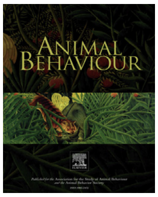
Animal Behaviour 188 (2022) 35–44

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Urban noise does not affect cognitive performance in wild Australian magpies

Farley Connelly [a], [b], *, Michelle L. Hall [a], [c], [d], Robin D. Johnsson [b], Shona Elliot-Kerr [a], Belinda R. Dow [a], John A. Lesku [b], Raoul A. Mulder [a]

[a] *School of BioSciences, The University of Melbourne, Melbourne, Victoria, Australia*
[b] *School of Agriculture, Biomedicine and Environment, La Trobe University, Melbourne, Victoria, Australia*
[c] *Bush Heritage Australia, Melbourne, Victoria, Australia*
[d] *School of Biological Sciences, The University of Western Australia, Perth, Western Australia, Australia*

ARTICLE INFO

Article history:
Received 8 September 2021
Initial acceptance 2 December 2021
Final acceptance 28 February 2022

MS. number: 21-00530R

Keywords:
anthropogenic noise
behavioural flexibility
bird
cognition
executive function
learning
memory
noise pollution
urban noise

City-living animals are exposed to pervasive human-generated noise from traffic and industry. There is growing evidence that this exposure may have deleterious physiological and behavioural effects. Cognitive processes could be particularly sensitive to the disruptive effects of noise, but little is known about the potential effects of noise on cognition and cognitive development. We compared the cognitive performance of wild, urban-dwelling Australian magpies, *Cracticus tibicen tyrannica*, in resident groups exposed to differing levels of environmental noise. We found no evidence that cognitive performance (measured across four behavioural tests estimating different aspects of cognitive ability) covaried with the amplitude of ambient anthropogenic noise across an urban gradient of noise levels. With the exception of one task (spatial memory), the cognitive development of adolescent magpies measured at two different developmental stages (on average 160 and 290 days postfledging) was also similar, irrespective of whether they had been exposed to relatively high or low levels of anthropogenic noise. Our results suggest that levels of anthropogenic noise typical of city parklands do not appear to negatively impact general cognitive performance.

Noise caused by human activity is rapidly changing Earth's natural soundscapes (Duarte et al., 2021; Kight & Swaddle, 2011; Shannon et al., 2016). Aircraft or vehicle noise can now be heard in some of the planet's most pristine and protected environments (Buxton et al., 2017). Negative effects of urban noise on humans are relatively well understood, including severe health-related impacts such as hearing damage (Passchier-Vermeer & Passchier, 2000), cardiovascular disease (Fyhri & Aasvang, 2010), heightened stress (Basner et al., 2014) and disturbed sleep (Frei et al., 2014; Halperin, 2014). There is emerging evidence that high levels of anthropogenic noise can have negative impacts on wildlife, both in terrestrial and aquatic environments (Grunst et al., 2021; Kunc & Schmidt, 2019). For instance, in terrestrial animals, noise can affect communication (Shannon et al., 2016; Slabbekoorn & Peet, 2003; Slabbekoorn & Ripmeester, 2008), decrease survival (Francis & Barber, 2013; Kight & Swaddle, 2011; Raap et al., 2017; Schroeder et al., 2012) and breeding success (Ernstes & Quinn, 2016; Potvin & MacDougall-Shackleton, 2015), augment stress responses (Chloupek et al., 2009; Kleist et al., 2018; Wright et al., 2007), alter the frequency and timing of vocalizations (Fuller et al., 2007; Guo et al., 2016; Kight & Swaddle, 2015; Potvin et al., 2014) and interfere with migratory paths (McClure et al., 2013, 2017).

While there is now some insight into the behavioural and physiological impacts of anthropogenic noise, surprisingly little is known about how noise might affect cognitive development and performance, including learning, memory, behavioural flexibility and executive function. This omission is significant because of putative mechanistic links between noise, cognition and fitness. For example, children exposed to environmental noise (i.e. planes, trains and automobiles) showed deficits in speech, reading comprehension and memory consolidation (Basner et al., 2014; Halperin, 2014). In nonhuman animals, noise exposure can negatively impact short-term memory in rats (Kight & Swaddle, 2011; Rabat et al., 2006) and learning, memory, development and motor

---

* Corresponding author.
E-mail address: charles.connelly@unimelb.edu.au (F. Connelly).

https://doi.org/10.1016/j.anbehav.2022.03.021

coordination in mice (Barzegar et al., 2015; Jafari et al., 2018). In addition, noise exposure impaired long-term memory (Funabiki & Konishi, 2003) and vocal development and learning in juvenile zebra finches, *Taeniopygia guttata* (Brumm et al., 2021; Searcy & Nowicki, 2019). Such individual differences in cognitive development may also translate to fitness differences: in some species, individuals that perform better on cognitive tasks show improved reproductive performance (Ashton et al., 2018; Keagy et al., 2009, 2011; Preiszner et al., 2017).

Urban environments can impact animal cognition in myriad ways (Lee & Thornton, 2021), but the contribution of anthropogenic noise to such impacts remains unknown. Birds from urban environments show differences in cognitive performance when compared to birds from rural environments on a variety of tests: reversal learning tasks in common mynas, *Acridotheres tristis* (Federspiel et al., 2017) and great tits, *Parus major* (Cauchoix et al., 2017); foraging tasks in Barbados bullfinches, *Loxigilla barbadensis* (Audet et al., 2016) and house finches, *Haemorhous mexicanus* (Cook et al., 2017) and obstacle removal tasks in great tits (Preiszner et al., 2017). However, urban and rural environments potentially differ in many respects other than soundscape (e.g. habitat type, density and quality, artificial light, predation risk), such that these impacts cannot be unambiguously attributed to noise.

In this study, we explored whether wild Australian magpies, *Cracticus tibicen tyrannica*, exposed to varying levels of urban noise throughout different life stages also varied in cognitive performance and in the acquisition of cognitive skills. Australian magpies are iconic Australian birds and ideal study subjects for investigating this question as they are common, inhabit urban, noise-polluted areas, occupy the same territory for much of their lives, and can be trained to complete cognitive tasks in close proximity to humans (Ashton et al., 2018; Mirville et al., 2016; Rollinson & Jones, 2006). Using a battery of cognitive tests developed and validated for this species (Ashton et al., 2018), we quantified individual performance on four tasks, each estimating a different cognitive function: (1) associative learning (the ability to acquire knowledge through repeated experiences; Morand-Ferron et al., 2016); (2) reversal learning (cognitive flexibility, sometimes referred to as behavioural flexibility; Bond et al., 2007; Izquierdo et al., 2017; Lea et al., 2020); (3) inhibitory control (self-control, or the inhibition of immediate responses; Isaksson et al., 2018; Kabadayi et al., 2016, 2018; MacLean et al., 2014); and (4) spatial memory (the ability to remember the location of resources, territorial borders or threats; Emery, 2006). We tested whether performance varied with the level of long-term urban noise exposure and whether changes in performance during development varied with the level of long-term urban noise exposure.

METHODS

Study Species

The study population consisted of 45 individual Australian magpies belonging to 25 resident groups. The Victorian subspecies *tyrannica* breeds cooperatively and lives in stable territorial groups ranging in size from two to five adults (Kaplan, 2004). Most groups in the study population comprised a dominant male, a dominant female and a subordinate female. Groups cooperate to defend the territory and subordinates are known to participate in alloparental care (Kaplan, 2004), although this was not ubiquitous in this population. Juveniles remained in their territory for about a year, at which point they were forced to leave by the adults. This expulsion usually coincided with the start of the breeding season. In other subspecies, juveniles will remain with their natal group and help raise the next season's brood (cooperative breeding: this was only witnessed in two of 25 groups). In the present study, the age of birds was assessed based on behavioural and physical characteristics. Each bird was assigned to one of two age groups: subadult (residing with natal family, begging behaviour; no or partial adult plumage, darker bill coloration; 0–2 years of age); or adult (breeding or parental behaviour; full adult plumage; 2+ years old). The ages of all birds used to investigate cognitive development were accurate to within a few days as these individuals were observed in the nest, prefledging.

