

# Cognitive performance is linked to group size and affects fitness in Australian magpies

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**The social intelligence hypothesis states that the demands of social life drive cognitive evolution<sup>1–3</sup>. This idea receives support from comparative studies that link variation in group size or mating systems with cognitive and neuroanatomical differences across species<sup>3–7</sup>, but findings are contradictory and contentious<sup>8–10</sup>. To understand the cognitive consequences of sociality, it is also important to investigate social variation within species. Here we show that in wild, cooperatively breeding Australian magpies, individuals that live in large groups show increased cognitive performance, which is linked to increased reproductive success. Individual performance was highly correlated across four cognitive tasks, indicating a ‘general intelligence factor’ that underlies cognitive performance. Repeated cognitive testing of juveniles at different ages showed that the correlation between group size and cognition emerged in early life, suggesting that living in larger groups promotes cognitive development. Furthermore, we found a positive association between the task performance of females and three indicators of reproductive success, thus identifying a selective benefit of greater cognitive performance. Together, these results provide intraspecific evidence that sociality can shape cognitive development and evolution.**

The social environment is commonly assumed to generate important cognitive challenges. According to the social intelligence (or social brain) hypothesis, these challenges, including the need to form and maintain social bonds, track third-party relationships and anticipate the actions of others, are the central drivers of cognitive evolution<sup>1–3</sup>. This argument receives widespread support from studies that link variation in social factors, such as group size or mating systems, with differences in cognitive performance or neuroanatomy across species of birds and mammals (for example, see refs 3–6). However, comparative analyses are subject to ecological and phylogenetic confounding effects, and have yielded conflicting results, with recent work calling into question the importance of social factors<sup>8–10</sup>. To understand the role of sociality in cognitive evolution, it is critical to examine the causes and fitness consequences of cognitive variation within species<sup>11,12</sup>.

For species that live in stable social groups, within-population variation in group size could generate differences in information-processing demands and so influence the expression of cognitive traits<sup>13</sup>. Measurements of brain structure correlate with group size in humans, captive cichlids (*Neolamprologus pulcher*) and captive macaques (*Macaca mulatta*)<sup>13–15</sup>, but the relationship between group size and cognition in wild animals is unknown. Furthermore, the potential for group-size-dependent cognitive traits to come under selection is not understood, as their fitness consequences have not been investigated. To address these critical gaps in our knowledge, we examined whether group size predicts individual variation in cognitive performance (controlling for morphological, nutritional and behavioural factors) within a population of wild, cooperatively breeding Australian magpies (Western Australian subspecies, *Cracticus tibicen dorsalis*, also known as *Gymnorhina tibicen dorsalis*). We quantified

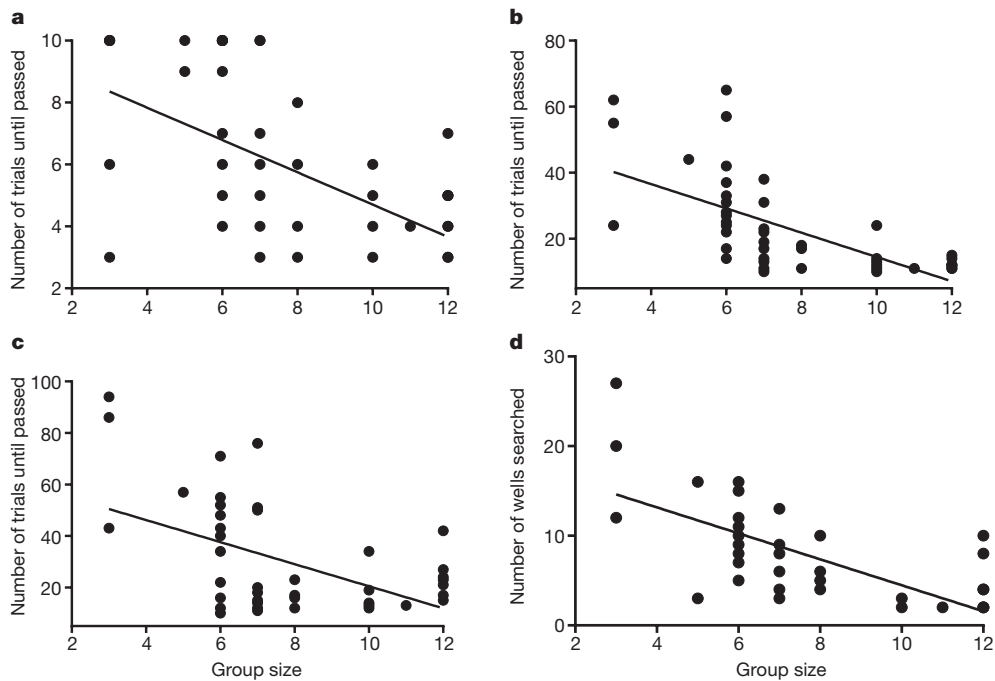
individual cognitive performance in 56 birds from 14 groups, which ranged in size from 3 to 12 individuals, using a variety of cognitive tasks designed to measure inhibitory control (the ability to inhibit prepotent responses), associative learning, reversal learning and spatial memory (Extended Data Fig. 1). These four domain-general cognitive processes are thought to have an important role in a range of fitness-related behaviours in both social and asocial contexts<sup>11,16</sup> (see Methods for details).

Group size was the strongest predictor of adult performance across all four tasks (Supplementary Tables 1–4), with individuals from larger groups performing better than those from smaller groups (Fig. 1). Individual performance was significantly positively correlated across all four tasks (Supplementary Table 5), suggestive of an underlying general intelligence factor akin to what has been reported in human psychometric studies<sup>17</sup>. A principal component analysis revealed that performance in all four tasks positively contributed to the first principal component (PC1; eigenvalue >1). This component (referred to hereafter as ‘general cognitive performance’) accounted for 64.6% of the total variance in task performance (Extended Data Table 1), a substantially higher proportion than has previously been shown for cognitive tasks in other species<sup>18–22</sup>. Group size was also the strongest predictor of PC1 (Fig. 2 and Supplementary Table 6). To confirm that our tasks provided robust measurements of individual cognitive performance, we ran a second set of cognitive tasks two weeks later using causally identical, but visually distinct, tasks (see Methods). Individual performance was highly repeatable in all four tasks: inhibitory control ( $r = 0.806$ ,  $P < 0.0001$ ), associative learning ( $r = 0.97$ ,  $P < 0.0001$ ), reversal learning ( $r = 0.975$ ,  $P < 0.0001$ ) and spatial memory ( $r = 0.932$ ,  $P < 0.0001$ ) (Extended Data Table 2).

