). Similarly, some studies have suggested that neophobia is a product of experience (Hauser 1988; Kelley and Magurran 2003; Benson-Amram and Holekamp 2012), which additionally supports the finding that older magpies, with more experience, are more hesitant to
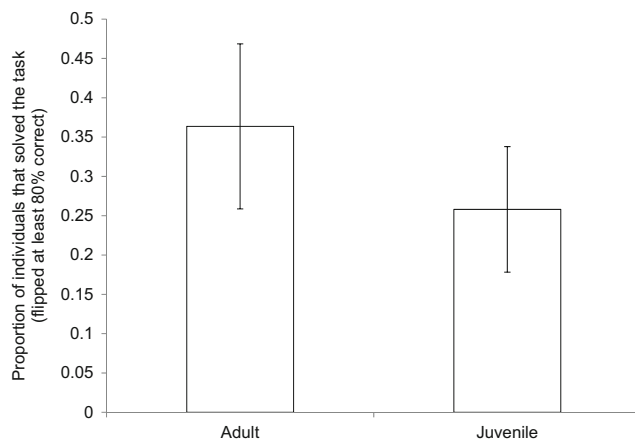
Fig. 4 The effect of age on the mean (±SE) frequency of individuals solving a novel foraging task. Data included 53 trials with a novel task to 18 individuals from four different groups
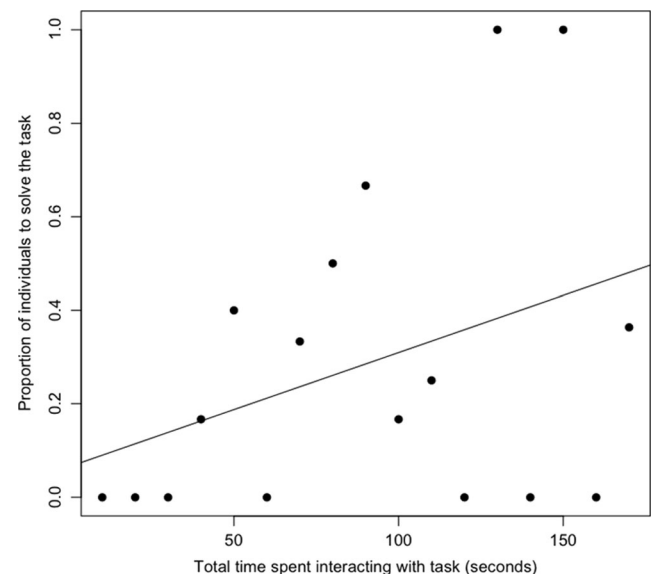
Fig. 5 Relationship between the time spent interacting with a task and the proportion of individuals that solved the colour-reward association task. The *trend lines* were generated from 53 trial presentations of a novel task to 18 individuals from four different groups

interact with novelty (Kelley and Magurran 2003; Benson-Amram and Holekamp 2012).

Associative learning among individuals

Our study revealed that adults were more likely to associate colour with a food reward (i.e. demonstrated higher flipping success) and displayed higher levels of learning success than juveniles. Adults are likely to possess a larger repertoire of prior experience and knowledge (Hauser 1988) from which to innovate in novel situations and may therefore succeed in learning more often where juveniles may fail (Morand-Ferron et al. 2011; Thornton and Samson 2012; Resende et al. 2014). Hauser (1999) suggested that maturity is associated with more successful learning mechanisms, as older individuals are less exploratory and have a higher capacity to reject non-beneficial options when interacting with a novel associative task. More experienced individuals may be more adept at overcoming novel situations because of their higher levels of learning strategies and problem-solving skills, characteristics more commonly associated with adults than juveniles (Reader and Laland 2001). Furthermore, the tendency for juveniles to be more exploratory than adults may have reduced their ability to demonstrate successful learning strategies. Younger magpies might have continued to explore the non-rewarding option even once the preference for the rewarding option was developed, demonstrating a difference in learning strategy depending on age (Thornton and Lukas 2012). Thus, although juveniles are more likely to engage in novel situations, efficient skills are most likely introduced into a group by adult individuals who are able to inhibit their explorative tendencies and generate more successful strategies to solve novel problems.

Among all individuals, the longer the time spent interacting with the foraging task, the higher the likelihood of solving it. A recent study on chimpanzees revealed that upon the presentation of a novel foraging puzzle, individuals that were more open to novel experiences were those that spent more time actively interacting with the task (Hopper et al. 2014). Although the current study found no correlation between associative learning and neophobia, it suggests that fear of novelty plays an important role in the exploration of novel objects and, thus, the ability to adapt to them. Learning is required for a one-time successful innovation to develop into a problem-solving strategy (Benson-Amran et al. 2013). Individuals that spent more time interacting with the task may therefore have the opportunity to invest more time in behaviours that enhance learning, and this may be an important factor in determining cognitive variation within a population.

There were several limitations to this research that should be acknowledged. Firstly, because our study was conducted on a wild population, the data were limited by the group sizes that were available (ranging between 3 and 12 magpies). This may have concealed the possible effect of group size on individual learning ability, because this range is lower than that of group sizes recorded in literature for magpies (average of 15 individuals (range 3–26), Farabaugh et al. 1992). Although our study did not show any evidence that some individuals are predisposed to engage with lids of a particular colour, repeating the experiment with the colour order reversed, or presenting half the population with yellow reward lids and the other half with blue reward lids, would further enhance evidence of this species' associative learning ability.

Implications of variation in cognitive abilities

Although group size did not directly influence the associative learning performance of individuals, it inhibited some individuals' likelihood of engaging with the task. Thus, individual differences in initial exploratory behaviour may be a key determinant of learning performance in wild magpies. This finding may provide some clues to the causes of cognitive diversity among individuals, because long-term group size may determine an individual's opportunity to acquire the skills necessary for overcoming social and ecological challenges. This could potentially have lasting implications; enhanced cognitive skills may allow individuals to escape novel predators, adjust to new or changing habitat conditions or locate new resources when existing ones become scarce (Leal and Powell 2011; Thornton and Lukas 2012; Cauchard et al. 2013; Resende et al. 2014). For example, a study on starlings (*Sturnus vulgaris*) demonstrated that individuals that rapidly solved a novel foraging task exhibited low neophobia and were quick to feed in a novel environment (Boogert et al. 2006). In addition, small group sizes may limit the introduction and transmission of novel skills through the population, ultimately limiting food acquisition and, therefore, nutritional intake (Bouchard 2002; Brosnan et al. 2010; Aplin et al. 2013; Thompson and Ridley 2013). Thus, small, stable group sizes may be limited in their opportunity to learn about novel situations, indicating a potential benefit of living within a large group (Croney and Newberry 2007; Krause et al. 2010; van Schaik et al. 2012; Cauchard et al. 2013). If individuals from smaller groups are less likely to interact with a novel task and subsequently solve a problem, they may be less adaptable and exhibit limited behavioural plasticity in changing environments. Although there are a number of factors contributing to an individual's ability to solve a novel problem, such as tendencies to explore novelty and variable environmental pressures, our study suggests that group size may be one important driver of this variation within a population of social animals. Enhanced cognitive ability may be of particular importance for an urban-dwelling bird, such as the magpie population observed in this study, and our results suggest that there is variable ability within the population to solve novel problems.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

Ethical approval   All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All observations performed on free-living magpies in this study were in accordance with the ethical standards of the Animal Ethics Committee, University of Western Australia (Approval number RA/100/1272).

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