We habituated magpies to human presence by repeatedly visiting territories, training the birds to approach us in response to a specific whistle and providing a small food reward (shredded mozzarella cheese). This level of habituation allowed us to easily capture birds, monitor their health (birds were trained to step onto a scale) and eventually test them. Individuals were initially captured using a manually triggered, baited walk-in trap. To reduce stress and minimize the possibility that birds would subsequently recognize us and react adversely to future encounters, we placed a hood over each individual's head during capture. Individuals were fitted with a uniquely numbered three-digit PVC band on one leg and a uniquely numbered metal band supplied by the Australian Bird and Bat Banding Scheme on the other. Most birds ($N = 38$) that were tested were banded; unbanded magpies ($N = 7$) were identified using a combination of group composition, geographical location and/or unique physical characteristics or plumage patterns. For captured individuals, we measured tarsus length (using dial callipers, to the nearest 0.1 mm) and wing chord (blunt-ended ruler, nearest 1 mm), and calculated scaled mass index (an estimate of body condition; Peig & Green, 2009).

Study Site

The study took place in Melbourne and the Greater Geelong area (Victoria, Australia) between January 2016 and July 2019. We selected groups for inclusion in the study that occupied territories spanning a range of environmental noise levels (sound levels were measured, dBA), and that responded to training. Sound levels across territories ranged from 40 to 65 dBA. The sites with the lowest levels of noise averaged between 40 and 45 dBA (equivalent to the sound of a library), while the loudest sites were between 60 and 65 dBA (equivalent to a busy restaurant). Using an NSRT Sound Level Logger (Convergence Instruments, Quebec, Canada) at 48 kHz sampling rates, we recorded sound levels (in dBA) at two or three geographically dispersed locations within each territory. Loggers were placed in trees approximately 5 m above the ground. The microphone was always directed downwards to protect the recorder from both potential rainfall and animals (walking or perching on them) and to maintain consistency across sites. Sound levels were recorded every second over one weekend and weekday (using sunrise/sunset as a starting point), as sound levels could vary between weekdays and weekends (Fig. A1). Recordings were always taken during or immediately following the testing period to best capture what the bird was experiencing during the testing process. To determine the noise level experienced by nestlings during early development, sound level loggers were placed close to active nests, either at the base of the nesting tree or in an adjacent tree (within 10 m of the nesting tree). If a nestling recording was taken, it was included in a site's overall sound level average (Table A1). These recordings estimated the amplitude of noise experienced by the nestlings during early development and the noise levels experienced by the parents which spent most of their time during incubation on or near the nest.

Cognitive Testing

Birds were first trained to use the test apparatus. We used a motor skill task to train the magpies to interact with the test boards. This task consisted of a wooden block (30 × 9 cm and 4 cm high) with four wells (3.0 cm deep and 3.3 cm diameter). Each well was covered by a coloured plastic cap (a dark and light shade of yellow and green) held in place by a rubber band looped around nails set on either side of each well, which allowed the caps to rotate. By prodding the cap with their bills, magpies could flip the lid, expose the contents of the well and learn to access a food reward (grated cheese) that was placed in each well. Magpies were presented with the training board until they successfully extracted food from the wells three times in a row. Once successful, they were presented with the first cognitive task.

To assess cognitive performance, 45 magpies (26 adults and 19 subadults) were presented with a test battery consisting of four tasks that differed in their cognitive demands: (1) associative learning; (2) reversal learning; (3) inhibitory control; and (4) spatial memory. Reversal learning constitutes cognitive/behavioural flexibility, and both reversal learning and inhibitory control represent executive functions, processes considered mechanistic or logically based (Grafman & Litvan, 1999; Lea et al., 2020). Tasks were always presented in the same order, and a new task only began once the previous test was completed (details of each task are provided below). We first determined whether an individual was motivated to participate in testing by tossing a piece of cheese across its line of sight. If the bird flew in and ate the cheese, the test board was presented, and testing began. If the bird did not interact with the test board for over 1 min, the board was removed, and another piece of cheese was tossed to assess motivation. If the bird did not eat the cheese, testing would stop. Testing was never conducted on an unmotivated bird. Isolation from other individuals was required during testing to reduce the likelihood of social learning. To do so, testing was suspended if another magpie approached to within 10 m of the focal bird being tested.

Associative learning

We used a colour discrimination task to test how quickly a magpie could associate a food reward with a novel-coloured cap. This task utilized a similar board as the training stage, and therefore required no additional training. The foraging grid (19 × 9 cm and 4 cm high) contained two wells (3.0 cm deep, 3.3 cm diameter; Fig. 1a, b). Each well was covered with a cap of a different shade of the same colour (i.e. blue: navy and sky, Fig. 1a; purple: violet and lilac, Fig. 1b). Shades were used instead of different colours to minimize any potential effects of colour preference (Ashton et al., 2018; Shaw et al., 2015, Teichmann et al., 2020), as in spotted bowerbirds, *Ptilonorhynchus maculatus* (Isden et al., 2013). One well contained a cheese reward; the other well was empty. The colour and shade of the rewarded cap were randomized.

As in the training stage, shredded cheese was used as a reward for a correct trial. In the first trial, magpies were allowed to search both wells to find the reward. In all consecutive trials, an incorrect choice (pecking the unbaited well) cued the removal of the board for 1 min. Test subjects had a maximum of 1 min to interact with the board before it was removed from the testing area. The starting position of the food reward (left or right) was pseudorandomized; we avoided having the reward on the same side for more than three consecutive trials. Fresh cheese was wiped into both wells prior to the start of testing to minimize olfactory cues to the location of the reward. The test was considered complete (the subject 'passed' the test) when the subject was able to select the correct well in 10 of 12