To examine the development of the relationship between group size and cognition, we repeatedly tested juveniles at 100, 200 and 300 days after fledging. There was no evidence of general cognitive performance at 100 days after fledging (see Supplementary Discussion); however, much like adults, there was strong evidence for general cognitive performance at 200 (PC1 accounted for over 64% of total variance in task performance; Extended Data Table 3 and Supplementary Table 7) and 300 days after fledging (more than 80% of total variance explained by PC1; Extended Data Table 4 and Supplementary Table 8). There was no relationship between group size and cognitive performance at 100 days (Supplementary Tables 9, 10), but PC1 was strongly positively correlated with group size at 200 and 300 days (Fig. 3, Supplementary Tables 11, 12; see Supplementary Discussion for discussion of influential data points). When analysed longitudinally, an interaction between age tested and group size was the best predictor of cognitive performance (Extended Data Fig. 2 and Supplementary Tables 13–18).

The emergence of a positive association between group size and cognitive performance through early life supports the possibility that living in large groups helps to drive cognitive development. Manipulations of group size would be required to demonstrate an unequivocal causal effect, which in wild populations would lead to

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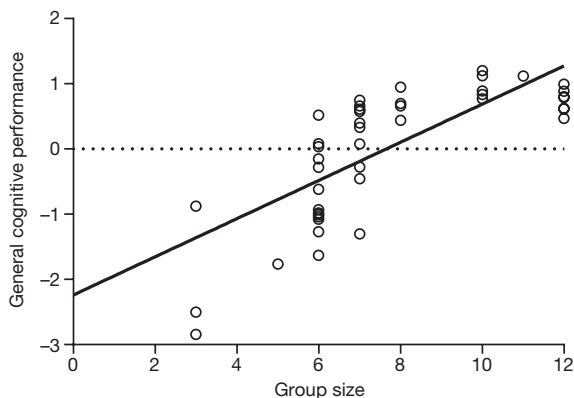


**Figure 1 | The relationship between group size and cognition.**

**a–d**, The relationship between group size and cognitive performance in an inhibitory control task (**a**;  $n = 56$  individuals), associative learning task (**b**;  $n = 48$  individuals), reversal learning task (**c**;  $n = 48$  individuals)

and spatial memory task (**d**;  $n = 49$  individuals). Lines represent best fit. Performance is measured as either the number of trials taken to succeed with the task, or the number of locations searched, so lower scores indicate better performance.

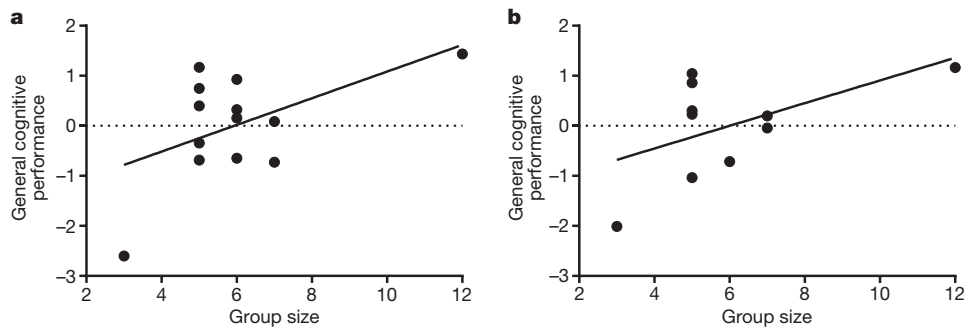
strong logistical and ethical challenges (see Supplementary Discussion). However, our analyses allow us to address key alternative explanations. First, the increased cognitive performance of birds in large groups is unlikely to be explained by reduced nutritional constraints on cognitive development<sup>23</sup>, because we found no effect of group size on offspring provisioning rates (Supplementary Table 19), and no relationship between body size and cognitive performance in either adults or juveniles (Supplementary Tables 1–4, 9–12). We also found no relationship between foraging efficiency and cognitive performance in adults (Supplementary Tables 1–4; foraging efficiency data were not available for juveniles). Second, the positive effects of group size cannot result from a reduced need for vigilance or reduced neophobia (the fear of something new): we recorded no anti-predator behaviour during any task presentations and neophobia was unrelated to performance on any tasks, except juveniles' performance on the spatial memory task at 100 days after fledging (adults: Supplementary Tables 1–4; juveniles: Supplementary Tables 9–12). There was also no



**Figure 2 | The relationship between group size and general cognitive performance.** Individual measurements of general cognitive performance derived from principal components analysis.  $n = 46$  individuals.

relationship between group size and the time that test subjects spent interacting with tasks (see Supplementary Discussion). Third, a link between cognitive performance and group size could potentially arise if magpies preferentially joined groups containing individuals with similar traits, but life-history data collected over more than four years provided no evidence of such social assortment (see Supplementary Discussion). Moreover, we found a clear difference in the frequency distribution of cognitive phenotypes between small and large groups (Extended Data Fig. 3), so it is not simply the case that large groups have a wider distribution of cognitive phenotypes, and are therefore more likely to contain some high-performing individuals by chance. Instead, we propose that, as suggested by captive studies<sup>13,15</sup>, living in larger groups presents wild animals with information-processing challenges that promote the development of cognitive traits. Determining precisely what those challenges are is a priority for future research. An important next step will be to determine whether individual cognitive development is specifically linked to the quantity and quality of their relationships within their social networks, as might be expected if the need to establish and maintain multiple relationships within groups places cognitive demands on individuals<sup>3</sup>.

To determine whether the group-size-dependent cognitive variation that we have identified may be subject to selection, we examined the relationship between individual cognitive performance and three measures of reproductive success. General intelligence has been linked to fitness-related traits in humans<sup>24</sup>, but few studies have examined the fitness consequences of cognitive variation in wild animals<sup>11</sup>, and the two studies that have used rigorous psychological tests found no effects<sup>19,25</sup>. In our magpie population, exceptionally high rates of extra-group paternity<sup>26</sup> mean that we were only able to reliably identify the mother of the brood (female reproductive skew in our population is low, and all females attempt to breed). Variation in female reproductive success was strongly linked to cognitive performance: general cognitive performance and foraging efficiency were the best predictors of the average number of hatched clutches per female per year (Fig. 4a, b and Supplementary Table 20), and general cognitive performance was the best predictor of the average number of fledglings produced and the