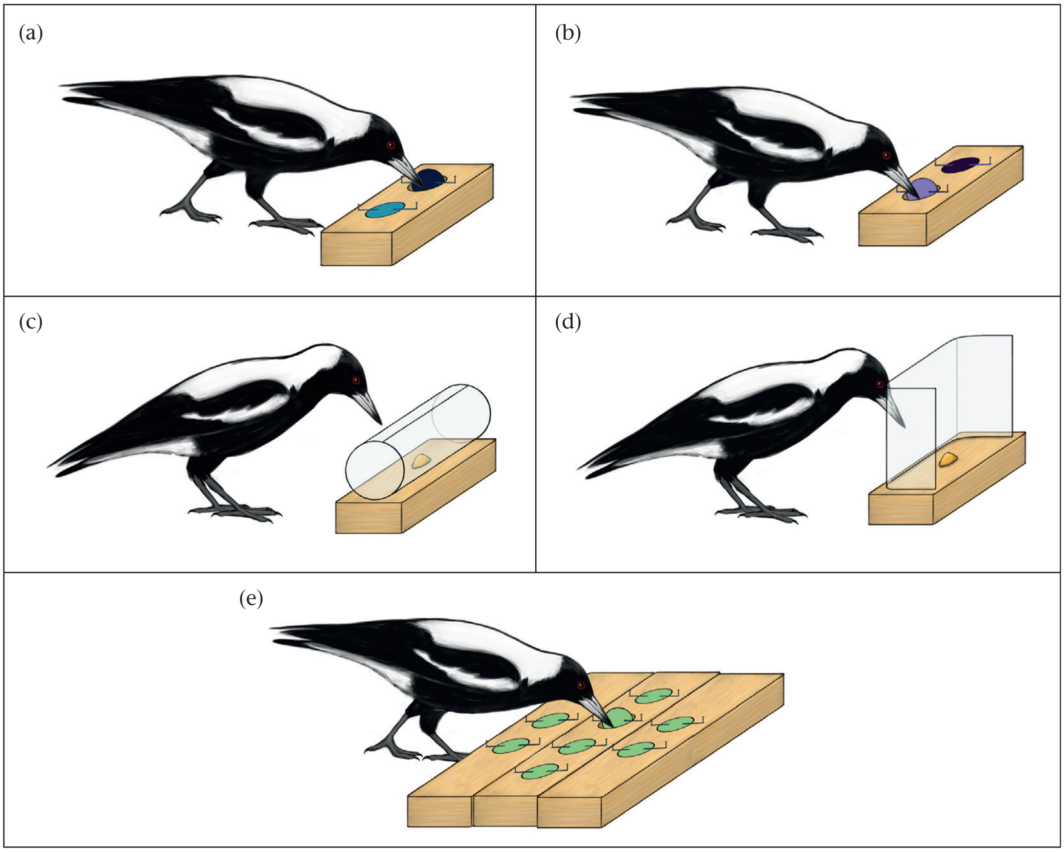


Figure 1. Five cognitive tasks. The cognitive test series presented to individuals to quantify cognitive performance: (a, b) associative and reversal learning (both blue and purple caps shown); (c, d) inhibitory control (cylinder: adult/subadults/age 160 days; wall: age 290 days); and (e) spatial memory. Illustrations by Laura X. Tan.

consecutive trials (10/12 correct choices represents a significant deviation from random binomial probability; binomial test: $P = 0.04$; as in Ashton et al., 2018). If the bird did not complete the task (10/12 correct trials) in a single day, the score would carry over to the next day and testing would continue with trials being added to the previous score. The total number of trials required to reach this criterion (including the final 12 trials) represented the associative learning score. At 290 days, juveniles were presented with the same test; however, to maintain novelty, the colour of the caps was different (i.e. if birds had blue the first time they completed the test, then they would be tested with violet/lilac the second time).

Reversal learning

The reversal learning task was used to test cognitive flexibility, quantifying the number of trials required for a magpie to dissociate the previous association made and learn a new association, inhibiting previously learned behaviours. This task was presented the day after the completion of the associative learning task. The same test board was used (Fig. 1a, b); however, for the reversal learning task, the shade of the cap covering the food reward was switched (i.e. the reward contingency was reversed; associative food well = violet; reversal food well = lilac). The experimental protocol and completion criterion were the same as in the associative learning task. At 290 days, juveniles were presented with the same test, but as described above, the cap colour of the food reward was different.

Inhibitory control

The inhibitory control test quantified a magpie's ability to inhibit a principal response and navigate around an obstacle to reach a reward. In this instance the principal response was to peck the plastic barrier to access the reward. To measure this, we presented magpies with a ‘detour reaching’ task. In this task a food reward (grated cheese) was placed inside a transparent open-ended cylinder (13 cm long × 5 cm diameter) mounted on a small wooden block (13 × 7 cm and 5 cm high; Fig. 1c). The cylinder was presented to the subject at a right angle to its body axis (open ends were positioned out of the magpie's eyeline), to see if it could solve the challenge of accessing the reward.

As with the associative learning task, when first presented with the detour task the subject was given time to explore the test board and find the food. Each trial thereafter counted towards their overall inhibitory score. To achieve a successful trial, the subject needed to avoid pecking the closed walls of the cylinder and instead move to the open ends and reach the food reward. Pecking the transparent cylinder counted as an incorrect score and cued the removal of the task for 1 min. The task was considered complete when the subject correctly detoured the task three consecutive times (same criterion as in Ashton et al., 2018). Magpies were allowed a maximum of 10 trials per day and trials were conducted at 1 min intervals. At 290 days, juveniles were presented with a similar detour task, a transparent plastic ‘wall’ (30 cm long, 15 cm high) mounted vertically onto a wooden block (25 × 9 cm and 4 cm high; Fig. 1d). The same methods and protocols were followed. We did not provide a training phase for this task as other studies have done (e.g. through the exposure of subjects to an opaque tube or wall prior to the transparent one; Kabadayi et al., 2018) because success on detour tests could arguably be linked to ‘a continued application of a learned rule’ in addition to inhibitory control (Ashton et al., 2018).

Spatial memory

The spatial memory task was used to determine a magpie's ability to memorize information regarding food placement and retrieve it later. The task consisted of a board (45 × 27 cm and 4 cm high) containing eight wells (3.0 cm deep, 3.3 cm diameter) to create a foraging grid (Fig. 1e). All the wells were covered with lime green caps (the same colour used in the training board) and utilized the same flipping mechanism as the associative and reversal learning tasks, so no additional training was necessary. Wells were numbered one to eight, front to back, starting with the leftmost well in the first front row. Each bird was randomly assigned a well number and that well contained the food reward for the entirety of the task.

Magpies were presented with the test board five times over a 72 h period: twice on the first day, once on the second day and twice on the third day (Ashton et al., 2018). Each testing event was deemed complete when the magpie found the reward (similar to Ashton et al., 2018). The first presentation of the board was the training event; magpies were presented with the board and allowed to search for the baited well. Once the baited well was discovered, the event was considered complete, and the board was removed. After 5 min the same well was rebaited, and the board was again presented for the initial event, which followed the same protocol. The third and fourth events occurred 24 h and 48 h later, respectively, following the same protocol as the training event. The final event, which controlled for olfactory cues (odour event), was performed 5 min after the fourth event. For the odour event, the board was rotated 180 degrees and no reward was placed in the previously baited well. The foraging grid appeared identical to the subject, but the previously baited well was on the opposite side of the test board. This allowed us to assess whether magpies were using olfactory cues to find the location of the rewarded well. The total number of trials required to find the reward in the 24 h and 48 h events determined a magpie's spatial score. At 290 days, the same methods and protocols were followed, but a different well was randomly assigned to hold the reward.

In total, 45 birds completed at least one of the tasks. Not all birds completed every task because sometimes birds disappeared before completing the full battery of tests primarily due to loss of territory. A subset of 12 birds completed a combination of tasks twice: four adults completed the associative and reversal learning tasks twice as testing was interrupted by the breeding season and the test series had to be reset, and eight subadults completed all tasks twice.

Cognitive Development

To test for longitudinal changes in cognitive performance through development, we presented eight magpies with the test battery at two different ages: mean 160 days (range 133–219) and mean 290 days (range 270–44) postfledging. Testing began at 160 days postfledging because at this age magpies begin to feed independently and can easily be isolated from their parents and siblings for testing. At 160 days, juveniles were presented with the same test battery as the adults. Minor aspects of the task were modified (i.e. the colour of the caps for associative and reversal learning) between the 160 and 290 days to introduce novelty and test for genuine learning while allowing the comparison of scores. The same protocol and criterion for success applied to the subadult and adult testing was used for juveniles at on average 160 and 290 days.

Statistical Analysis

We conducted all analyses in the statistical environment R version 3.5.2 (R Development Core Team, 2018). Using the R package lme4, we fitted generalized linear mixed models (GLMM) with a Poisson error structure and logarithmic link to investigate variables affecting performance of all birds across associative learning ($N = 45$ birds), reversal learning ($N = 43$), inhibitory control ($N = 37$) and spatial memory ($N = 33$) tasks. The GLMM contained all probable explanatory values: sound level, age, sex, body condition (scaled mass index) and group size. Random effects included individual birds and the identity of the group the birds belonged to. We fitted a linear mixed-effect model (LMM) with the explanatory value sound levels, controlling for group, to compare performance between the two developmental ages (160 and 290 postfledging) calculated as the proportional difference: (number of trials to reach criterion at 290 − number of trials to reach criterion at 160)/total number of trials to reach criterion at both ages. An LMM was used instead of a GLMM because of the small sample size of birds that completed the test at two age classes ($N = 8$). A series of GLMMs and LMMs were conducted to determine which factors impacted cognitive performance in each task. The final models included the most significant predictors of performance in each of the cognitive tasks, while preventing overfitting and reducing variance. In addition, a paired t test was used to determine whether magpies used olfactory cues during spatial testing. All P values for significant terms were obtained from these analyses.