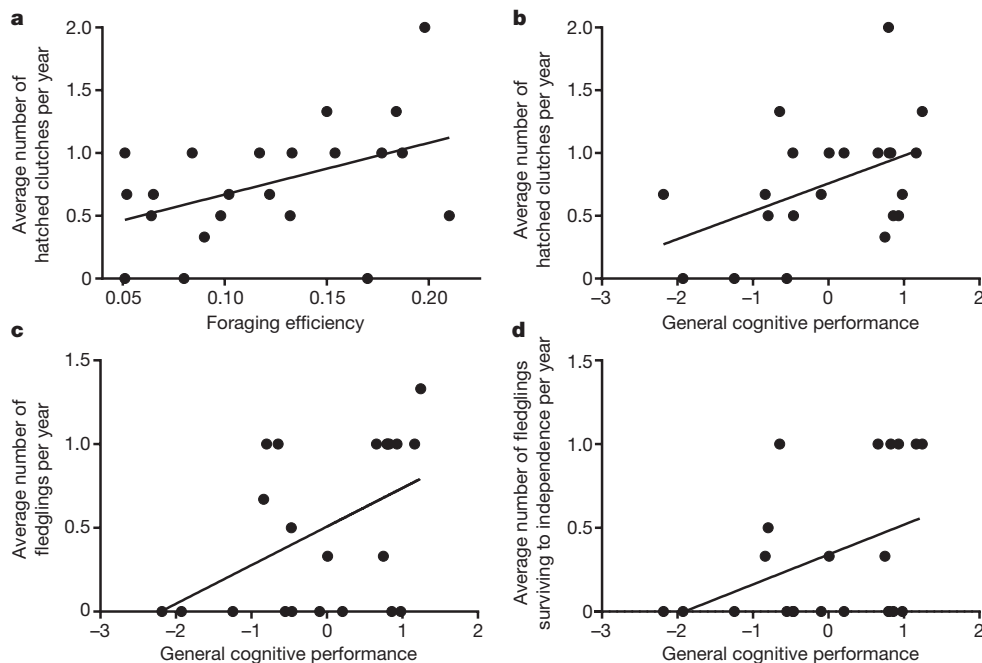
**Figure 3 | The relationship between general cognitive performance and group size in juveniles. a, b,** The relationship between general cognitive performance and group size at 200 days after fledging

(a;  $n = 15$  individuals) and 300 days after fledging (b;  $n = 10$  individuals). General cognitive performance could not be computed at 100 days after fledging.

average number of fledglings surviving to independence per female per year (Fig. 4c, d and Supplementary Tables 21, 22). These effects were independent of group size (Supplementary Tables 20–22), indicating that fitness benefits arise as a direct consequence of increased cognitive performance and are not simply the result of the non-cognitive advantages of living in larger groups. These results provide the evidence of a potential selective benefit of high levels of general cognitive performance in a wild population of non-human animals. Precisely how these benefits arise, and whether increased cognitive performance incurs any costs<sup>27</sup>, has yet to be determined. General cognitive performance and foraging efficiency are not correlated in female magpies ( $r = 0.06$ ,  $P = 0.791$ ,  $n = 22$ ), but it is possible that cognitively adept females may boost their reproductive success through improvements not in the quantity, but in the quality or variety of food given to offspring<sup>28</sup>. Additional, non-mutually exclusive explanations for the relationship between cognition and reproductive success could include enhanced abilities to defend young by avoiding inter- and intraspecific conflict<sup>29</sup>, or heritable cognitive abilities that promote offspring survival<sup>30</sup>. It is also possible that the fitness benefits of cognitive performance may account for the relation between group size and cognition, if females with increased cognitive performance produce large numbers of

cognitively adept offspring. However, this explanation is unlikely, given that group size is stable over time (see Methods), and the extraordinarily high rates of extra-group paternity<sup>26</sup> are likely to preclude substantial genetic differentiation between groups.

Since its inception, the social intelligence hypothesis has focused on cognitive differences between species that result from selection in response to the challenges of social life. Our results indicate that social factors can also have developmental effects on cognition within species, with important consequences for individual fitness. In summary, we have shown that wild Australian magpies living in larger groups show increased cognitive performance, which is associated with increased reproductive success. The association between group size and cognition emerges through early life and cannot be explained by food intake, body size, neophobia, attention to tasks or social assortment. Although we cannot rule out the possibility that some other, unmeasured factor could have a role in driving the relationship, our findings strongly suggest that the social environment has developmental effects on fundamental, domain-general cognitive traits. Furthermore, we provide rare evidence that cognitive performance provides benefits for female reproductive success. Recent comparative studies have brought into question the notion that variation in social structure drives cognitive



**Figure 4 | The relationship between female traits and reproductive success. a–d,** The relationship between foraging efficiency and the average number of hatched clutches per female per year (a), general cognitive performance and the average number of hatched clutches per female

per year (b), general cognitive performance and the average number of fledglings per female per year (c) and general cognitive performance and the average number of fledglings surviving to independence per female per year (d).  $n = 22$  individuals.

evolution<sup>9,10</sup>. However, our work highlights the critical importance of considering intraspecific variation, which is typically overlooked by comparative analyses. Together, our results point to a major role for the social environment in driving both the development and evolution of cognitive traits.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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**Supplementary Information** is available in the online version of the paper.

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## METHODS

**Data reporting.** No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

**Study site and species.** The study took place in Guildford, Western Australia, between September 2013 and February 2016. The study population consists of 14 groups of ringed, habituated Australian magpies (Western Australian subspecies *Cracticus tibicen dorsalis*), with groups ranging in size from 3 to 12 individuals (for composition of study population, see Supplementary Table 23). The Western Australian subspecies breeds cooperatively and lives in territorial groups, in which the number of adults remains stable (individuals within our study population have remained in the same group since research commenced in 2013, and there have been no recordings of ringed birds moving between groups)<sup>26,31</sup>. Individuals exhibit a range of cooperative behaviours such as territory defence and alloparental care<sup>32</sup>. Reproductive skew among females is very low, with all adult females typically attempting to breed each year<sup>33</sup>, but extra-group paternity is the highest recorded for any bird species (>82%)<sup>26</sup>, indicating high gene flow between groups. All of the group territories for our study population are located in urban parklands. Although individuals have access to food from anthropogenic sources, it is worth noting that all territories cover similar habitats and none contain dumps or landfills that could provide a glut of food sources.

The majority of birds within our study population are colour-ringed and habituated to close human observation, allowing us to present cognitive tests to most individuals. Individuals are trained to hop onto electronic top-pan scales in return for a crumb of mozzarella cheese, allowing us to collect daily records of individual body mass. Mozzarella was also used as the food reward in the cognitive tests. Weekly behavioural focal follows are carried out on all individuals in the study population<sup>33</sup>, from which foraging efficiency is calculated (defined as the mass of food (in grams), caught per foraging minute; biomass of food items was calculated using ref. 33).

**Adult cognitive test battery.** We carried out a series of cognitive tests on 56 adult Australian magpies. The battery consisted of four tasks designed to measure inhibitory control, associative learning, reversal learning and spatial memory (Extended Data Fig. 1a–c). All individuals were tested on the tasks in this order. We chose these tasks, because (i) they target well-understood and widely studied cognitive traits spanning cognitive domains<sup>11,20,34</sup> and (ii) they are likely to be highly ecologically relevant: spatial memory is likely to be important in remembering locations of resources and territory boundaries<sup>35</sup>, while associative and reversal learning enable the acquisition and flexible readjustment of predictive contingencies between cues in the environment, including learning from conspecifics' behaviour<sup>11,34,36,37</sup>. Finally, inhibitory control, the ability to inhibit prepotent responses, has been implicated in adaptive decision-making in both social and asocial contexts<sup>16,25,38</sup>.

**Inhibitory control.** To quantify individuals' ability to inhibit ineffective prepotent responses towards food, we presented individuals with a detour reaching task<sup>25</sup>. This consisted of a transparent open-ended cylinder (13 cm length, 5 cm diameter; Extended Data Figs 1a, 4a) in which a food reward was placed in the centre. Test subjects were presented with the task such that the open ends of the cylinder were facing away from the individual's direction of gaze. A trial was deemed successful if the test subject inhibited the prepotent response of pecking the transparent cylinder, and detoured around to the open ends of the cylinder to gain access to the food reward. Once an individual successfully detoured to the open ends of the cylinder without pecking the transparent walls three times in a row, it was considered to have succeeded at the inhibitory control task. The number of trials taken to succeed was the measure of success. Trials were carried out at one-minute intervals with a maximum of 10 trials, and when possible, all trials were carried out on the same day. Individuals that failed to pass were assigned the maximum score of 10 for statistical analyses. Other studies using the detour reaching task commonly include a training phase in which test subjects are presented with an opaque tube before being exposed to the transparent tube (for example, ref. 25). We did not include the opaque phase in our study, because it generates difficulties in interpretation: success in the transparent condition could be linked to inhibitory control, or could result from the continued application of a learned rule: pecking at the open ends of the cylinder was rewarded in the opaque condition, so individuals may persist with this behaviour in the transparent condition.

**Associative learning.** To test associative learning, we used a colour-discrimination task consisting of a wooden foraging grid (31 × 9 × 4 cm) containing two wells (3.5 cm diameter, 2.5 cm deep; Extended Data Fig. 1b). The presence of only two wells allowed experimental trials to be carried out quickly, reducing the chance of non-focal birds detecting and approaching the task. The wells were covered with PVC lids that fitted exactly into the wells, and were held in place by elastic bands that were threaded through drilled holes in the lids and fastened to either side of the well (Extended Data Fig. 5). This created an axis on which the lids could swivel when pecked. Birds were first trained to search the wells using a shaping

procedure similar to what is described in ref. 39: magpies could gain access to a food reward (a small amount of grated mozzarella cheese) by first being exposed to the wells without any lids covering them, second with the lids partially covering the well, and third with the lid fully covering the well. Lid colour in the training phase was yellow, a colour not used in any of the experimental trials. Once a bird had successfully searched the wells when fully covered by lids three times in a row, it moved onto the experimental trials of the associative learning task.

During experimental trials, the wells were covered by either a dark-blue or light-blue lid. One of these two colours was randomly assigned to be the rewarded colour for each of the test subjects. We used dark and light shades of one colour, rather than distinct colours (for example, red versus yellow), in order to minimize any potential effects of past experience with particular colours on task performance<sup>40</sup>. Following ref. 20, test subjects were allowed to search both wells in the first trial to demonstrate that only one of the wells contained a food reward. In all subsequent trials, the bird was only allowed to search one well before the task was removed. Test subjects had a maximum of one minute to complete the task. There was a minimum interval of one minute between trials (mean ± s.d. = 1.06 ± 0.35 min; range = 1–6 min) with a maximum of 50 trials per individual per day; differences in inter-trial interval were unrelated to group size (Spearman's correlation,  $r_s = 0.048$ ,  $P = 0.121$ ,  $n = 1,027$  trials). If the maximum number of trials was reached on one day, trials were continued the following day. To ensure that the colour was the cue being associated with a food reward, rather than location, the position of the baited well was pseudo-randomized and was never on the same side of the foraging grid for more than three consecutive trials. Furthermore, both wells were wiped with cheese to control for olfactory cues. Following ref. 20, an individual was considered to have succeeded at the task when it pecked the rewarded colour in at least 10 out of 12 consecutive trials (10/12 correct represents a significant deviation from random binomial probability; binomial test:  $P = 0.039$ ). The number of trials taken to reach this criterion (including the final 12 trials) was the associative learning score.

**Reversal learning.** Twenty-four hours after the completion of the associative learning task, individuals were tested on a reversal learning task. The same foraging grid was presented; the only difference being the colour of the rewarded lid was reversed from that of the associative learning task. Otherwise the experimental protocol and the criteria for passing were the same as the associative learning task described above.

**Spatial memory.** The spatial memory task consisted of a wooden foraging grid (40 × 36 × 4.5 cm), containing eight wells (3.5 cm diameter, 2.5 cm deep). The wells were equidistant from one another (6 cm between wells) and were arranged in three rows, with the first row containing two wells, the second row four wells and the third row two wells (Extended Data Fig. 1c). The wells were covered with light-blue lids that were the same as those used in the associative and reversal learning experiments, so no training phase was necessary. Following the protocol described in ref. 20, the experiment consisted of five phases. One of the eight wells was randomly chosen to be the baited well, containing a food reward in all phases of the experiment. The first phase was a 'baseline' trial in which individuals searched the foraging grid for the baited well. Once the test subject had located and eaten the food reward, the foraging grid was removed. Five minutes after the baseline trial, the second 'training' phase was carried out, during which the same well was baited, and the test subjects had to search for the food reward again. The third and fourth phases were test trials in which subjects were presented with the foraging grid 24 and 48 h after the training phase, respectively. The cumulative number of wells searched before locating the rewarded well in the third and fourth phases of the experiment was the spatial memory score, thus higher scores indicate worse performance. To control for olfactory cues, the foraging grid was presented a fifth time as an unrewarded 'probe' trial<sup>20</sup> (five minutes after the 48-h post-training phase trial), in which the grid was rotated 180 degrees, and without a baited well. The foraging grid would appear identical to the magpie, but the position of the previously baited well would be on the opposite side of the grid compared to the other phases of the experiment. If the test subject had remembered the location of the rewarded well in the experimental phases, one would predict that it would search the well opposite the previously baited well. If the test subjects were using olfactory cues to locate the rewarded well, one would predict that the previously baited well would be searched first. To investigate whether birds were using olfactory cues to locate the food reward a paired *t*-test was carried out to see whether there was a difference between the number of wells searched in the 48-h post-training phase trial and the fifth trial (see Supplementary Discussion for results). The number of wells searched in the fifth presentation did not count towards the spatial memory score.