Ethical Note

All methods were performed in accordance with the guidelines and regulations of The University of Melbourne and were approved by The University of Melbourne Office for Research Ethics and Integrity, Animal Ethics (ID No. 1714094). Permission to capture, band and test birds was granted by the Department of Environment, Land, Water and Planning (10008264) and the Australian Bird and Bat Banding Scheme (ABBBS number 1405).

RESULTS

Effect of Urban Noise Level and Age on Cognitive Performance

There was no relationship between performance on any of the tasks and the sound level within the territory, sex or body condition (Table 1, Fig. 2).

For the associative learning task, there was no significant difference in the number of trials to reach criterion by adults (27.8 ± 26.7; $N = 26$) and subadults (40.7 ± 36.0; $N = 19$; Table 1). For the reversal learning task, there was similarly no difference between the number of trials to reach criterion for adults (50.1 ± 26.8; $N = 24$) and subadults (54.7 ± 33.2; $N = 19$; Table 1). Adults took fewer trials to reach criterion than subadults to pass the inhibitory control task (8.3 ± 7.0 trials by 19 adults; 16.3 ± 14.1 by 18 subadults; Table 1). Finally, adults required fewer trials to reach criterion (6.1 ± 3.7; $N = 17$) than subadults (9.6 ± 7.2; $N = 16$; Table 1) in the spatial memory task. In the olfactory test, we determined that the chances of using olfactory cues compared to randomly selecting a different well was not statistically significant ($t = 1.90$, $P = 0.07$).

Table 1
Effects of model variables on performance in the four cognitive tasks

Model variables	Estimate ± SE	z	P
Associative learning			
Sound level	0.01 ± 0.02	0.50	0.62
Age	0.46 ± 0.33	1.40	0.16
Sex	−0.04 ± 0.38	−0.11	0.91
Body condition	0.003 ± 0.004	0.82	0.41
Group size	**0.43 ± 0.20**	**2.11**	**0.03**
Reversal learning			
Sound level	−0.003 ± 0.01	−0.22	0.83
Age	0.02 ± 0.20	0.08	0.94
Sex	−0.21 ± 0.24	−0.87	0.39
Body condition	−0.002 ± 0.002	−0.99	0.32
Group size	−0.01 ± 0.05	0.28	0.78
Inhibitory control			
Sound level	−0.01 ± 0.02	−0.76	0.45
Age	**0.83 ± 0.28**	**2.92**	**<0.01**
Sex	0.08 ± 0.38	0.22	0.82
Body condition	−0.002 ± 0.004	−0.63	0.53
Group size	−0.25 ± 0.20	−1.24	0.22
Spatial memory			
Sound level	−0.02 ± 0.02	−1.12	0.26
Age	**0.56 ± 0.27**	**2.04**	**0.04**
Sex	−0.08 ± 0.34	−0.22	0.82
Body condition	−0.001 ± 0.005	−0.24	0.80
Group size	−0.04 ± 0.18	−0.21	0.83

Results of GLMM analysis of the factors affecting performance (defined as the number of trials to reach completion criteria) of all birds across associative learning ($N = 45$ birds), reversal learning ($N = 43$), inhibitory control ($N = 37$) and spatial memory ($N = 33$) tasks. Random effects included individual birds and their natal group. Data were fitted to a Poisson distribution with a logarithmic link function. Statistically significant results are in bold.

Birds in larger groups completed the associative learning task in fewer trials than birds in smaller groups (Table 1). This relationship was not observed with any other task (Table 1).

Effect of Urban Noise on Cognitive Development

Eight individuals completed all four tasks at both 160 and 290 days postfledging. At 160 days, birds averaged 51.1 ± 44.4 trials to reach criterion on the associative learning task, 75.8 ± 42.0 trials to reach criterion reversal learning task, 24.8 ± 20.3 trials to reach criterion on the inhibitory control task and 11.8 ± 9.7 trials to reach criterion on the spatial memory task. At 290 days postfledging, birds performed significantly better on the inhibitory task averaging 6.1 ± 3.2 trials to reach criterion ($t = -2.69$, $P = 0.03$). No difference was seen on any of the other tasks at 290 days postfledging: birds averaged 31.9 ± 29.6 trials to reach criterion on the associative learning task ($t = -1.02$, $P = 0.32$), 56.5 ± 19.4 trials to reach criterion on the reversal learning task ($t = -1.18$, $P = 0.26$) and 7.1 ± 5.9 trials to reach criterion on the spatial memory task ($t = -1.15$, $P = 0.27$).

Change in performance (proportional difference) on all tasks at 160 and 290 days was unaffected by sound level with the exception of spatial memory: magpies from habitats with increased sound levels required more trials to reach criterion on the spatial memory task at 290 days than at 160 days compared to birds from habitats exposed to lower sound level (Table 2, Fig. 3).

DISCUSSION

Urban Noise and Cognitive Performance

Our results suggest that variation in the long-term exposure of anthropogenic noise has little or no effect on cognitive performance of either juvenile or adult magpies. We found no effect of noise on cognitive performance on any of the tasks. Age was the best predictor of performance on tasks, with adults performing better than subadults on two of the four tasks (inhibitory control and spatial memory).

While noise levels of comparable amplitude to those measured in our study population can affect reproductive success in other species in a laboratory context (zebra finches, Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2019), it is possible that deleterious impacts of prolonged ambient noise on cognitive performance in magpies only occur at higher noise amplitudes. Other studies exploring the impact of noise exposure on cognitive performance included noise levels above 70 dBA (Barber et al., 2010; Irgens-Hansen et al., 2015; Rabat et al., 2005); in a few cases, the study animals were exposed to noise levels with double the amplitude (10 or more dBA higher) of our loudest site. If the study sites we used were comparatively ‘quiet’, chronic exposure to noise at louder sites might still result in declines in performance on the cognitive tests. We were unable to test this because in our study such areas were either inaccessible (at airports or directly adjacent

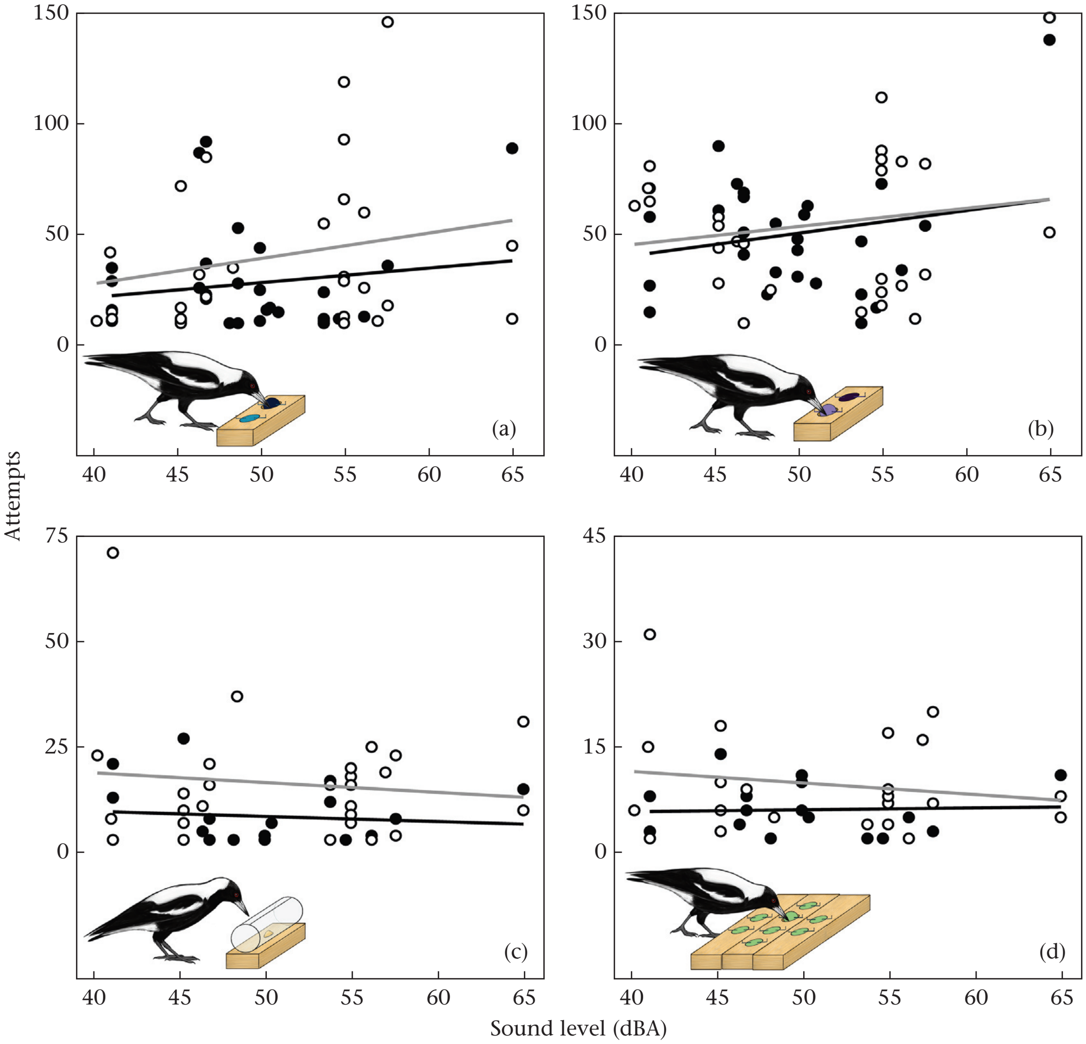


Figure 2. Effect of sound level on cognitive performance. A total of 45 magpies from territories spanning a range of sound levels, tested on one or more of the tasks within the test battery: (a) associative learning (*N* = 45), (b) reversal learning (*N* = 43), (c) inhibitory control (*N* = 37) and (d) spatial memory (*N* = 33). Performance (number of attempts) on each task for each bird is shown for adults (black circles) and subadults (open circles). Illustrations by Laura X. Tan.

Table 2
Effect of sound level on cognitive development from 160 to 290 days postfledging

Task	Estimate ± SE	*t*	*P*
Associative learning	−0.02 ± 0.05	−0.43	0.68
Reversal learning	−0.04 ± 0.04	−1.07	0.35
Inhibitory control	0.01 ± 0.03	0.27	0.80
Spatial memory	**0.10 ± 0.03**	**3.16**	**0.02**

Results of linear mixed-effect models analysing the effect of sound levels on the proportional differences in performance ([performance at 290 days − performance at 160 days]/cumulative performance at each age) on associative learning, reversal learning, inhibitory control and spatial memory tasks. *N* = 8 birds. Social group was treated as a random effect. Statistically significant result is in bold.

to freeways), lacked resident magpies, or included resident populations of magpies unaccustomed to human interaction, which we were unable to train. Nevertheless, several studies suggest that the range across which we measured noise is typical of urban environments. For instance, Potvin et al. (2011) found that over 99% of all ambient noise measured over more than 1 million km^2 of rural and urban habitats across southeast Australia land was below 70 dBA. Thus, while habitats with noise at such high amplitudes exist (Kleist et al., 2018; Wolfenden et al., 2019), they are uncommon, and may not be representative of the conditions experienced by most urban wildlife.

Adults did not outperform subadults on association or reversal learning. This suggests that these tasks (single tests, not serial) can easily be learned by magpies early in life, before they become nutritionally independent (when we began testing), perhaps due to the highly exploratory nature of subadult magpies. Birds are skilled at performing associative and discrimination tasks (Emery, 2006), and pigeons, *Columba livia*, have been shown to discriminate between photos of other pigeons (Poole & Lander, 1971), cars, humans and flowers (Bhatt et al., 1988). While providing a measure of cognitive performance for which to compare magpies, the simple associative learning task presented does not represent a higher cognitive process (Emery, 2006; Wasserman & Miller, 1997) and therefore may not be strongly impacted by age. In contrast, reversal learning is a complex task that challenges an executive function, cognitive flexibility (Aljadeff & Lotem, 2021; Bond et al., 2007; Izquierdo et al., 2017; Lea et al., 2020). However, it is possible that the reversal task we presented would have been more effective if performed repeatedly instead of only once. Research suggests that serial reversal and midsession reversal tasks may provide a better measure of individual variation through the comparison of improving performances across successive reversals (Bond et al., 2007; Emery, 2006; Laschober et al., 2021). Moreover, a recent study showed that a two-step, multiple-choice reversal test with

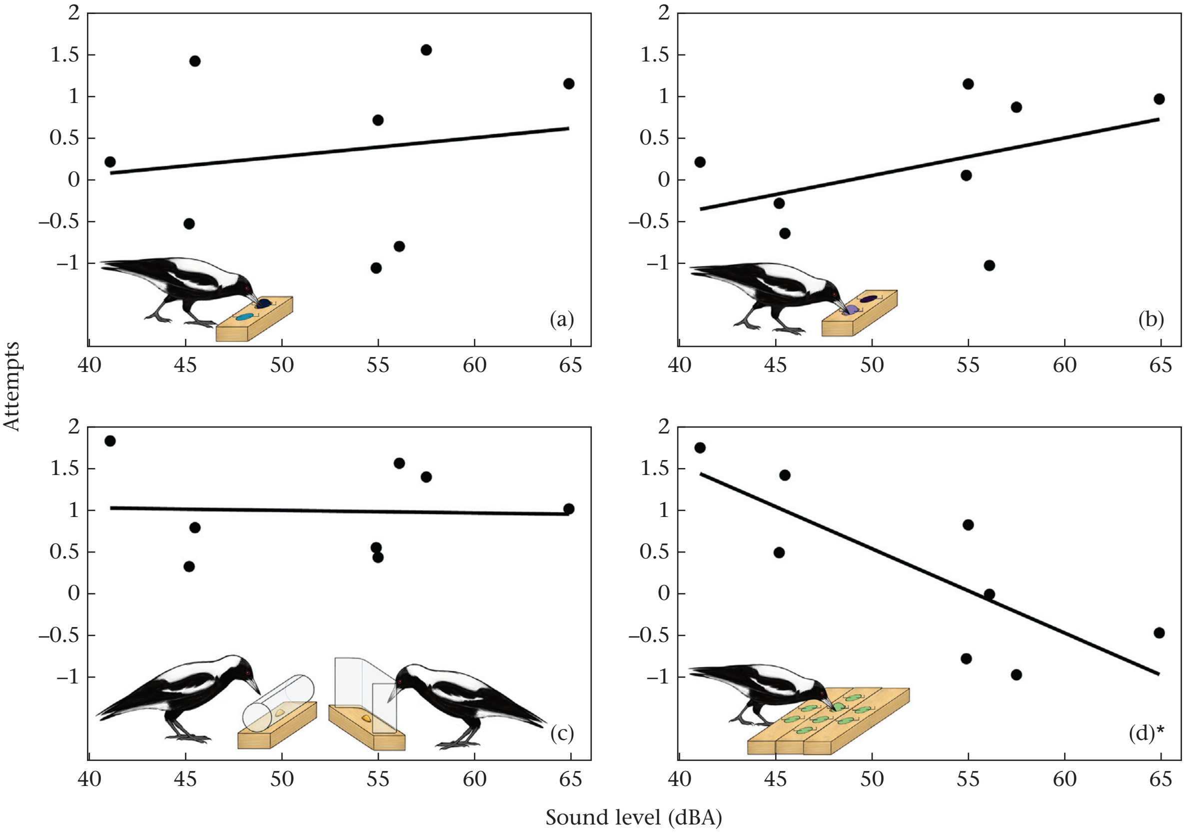


Figure 3. Proportional difference in performance on the four tasks between birds aged 160 and 290 days across a noise gradient. (a) Associative learning, (b) reversal learning, (c) inhibitory control and (d) and spatial memory. Magpies ($N = 8$) were tested twice during 2017 and 2018. The change in their performance on each test is represented by the proportional difference between the two testing ages ([performance at 290 days − performance at 160 days]/total performance at both ages), with positive scores indicating improved (faster) performance with age. *$P<0.05$. Illustrations by Laura X. Tan.