To ensure that we tested individual performance, and to control for the potentially confounding effect of social learning or social interference, all trials were carried out in conditions as close as possible to social isolation. This was achieved by ensuring that no other birds were within 10 m of the bird being tested. This was

possible as magpies often forage over 10 m away from each other. If another bird approached during an experimental trial, the trial was discontinued. To investigate whether individual performance was affected by social learning, we included 'test order' as an explanatory term in the analyses investigating factors affecting performance. This allowed us to verify that individuals tested later within a group (who could therefore have had opportunities to observe previous group members being tested) did not perform better than those tested earlier. Tasks were placed directly in front of the test subjects. Experiments were run between 05:00 and 10:00 and were recorded live by the observers (B.J.A. and E.K.E.). One observer recorded individual performance, while the other recorded neophobia (defined as the time elapsed between the test subject first came within 5 m of the apparatus and first touching the apparatus), the time spent interacting with the task, and anti-predator behaviour within the group.

**Individual consistency in adult performance—repeatability testing.** Apparent individual differences in cognitive performance in a single round of testing could simply result from stochastic variation or extraneous confounding variables<sup>41</sup>. To determine whether individuals were consistent in their performance, we carried out a second test battery two weeks after the first test battery to test the repeatability of adult cognitive performance. To ensure that individuals could not simply use memory of visual cues from the first round of testing to solve tasks in the second round, we changed the visual appearance of each task, while keeping the causal structure of the task the same. In the associative and reversal learning task the colour of lids was changed to dark green and light green. In the spatial memory task, the location of the rewarded well was changed from the first test battery. In the inhibitory control task, rather than using an open-ended cylinder, we presented food rewards behind a transparent curved wall (30 cm length, 10 cm height; Extended Data Fig. 4d). Other than these changes in the appearance of the tasks, the protocol and criteria for passing were exactly the same as the first cognitive test battery.

**Juvenile cognitive test battery.** Juveniles were presented with a battery of four cognitive tasks at three ages: 100, 200 and 300 days after fledging (Extended Data Fig. 4). Cognitive testing commenced at 100 days after fledging, because by this time, individuals spend most of their time foraging independently<sup>31</sup>. The same four cognitive traits (inhibitory control, associative learning, reversal learning and spatial memory) were quantified at each age by presenting individuals with cognitive test batteries containing causally identical but visually distinct versions of each of the four tasks (Extended Data Fig. 4). This ensured the same cognitive traits were tested at each age, while making sure the tasks were not the same in appearance, minimizing the potentially confounding effect of memory.

To quantify inhibitory control at 100 days after fledging, we presented individuals with the same detour reaching task used in the adult cognitive test battery (Extended Data Figs 1a, 4a), and used the same experimental protocols and criteria for succeeding at the task. At 200 days after fledging, rather than using a transparent open-ended cylinder, food rewards were presented behind a transparent curved wall (32 cm length, 12 cm height; Extended Data Fig. 4d). At 300 days after fledging, individuals were presented with a detour reaching task consisting of a transparent 'umbrella'; the food reward could be accessed by detouring underneath the transparent Perspex dome (55 cm circumference, 8 cm height; Extended Data Fig. 4g). Regardless of the differences in appearance, the criteria for passing the inhibitory control tasks at 200 and 300 days after fledging were the same as for the first detour reaching task presented at 100 days after fledging.

Spatial memory was quantified at 100 days after fledging by presenting individuals with a wooden foraging grid (40 × 26 × 4 cm) containing six wells (3.5 cm diameter, 2.5 cm deep) covered with lids as used for the associative and reversal learning tasks (Extended Data Fig. 4c). One of the six wells was randomly assigned to be the rewarded location for all phases of the experiment. The spatial memory experiment consisted of two phases; first the grid was presented in a baseline trial, in which individuals were able to search for the rewarded location. A memory trial was carried out five minutes later, during which individuals were presented with the foraging grid in the exact same arrangement a second time. The number of wells searched before locating the food reward in the memory trial was the spatial memory score. At 200 and 300 days after fledging the same experiment was carried out, although we ensured that a different well was randomly assigned as the rewarded location (Extended Data Fig. 4f, i).

We were unable to quantify individual performance in associative and reversal learning at 100 days after fledging, because individuals took a prohibitive amount of trials to complete the tasks (no individuals succeeded within 20 trials). Associative learning was quantified at 200 days after fledging by presenting test subjects with a wooden foraging grid (41 × 35 × 4 cm) containing 20 wells (3.5 cm diameter, 2.5 cm deep), covered with 20 plastic lids; 10 a light-blue colour and 10 a dark-blue colour (Extended Data Fig. 4e). Wells covered with lids of one colour were randomly assigned to be rewarded for the duration of the trials, when these lids were pecked, a food reward could be accessed. Test subjects were considered to have passed the

associative learning task when they chose the rewarded well in eight out of the first nine wells searched; this represents a significant deviation from binomial probability (binomial test:  $P = 0.039$ ). The number of trials taken to reach this criterion was the associative learning score. Individuals received a maximum of 10 trials; those that failed to pass were assigned a score of 10 for statistical analyses. At 300 days after fledging rather than light- and dark-blue lids, light- and dark-green lids were used (Extended Data Fig. 4h). Other than the change in lid colour, all protocols and criteria for passing remained the same.

At each developmental stage (200 and 300 days after fledging), reversal learning was quantified 24 h after the successful completion of the associative learning task. The protocol and criteria for passing the reversal learning tasks were the same as the associative learning task, except that the previously unrewarded colours were now rewarded.

Similar to the cognitive testing carried out on adults, all trials were carried out on juveniles in isolation. This was achievable because by 100 days after fledging, juveniles are foraging independently.