several cue types (e.g. colours and shapes) may present a greater challenge and provide more insight into cognitive flexibility (Aljadeff & Lotem, 2021). Presenting the test in these ways may have provided more insight into how age and other factors affect performance. Additionally, subadult magpies may be less neophobic and possess exaggerated exploratory tendencies compared to adults. These traits may contribute to an individual's willingness to trial a novel task such as those presented and potentially perform better than a more reserved individual (i.e. an adult; Biondi et al., 2010; Greenberg, 2003; Kendal et al., 2005; Mirville et al., 2016).

Unsurprisingly, adults performed better than subadults on the inhibitory and spatial tasks. In both humans and laboratory rodents, performance on tasks, including inhibitory control and spatial memory, increases with age and experience, as well as across adolescence and into adulthood (Ainge & Langston, 2012; Anderson et al., 2001; Meyer & Bucci, 2014). Studies of adolescent ravens, *Corvus corax*, also found that caching skills (a behaviour that relies on spatial memory) improved with age (Bugnyar et al., 2007). Perhaps these age-related differences are due to incomplete brain maturation of specific brain regions involved with executive control and spatial memory in juveniles.

How Does Urban Noise Affect Cognitive Development?

Birds from habitats that routinely experienced higher sound levels required more trials to reach criterion on the spatial memory task at 290 days postfledging than at 160 days compared to birds from habitats exposed to lower sound levels. In addition, birds performed significantly better on the inhibitory task at 290 days than at 160 days. Overall, individuals required fewer trials to reach criterion at 290 than 160 days postfledging, and, with the exception of the listed examples, improvements in performance with age were not statistically significant and not affected by sound levels.

The correlation between sound levels and performance on spatial memory matches other findings in the literature. Cognitive declines in memory, including spatial memory, were observed in rats exposed to noise both early in life (Barzegar et al., 2015) and during later life stages (Hu et al., 2014). It is therefore possible that noise has a stronger impact on spatial memory than it does on other cognitive functions; a future study in a noise-controlled, laboratory setting may provide insight into whether spatial memory is more sensitive to noise. While the association between performance on the spatial task and age was strong, the sample of birds available to estimate this effect ($N = 8$) was relatively small, due to fledgling mortality and early departure of birds from their natal territory. Other than for spatial memory, we found no evidence that noise negatively impacted performance. Taken together, these results suggest that exposure to anthropogenic noise has the potential to impact development of spatial memory but does not appear to impair the execution of other cognitive tasks in magpies.

Despite evidence that urban environments include many potentially disruptive environmental elements (e.g. light, noise and chemical pollution), many species thrive in these habitats. Indeed, studies of certain species have reported comparable or better performance on cognitive tasks by urban individuals compared to their rural conspecifics, which are presumably exposed to lower levels of disturbance (Audet et al., 2016; Preiszner et al., 2017; Sol et al., 2012). Magpies possess many of the traits that have been proposed to enable species to prosper in highly urbanized environments (Kark et al., 2007). These include the ability to live and forage without fear in the vicinity of humans, the ability to exploit human-related resources such as food waste and the ability to compete effectively with conspecifics and other species because of large body size and behavioural flexibility. Thus, magpies may be well adapted to survive and indeed flourish in cities. While there is evidence for short-term impacts of anthropogenic pollution on sleep in several bird species including magpies (light: Aulsebrook et al., 2020; noise: Connelly et al., 2020), great tits (noise: Grunst et al., 2021; light: Raap et al., 2016) and zebra finches (noise: Brumm et al., 2021), it is not clear that such impacts are sustained. Ultimately, the fitness consequences of long-term exposure to noise will need to be quantified in magpies and other species to assess whether anthropogenic noise is merely an environmental annoyanceor a persistent disruptive phenomenon with long-term effects on ontogeny and fitness.

Author Contributions

Farley Connelly: Conceptualization, Methodology, Formal analysis, Validation, Investigation, Writing – Original Draft, Visualisation, Project administration, Funding acquisition. **Michelle L. Hall**: Conceptualization, Methodology, Formal analysis, Validation, Writing–Review & Editing, Supervision. **Robin D. Johnsson**: Investigation, Writing–Review & Editing. **Shona Elliot-Kerr**: Investigation, Writing–Review & Editing. **Belinda R. Dow**: Investigation, Writing–Review & Editing. **John A. Lesku**: Conceptualization, Methodology, Formal analysis, Validation, Writing–Review & Editing, Supervision. **Raoul A. Mulder**: Conceptualization, Methodology, Formal analysis, Validation, Writing–Review & Editing, Supervision.

Acknowledgments

This project was supported by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia. We thank Parks Victoria and the City of Melbourne for permission to catch and test birds, staff at Serendip Sanctuary for their assistance and EPA Victoria and VicRoads for access to road and rail noise data. We are grateful to the many volunteers who helped catch and train birds, especially Eliza Thompson. Finally, thank you Laura X. Tan for the Australian magpie artwork.

References

Ainge, J. A., & Langston, R. F. (2012). Ontogeny of neural circuits underlying spatial memory in the rat. *Frontiers in Neural Circuits, 6*, 1–10. https://doi.org/10.3389/fncir.2012.00008

Aljadeff, N., & Lotem, A. (2021). Task-dependent reversal learning dynamics challenge the reversal paradigm of measuring cognitive flexibility. *Animal Behaviour, 179*, 183–197. https://doi.org/10.1016/j.anbehav.2021.07.002

Anderson, V. A., Anderson, P., Northam, E., Jacobs, R., & Catroppa, C. (2001). Development of executive functions through late childhood and adolescence in an Australian sample. *Developmental Neuropsychology, 20*(1), 385–406. https://doi.org/10.1207/S15326942DN2001_5

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature, 554*(7692), 364–367. https://doi.org/10.1038/nature25503

Audet, J. N., Ducatez, S., & Lefebvre, L. (2016). The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behavioral Ecology, 27*(2), 637–644. https://doi.org/10.1093/beheco/arv201

Aulsebrook, A. E., Connelly, F., Johnsson, R. D., Jones, T. M., Mulder, R. A., Hall, M. L., et al. (2020). White and amber light at night disrupt sleep physiology in birds. *Current Biology, 30*(18), 3657–3663. https://doi.org/10.1016/j.cub.2020.06.085. e5.

Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution, 25*(3), 180–189. https://doi.org/10.1016/j.tree.2009.08.002

Barzegar, M., Sajjadi, F. S., Talaei, S. A., Hamidi, G., & Salami, M. (2015). Prenatal exposure to noise stress: Anxiety, impaired spatial memory, and deteriorated hippocampal plasticity in postnatal life. *Hippocampus, 25*(2), 187–196. https://doi.org/10.1002/hipo.22363

Basner, M., Babisch, W., Davis, A., Brink, M., Clark, C., Janssen, S., & Stansfeld, S. (2014). Auditory and non-auditory effects of noise on health. *The Lancet, 383*(9925), 1325–1332. https://doi.org/10.1016/S0140-6736(13)61613-X

Bhatt, R. S., Wasserman, E. A., Reynolds, W. F., & Knauss, K. S. (1988). Conceptual behavior in pigeons: Categorization of both familiar and novel examples from four classes of natural and artificial stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 14*(3), 219–234.