**Life-history data collection.** To obtain measures of reproductive success for individual birds, we collected life-history data on the study population over three years. This was collected through a combination of behavioural focal follows on individuals, brood observations and ad libitum data collected while watching the whole group (for details see refs 31, 33). The extensive life-history database developed from these observations allowed us to determine the number of hatched clutches, the number of nestlings that fledged and the number of fledglings surviving to independence for each adult female in the study population per annum. In addition, the behavioural focal observations, brood observations and ad libitum data allowed us to quantify the amount of food adults provisioned to young. Fledglings were considered to have survived to independence when they reached three months after fledging. At this age, magpies forage independently and are fed by adults infrequently<sup>31</sup>. In addition to these three proxies of fitness, we also recorded the number of breeding attempts by females—a breeding attempt was considered to have occurred if a female was observed incubating on a nest. The mother was assumed to be the bird incubating at the nest (there is no evidence of egg-dumping or shared incubation in this subspecies, so there was only ever one female incubating a given nest). Groups were visited at least once a week during the breeding season, providing accurate measurements of the number of breeding attempts made per female, and accurate hatch and fledge dates for all nests. Clutches were considered to have hatched when adults started bringing food to the nest, or if we could see young in the nest. As many nests were upwards of 20 m high, we were unable to accurately determine clutch size to use as an additional measure of reproductive success.

All methods were performed in accordance with the guidelines and regulations of the University of Western Australia, and were approved by the University of Western Australia Animal Ethics Office (RA/3/100/1272).

**Statistical analyses. Adult cognitive performance.** To determine the factors influencing individual variation in cognitive ability, we analysed cognitive performance using generalized linear mixed models (GLMM) with either a Poisson distribution with a logarithmic link (inhibitory control) or a negative binomial distribution with a logarithmic link to account for overdispersion (associative learning, reversal learning and spatial memory). Cognitive performance was measured as the number of trials taken to pass the task. In addition to the potential cognitive demands of living in larger social groups, it is possible that indirect effects of group size on energy intake and task attention could generate group-size effects on cognitive performance<sup>41,42</sup>. We therefore included neophobia (defined as the time taken to interact with the task once being within 5 m of it), body mass and foraging efficiency as explanatory terms in the analysis, as well as sex, the sex ratio of males to females in the group, the order tested within the group and group size. Group identity was included as a random term in all models.

To determine whether body condition (body mass, accounting for skeletal size) could explain the variation in cognitive performance, we included mass (in grams) and tarsus size (in mm; a common analysis of skeletal size in birds) as covariates in an additional analysis on a subset of individuals for which both of these morphometric analyses were available ( $n = 27$ ). Dominance status was not included as an explanatory variable, because there is no clear dominance hierarchy within magpie groups. Adult age and immigration status were not included as explanatory variables, because the fledge date and natal origins of some of the adults in our population is unknown (Australian magpies are very long-lived, living up to 25 years in the wild<sup>32</sup>). We note that among the birds for which the complete life-history is known ( $n = 19$  individuals), there has been no movement between groups.

We analysed our data using a model selection process; terms were ranked in order of their corrected quasi-information criterion (QICc) values (the lowest QICc value has the greatest explanatory power<sup>43</sup>). If a term was more than two QICc units smaller than any other term, then this was judged to explain the observed

relationship in the data better than any other term. If there was more than one term with  $\Delta QICc < 2$  from the 'best' term, had confidence intervals that did not intersect zero and explained more variation than the basic model (the model containing no predictors, just the constant and the random terms), then model averaging was carried out on this top set of models as described in ref. 44. All statistical analyses were carried out using IBM SPSS Statistics software (v.22).

To examine the relationship in performance across tasks, we conducted Spearman's rank pairwise correlations between all four tasks. To determine whether a general cognitive factor explained cognitive performance across all four tasks, we performed a principal component analysis with a varimax rotation. Only principal components with an eigenvalue  $> 1$  were extracted from the analysis. A general intelligence factor has been argued to exist when all four tasks positively contributed to the first principal component and explain  $> 30\%$  of total task variance<sup>22</sup>. Following ref. 20, to assess whether the tasks were associated with the first principal component by chance, we compared the mean and standard deviation of the first component factor weights to the 95% confidence intervals of the means and standard deviations of the first component factor weights from 10,000 simulations. For each simulation, performance within each task was randomized between individuals (using the `randomizeMatrix` function in the `picante` R package<sup>45</sup>), a principal component analysis was performed, and the mean and standard deviation of the first component factor weights were obtained. The 95% confidence intervals were then calculated from the stored means and standard deviations from all the simulations.

Statistical analyses used to calculate estimates of repeatability in cognitive performance between the first and second cognitive test batteries were carried out in R (v.3.1.1, <http://www.r-project.org>) with the `rptR` package<sup>46</sup> using a linear mixed model repeatability estimate, with a restricted maximum likelihood function (REML).

**Juvenile cognitive performance.** A series of GLMMs were carried out to determine which factors affect cognitive performance in each task. Model selection (using the same approach as for analyses on adult cognitive performance) was then used to determine the most significant predictors of performance in each of the cognitive tasks<sup>43</sup>.

At 100 days after fledging, the response terms used were cognitive performance, in the detour reaching task this was the number of trials until passed and in the spatial memory task it was the number of wells searched. As these were count data, GLMMs with a Poisson distribution were used. The relationship between performance in the detour reaching task and the spatial memory task were examined using a Spearman rank correlation. At 200 and 300 days after fledging, we found evidence of general cognitive performance in juvenile magpies (Extended Data Tables 3, 4); this parameter was therefore used as the response term for analyses investigating factors affecting cognitive performance at 200 and 300 days after fledging.

Explanatory terms included in the models were neophobia, body mass, the stage of the breeding season (early or late), the presence or absence of siblings (from the same brood), group size and the sex ratio of adult males to females in the group. We were unable to include provisioning rate from adults to fledglings as an explanatory term in analyses as these data were only available for a small subset of individuals. Group ID was included as a random term in all models.