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Animal Cognition, 13*, 701–710.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica*). *Journal of Comparative Psychology, 121*(4), 372–379. https://doi.org/10.1037/0735-7036.121.4.372

Brumm, H., Goymann, W., Derégnaucourt, S., Geberzahn, N., & Zollinger, S. A. (2021). Traffic noise disrupts vocal development and suppresses immune function. *Science Advances, 7*(20), Article eabe2405. https://doi.org/10.1126/sciadv.abe2405

Bugnyar, T., Stöwe, M., & Heinrich, B. (2007). The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour, 74*(4), 757–767. https://doi.org/10.1016/j.anbehav.2006.08.019

Buxton, R. T., McKenna, M. F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., & Wittemyer, G. B. R. (2017). Noise pollution is pervasive in U.S. protected areas. *Science, 533*(356), 531–533.

Cauchoix, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field: Comparison of reversal learning performance in captive and wild passerines. *Scientific Reports, 7*(1), 12945. https://doi.org/10.1038/s41598-017-13179-5

Chloupek, P., Voslářová, E., Chloupek, J., Bedáňová, I., Pištěková, V., & Večerek, V. (2009). Stress in broiler chickens due to acute noise exposure. *Acta Veterinaria Brno, 78*(1), 93–98. https://doi.org/10.2754/avb200978010093

Connelly, F., Johnsson, R. D., Aulsebrook, A. E., Mulder, R. A., Hall, M. L., Vyssotski, A. L., & Lesku, J. A. (2020). Urban noise restricts, fragments, and lightens sleep in Australian magpies. *Environmental Pollution, 267*, 115484. https://doi.org/10.1016/j.envpol.2020.115484

Cook, M. O., Weaver, M. J., Hutton, P., & McGraw, K. J. (2017). The effects of urbanization and human disturbance on problem solving in juvenile house finches (*Haemorhous mexicanus*). *Behavioral Ecology and Sociobiology, 71*(5). https://doi.org/10.1007/s00265-017-2304-6

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., Erbe, C., Gordon, T. A. C., Halpern, B. S., Harding, H. R., Havlik, M. N., Meekan, M., Merchant, N. D., Miksis-Olds, J. L., Parsons, M., Predragovic, M., Radford, A. N., Radford, C. A., Simpson, S. D., … Juanes, F. (2021). The soundscape of the Anthropocene ocean. *Science, 371*(6529), eaba4658. https://doi.org/10.1126/science.aba4658

Emery, N. J. (2006). Cognitive ornithology: The evolution of avian intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1465), 23–43. https://doi.org/10.1098/rstb.2005.1736

Ernstes, R., & Quinn, J. E. (2016). Variation in bird Vocalizations across a gradient of traffic noise as a measure of an altered urban soundscape. *Cities and the Environment, 8*(1), 1–13.

Federspiel, I. G., Garland, A., Guez, D., Bugnyar, T., Healy, S. D., Güntürkün, O., et al. (2017). Adjusting foraging strategies: A comparison of rural and urban common mynas (*Acridotheres tristis*): Erratum. *Animal Cognition, 20*(1), 75. https://doi.org/10.1007/s10071-017-1070-1

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: An urgent conservation priority. *Frontiers in Ecology and the Environment, 11*(6), 305–313. https://doi.org/10.1890/120183

Frei, P., Mohler, E., & Röösli, M. (2014). Effect of nocturnal road traffic noise exposure and annoyance on objective and subjective sleep quality. *International Journal of Hygiene and Environmental Health, 217*(2–3), 188–195. https://doi.org/10.1016/j.ijheh.2013.04.003

Fuller, R. A., Warren, P. H., & Gaston, K. J. (2007). Daytime noise predicts nocturnal singing in urban robins. *Biology Letters, 3*(4), 368–370. https://doi.org/10.1098/rsbl.2007.0134

Funabiki, Y., & Konishi, M. (2003). Long memory in song learning by zebra finches. *Journal of Neuroscience, 23*(17), 6928–6935. https://doi.org/10.1523/JNEUROSCI.23-17-06928.2003

Fyhri, A., & Aasvang, G. M. (2010). Noise, sleep and poor health: Modeling the relationship between road traffic noise and cardiovascular problems. *The Science of the Total Environment, 408*(21), 4935–4942. https://doi.org/10.1016/j.scitotenv.2010.06.057

Grafman, J., & Litvan, I. (1999). Importance of deficits in executive functions. *The Lancet, 354*(9194), 1921–1923. https://doi.org/10.1016/S0140-6736(99)90438-5

Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 175–196). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198526223.003.0008.

Grunst, M. L., Grunst, A. S., Pinxten, R., & Eens, M. (2021). Variable and consistent traffic noise negatively affect the sleep behavior of a free-living songbird. *The Science of the Total Environment, 778*, 146338. https://doi.org/10.1016/j.scitotenv.2021.146338

Guo, F., Bonebrake, T. C., & Dingle, C. (2016). Low frequency dove coos vary across noise gradients in an urbanized environment. *Behavioural Processes, 129*, 86–93. https://doi.org/10.1016/j.beproc.2016.06.002

Halperin, D. (2014). Environmental noise and sleep disturbances: A threat to health? *Sleep Science, 7*(4), 209–212. https://doi.org/10.1016/j.slsci.2014.11.003

Hu, L., Zhao, X., Yang, J., Wang, L., Yang, Y., Song, T., et al. (2014). Chronic scream sound exposure alters memory and monoamine levels in female rat brain.

Physiology & Behavior, 137, 53–59. https://doi.org/10.1016/j.physbeh.2014.06.012

Irgens-Hansen, K., Gundersen, H., Sunde, E., Baste, V., Harris, A., Bråtveit, M., & Moen, B. (2015). Noise exposure and cognitive performance: A study on personnel on board Royal Norwegian navy vessels. *Noise and Health, 17*(78), 320–327. https://doi.org/10.4103/1463-1741.165057

Isaksson, E., Utku Urhan, A., & Brodin, A. (2018). High level of self-control ability in a small passerine bird. *Behavioral Ecology and Sociobiology, 72*(7), 1–7. https://doi.org/10.1007/s00265-018-2529-z

Isden, J., Panayi, C., Dingle, C., & Madden, J. (2013). Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. *Animal Behaviour, 86*(4), 829 838. https://doi.org/10.1016/j.anbehav.2013.07.024

Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H., & Holmes, A. (2017). The neural basis of reversal learning: An updated perspective. *Neuroscience, 345*, 12–26. https://doi.org/10.1016/j.neuroscience.2016.03.021

Jafari, Z., Kolb, B. E., & Mohajerani, M. H. (2018). Chronic traffic noise stress accelerates brain impairment and cognitive decline in mice. *Experimental Neurology, 308*, 1–12. https://doi.org/10.1016/j.expneurol.2018.06.011

Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition, 21*(1), 21–35. https://doi.org/10.1007/s10071-017-1152-0

Kabadayi, C., Taylor, L. A., von Bayern, A. M. P., & Osvath, M. (2016). Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. *Royal Society Open Science, 3*(4), 160104. https://doi.org/10.1098/rsos.160104

Kaplan, G. (2004). *Australian Magpie. Biology and Behaviour of an Unusual Songbird* (Vol. 142).