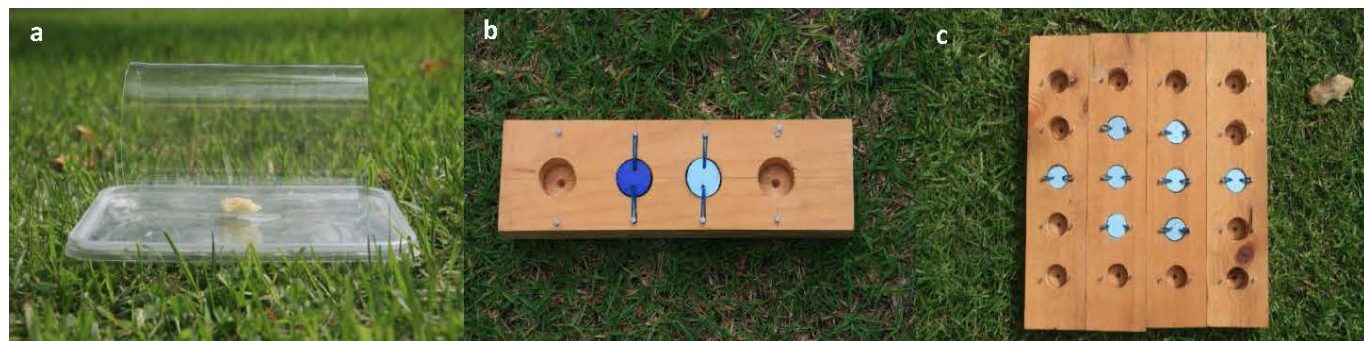
Factors affecting performance across all ages were analysed for each of the four cognitive traits quantified, using GLMMs. Four separate analyses were carried out, with cognitive performance used as the response term. Two additional analyses were carried out. First, to determine factors affecting performance across all ages for both inhibitory control and spatial memory (associative and reversal learning were omitted from this analysis as we only quantified performance at 200 and 300 days after fledging for these traits). Second, we investigated factors affecting

general cognitive performance measured at 200 and 300 days after fledging. Group ID and individual ID were included as random terms. Explanatory terms included were those used for the previous analyses. A model-selection approach was used to determine the most significant terms affecting performance.

**Relationship between cognitive performance and measures of reproductive success.** We carried out three separate analyses to determine the factors affecting three measures of reproductive success: the average number of hatched clutches per year, the average number of nestlings fledged per year and the average number of fledglings surviving to independence per year. We carried out GLMMs, with the analysis of reproductive success as the response term, and group ID was included as a random term. Explanatory terms included in the analyses were body mass, foraging efficiency, group size, the sex ratio of the group and general cognitive performance. General cognitive performance was used as an explanatory term for cognitive performance, because the principal component analysis revealed robust evidence for its existence within females (PC1 accounted for  $> 70\%$  of total variance in female task performance, Supplementary Table 25). We did not include age, because we do not know the exact fledge date for the majority of adult females in the population.

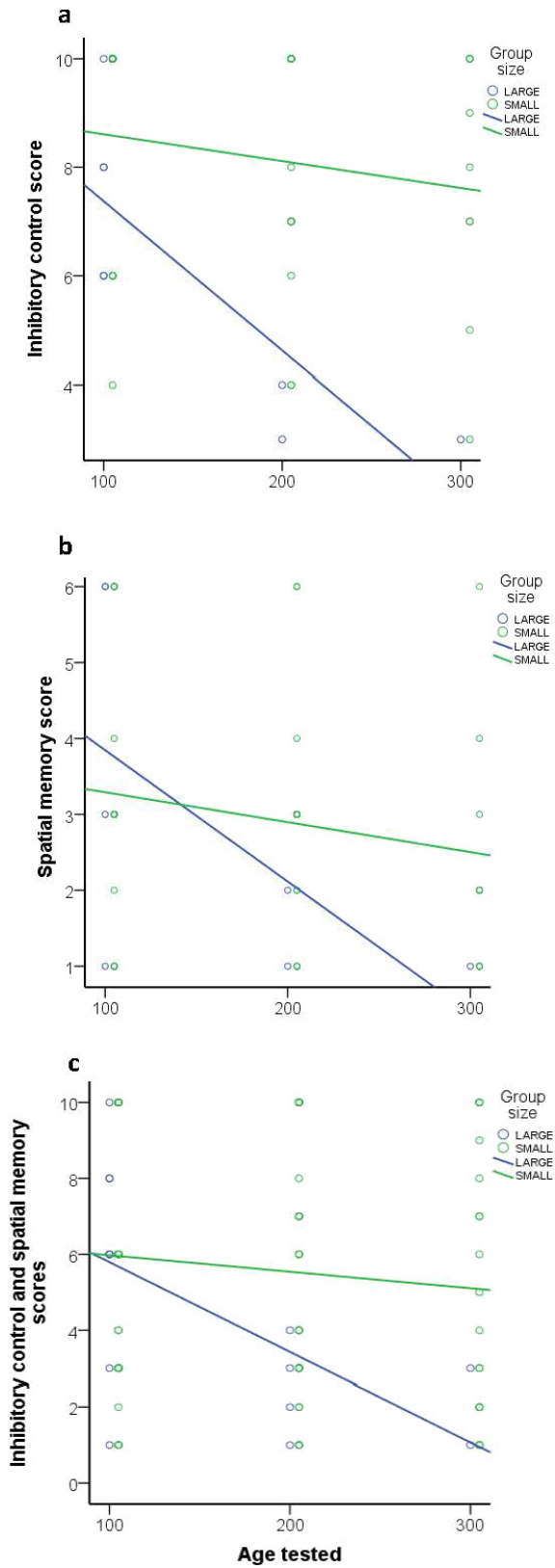
**Data availability.** The data that support the findings of this study have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.ph3h8>). Source Data have been provided for Figs 1–4 and Extended Data Figs 2, 3.

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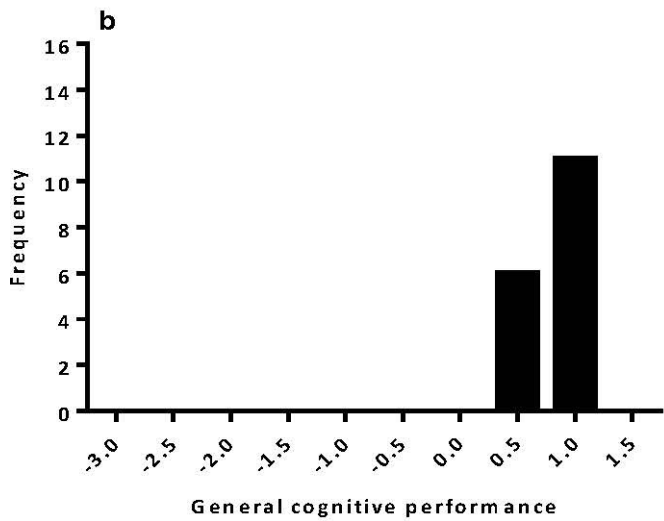
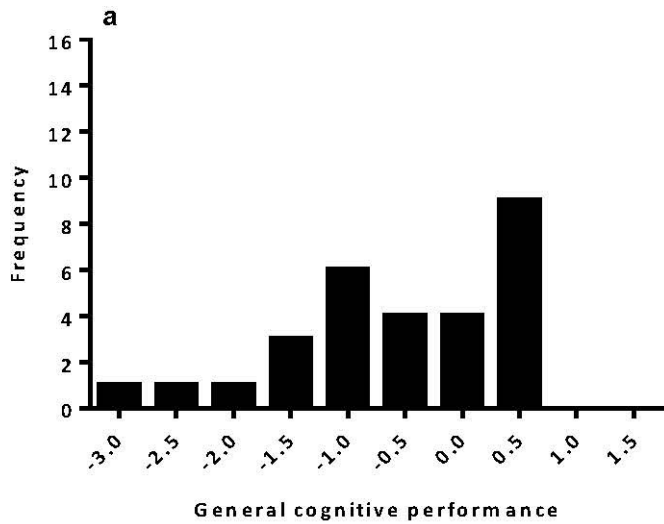


**Extended Data Figure 1 | Adult cognitive test set. a–c,** The cognitive test series used to quantify individual variation in inhibitory control (a), associative and reversal learning (b) and spatial memory (c).





**Extended Data Figure 2 | Developmental trajectory of cognitive performance.** **a, b,** The developmental trajectory of Australian magpies at 100, 200 and 300 days after fledging for two cognitive traits: behavioural inhibition (**a**;  $n = 48$  trials) and spatial memory (**b**;  $n = 46$  trials). **c,** Developmental trajectory for behavioural inhibition and spatial memory combined ( $n = 94$  trials). Green dots, individuals from small groups (containing 1–7 individuals); blue dots, individuals from large groups ( $\geq 8$  individuals). Scores are measured as either the number of trials taken to succeed at the task or the number of locations searched, so lower scores indicate better performance.



**Extended Data Figure 3 | Frequency distribution of general cognitive performance in relation to group size. a, b, Frequency distribution of general cognitive performance among individuals in small groups (a; containing <8 individuals,  $n = 29$  individuals) and large groups (b, >8 individuals,  $n = 17$  individuals).**



**Extended Data Figure 4 | Juvenile cognitive test batteries.** a–i, Cognitive test batteries presented to individuals at 100 (a–c), 200 (d–f) and 300 (g–i) days after fledging, containing four tasks designed to quantify inhibitory control (a, d, g), associative and reversal learning (b, e, h) and spatial memory (c, f, i). b is shown in black and white, because individuals were

unable to complete the associative and reversal learning tasks at 100 days after fledging. Red circles indicate that individuals had to search a different location at each age tested in order to obtain the food reward in the spatial memory task.



**Extended Data Figure 5 | Example of the lids used in the cognitive tasks.** The lids used in the associative learning, reversal learning and spatial memory tasks. The lids were held firmly in place by elastic bands,

and swivelled when pecked, allowing individuals to search wells for their contents.

**Extended Data Table 1 | Principal component analysis (adults)**

Task	PC1
Inhibitory control	0.703
Associative learning	0.789
Reversal learning	0.870
Spatial memory	0.841
Eigenvalue	2.582
% of total variance explained	64.56

Results of the principal component analysis for adult magpies that completed all four tasks. All four tasks positively contributed to the first principal component extracted with an eigenvalue >1.  $n = 46$  individuals.

**Extended Data Table 2 | Repeatability of cognitive performance**

Task	Repeatability	SE	Confidence intervals	P
Inhibitory control	0.806	0.049	0.691, 0.882	<0.0001
Associative learning	0.970	0.01	0.946, 0.983	<0.0001
Reversal learning	0.975	0.008	0.954, 0.986	<0.0001
Spatial memory	0.932	0.021	0.879, 0.963	<0.0001

Estimations of repeatability for the first and second series of cognitive tests. Inhibitory control,  $n = 56$  individuals; associative learning,  $n = 46$  individuals; reversal learning,  $n = 46$  individuals; spatial memory,  $n = 46$  individuals.

**Extended Data Table 3 | Principal component analysis (200 days after fledging)**

Task	PC1
Inhibitory control	0.571
Associative learning	0.916
Reversal learning	0.941
Spatial memory	0.737
Eigenvalue	2.593
% of total variance explained	64.837

Results of the principal component analysis for magpies that completed all four tasks at 200 days after fledging. All four tasks positively contributed to the first principal component extracted with an eigenvalue  $>1$ .  $n = 15$  individuals.

**Extended Data Table 4 | Principal component analysis (300 days after fledging)**

Task	PC1
Inhibitory control	0.675
Associative learning	0.947
Reversal learning	0.972
Spatial memory	0.957
Eigenvalue	3.215
% of total variance explained	80.363

Results of the principal component analysis for magpies that completed all four tasks at 300 days after fledging. All four tasks positively contributed to the first principal component extracted with an eigenvalue  $>1$ .  $n = 10$  individuals.



## Life Sciences Reporting Summary

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### ▶ Experimental design

#### 1. Sample size

Describe how sample size was determined.

No sample size calculation was performed. Sample size was dictated by the number of individuals in our study population. These sample sizes were sufficient for the analyses we carried out, taking into account the number of explanatory terms and repeated terms in the models used for statistical analyses.

#### 2. Data exclusions

Describe any data exclusions.

No data were excluded from the analyses.

#### 3. Replication

Describe whether the experimental findings were reliably reproduced.

All attempts at replication were successful; the second cognitive test battery was carried out on adults in the study population to determine repeatability of cognitive performance. Individual performance was highly repeatable.

#### 4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Randomization was not relevant to this study. All individuals in the study were tested on the same cognitive tests.

#### 5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Blinding was not relevant to the study as cognitive testing was carried out on a wild population of Australian magpies.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

#### 6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g.  $P$  values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

## ► Software

Policy information about [availability of computer code](#)

### 7. Software

Describe the software used to analyze the data in this study.

IBM SPSS Statistics software (version 22) was used to carry out generalized linear mixed modeling. R (version 3.1.1, <http://www.r-project.org>) was used to calculate repeatability estimates, using the rptR package.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

## ► Materials and reagents

Policy information about [availability of materials](#)

### 8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

No unique materials were used.

### 9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used.

### 10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No eukaryotic cell lines were used.

b. Describe the method of cell line authentication used.

No eukaryotic cell lines were used.

c. Report whether the cell lines were tested for mycoplasma contamination.

No eukaryotic cell lines were used.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

No commonly misidentified cell lines were used.

## ► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

### 11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

Australian magpies (*Cracticus tibicen dorsalis*) were used in the study. Both males and females, and fledglings, juveniles and adults were tested on cognitive test batteries.

Policy information about [studies involving human research participants](#)

### 12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

The study did not involve human research participants.