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: Can anyone become an urban exploiter? *Journal of Biogeography, 34*(4), 638–651. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Keagy, J., Savard, J.-F., & Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour, 78*(4), 809–817. https://doi.org/10.1016/j.anbehav.2009.07.011

Keagy, J., Savard, J. F., & Borgia, G. (2011). Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. *Animal Behaviour, 81*(5), 1063–1070. https://doi.org/10.1016/j.anbehav.2011.02.018

Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology, 66*(2), 167–188. https://doi.org/10.1002/ajp.20136

Kight, C. R., & Swaddle, J. P. (2011). How and why environmental noise impacts animals: An integrative, mechanistic review. *Ecology Letters, 14*(10), 1052–1061. https://doi.org/10.1111/j.1461-0248.2011.01664.x

Kight, C. R., & Swaddle, J. P. (2015). Eastern bluebirds alter their song in response to anthropogenic changes in the acoustic environment. *Integrative and Comparative Biology, 55*(3), 418–431. https://doi.org/10.1093/icb/icv070

Kleist, N. J., Guralnick, R. P., Cruz, A., Lowry, C. A., & Francis, C. D. (2018). Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proceedings of the National Academy of Sciences, 115*(4), E648–E657. https://doi.org/10.1073/pnas.1709200115

Kunc, H. P., & Schmidt, R. (2019). The effects of anthropogenic noise on animals: A meta-analysis. *Biology Letters, 15*(11), 20190649. https://doi.org/10.1098/rsbl.2019.0649

Laschober, M., Mundry, R., Huber, L., & Schwing, R. (2021). Kea (*Nestor notabilis*) show flexibility and individuality in within-session reversal learning tasks. *Animal Cognition, 24*(6), 1339–1351. https://doi.org/10.1007/s10071-021-01524-1

Lea, S. E. G., Chow, P. K. Y., Leaver, L. A., & McLaren, I. P. L. (2020). Behavioral flexibility: A review, a model, and some exploratory tests. *Learning & Behavior, 48*(1), 173–187. https://doi.org/10.3758/s13420-020-00421-w

Lee, V. E., & Thornton, A. (2021). Animal cognition in an urbanised world. *Frontiers in Ecology and Evolution, 9*, 120. https://doi.org/10.3389/fevo.2021.633947

MacLean, E. L., Hare, B., Nun, C. L., Addess, E., Amic, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, L. J. N., Burkart, J. M., Call, J., Cantlo, J. F., Chek, L. G., … Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences, 111*(20), E2140–E2148. https://doi.org/10.1073/pnas.1323533111

McClure, C. J. W., Ware, H. E., Carlisle, J. D., & Barber, J. R. (2017). Noise from a phantom road experiment alters the age structure of a community of migrating birds. *Animal Conservation, 20*(2), 164–172. https://doi.org/10.1111/acv.12302

McClure, C. J. W., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (2013). An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences, 280*(1773). https://doi.org/10.1098/rspb.2013.2290

Meyer, H. C., & Bucci, D. J. (2014). The ontogeny of learned inhibition. *Learning & Memory, 21*(3), 143–152. https://doi.org/10.1101/lm.033787.113

Mirville, M. O., Kelley, J. L., & Ridley, A. R. (2016). Group size and associative learning in the Australian magpie (*Cracticus tibicen dorsalis*). *Behavioral Ecology and Sociobiology, 70*(3), 417–427. https://doi.org/10.1007/s00265-016-2062-x

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: A review of practical and conceptual challenges. *Biological Reviews, 91*(2), 367–389. https://doi.org/10.1111/brv.12174

Passchier-Vermeer, W., & Passchier, W. F. (2000). Noise exposure and public health. *Environmental Health Perspectives, 108*(1), 123–131. https://doi.org/10.2307/3454637

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos, 118*(12), 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Poole, J., & Lander, D. G. (1971). The pigeon's concept of pigeon. *Psychonomic Science, 25*, 157–158. https://doi.org/10.3758/BF03332483

Potvin, D. A., & MacDougall-Shackleton, S. A. (2015). Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 323*(10), 722–730. https://doi.org/10.1002/jez.1965

Potvin, D. A., Mulder, R. A., & Parris, K. M. (2014). Silvereyes decrease acoustic frequency but increase efficacy of alarm calls in urban noise. *Animal Behaviour, 98*, 27–33. https://doi.org/10.1016/j.anbehav.2014.09.026

Potvin, D. A., Parris, K. M., & Mulder, R. A. (2011). Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*). *Proceedings of the Royal Society B: Biological Sciences, 278*, 2464–2469. https://doi.org/10.1098/rspb.2010.2296

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A., et al. (2017). Problem-solving performance and reproductive success of great tits in urban and forest habitats. *Animal Cognition, 20*(1), 53–63. https://doi.org/10.1007/s10071-016-1008-z

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Raap, T., Pinxten, R., Casasole, G., Dehnhard, N., & Eens, M. (2017). Ambient anthropogenic noise but not light is associated with the ecophysiology of free-living songbird nestlings. *Scientific Reports, 7*(1), 1–8. https://doi.org/10.1038/s41598-017-02940-5

Raap, T., Pinxten, R., & Eens, M. (2016). Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environmental Pollution, 215*, 125–134. https://doi.org/10.1016/j.envpol.2016.04.100

Rabat, A., Bouyer, J. J., Aran, J. M., Le Moal, M., & Mayo, W. (2005). Chronic exposure to an environmental noise permanently disturbs sleep in rats: Inter-individual vulnerability. *Brain Research, 1059*(1), 72–82. https://doi.org/10.1016/j.brainres.2005.08.015

Rabat, A., Bouyer, J. J., George, O., Le Moal, M., & Mayo, W. (2006). Chronic exposure of rats to noise: Relationship between long-term memory deficits and slow wave sleep disturbances. *Behavioural Brain Research, 171*(2), 303–312. https://doi.org/10.1016/j.bbr.2006.04.007

Rollinson, D. J., & Jones, D. N. (2006). Tolerance of Australian magpie *Gymnorhina tibicen* towards human: A comparison along an urban gradient. *Australian Field Ornithology, 23*, 29–35.

Schroeder, J., Nakagawa, S., Cleasby, I. R., & Burke, T. (2012). Passerine birds breeding under chronic noise experience reduced fitness. *PLoS One, 7*(7), Article e39200. https://doi.org/10.1371/journal.pone.0039200

Searcy, W. A., & Nowicki, S. (2019). Birdsong learning, avian cognition and the evolution of language. *Animal Behaviour, 151*, 217–227. https://doi.org/10.1016/j.anbehav.2019.01.015

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., Warner, K. A., Nelson, M. D., White, C., Briggs, J., McFarland, S., & Wittemyer, G. (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews, 91*(4), 982–1005. https://doi.org/10.1111/brv.12207

Shaw, R. C., Boogert, N. J., Clayton, N. S., & Burns, K. C. (2015). Wild psychometrics: Evidence for "general" cognitive performance in wild New Zealand robins, *Petroica longipes*. *Animal Behaviour, 109*, 101–111. https://doi.org/10.1016/j.anbehav.2015.08.001

Slabbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature, 424*, 267. https://doi.org/10.1038/424267a

Slabbekoorn, H., & Ripmeester, E. A. (2008). Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology, 17*(1), 72–83. https://doi.org/10.1111/j.1365-294X.2007.03487.x

Sol, D., Bartomeus, I., & Griffin, A. S. (2012). The paradox of invasion in birds: Competitive superiority or ecological opportunism? *Oecologia, 169*, 553–564. https://doi.org/10.1007/s00442-011-2203-x

Teichmann, M., Thorogood, R., & Hämäläinen, L. (2020). Seeing red? Colour biases of foraging birds are context dependent. *Animal Cognition, 23*(5), 1007–1018. https://doi.org/10.1007/s10071-020-01407-x

Wasserman, E. A., & Miller, R. R. (1997). What's elementary about associative learning? *Annual Review of Psychology, 48*(1), 573–607. https://doi.org/10.1146/annurev.psych.48.1.573

Wolfenden, A. D., Slabbekoorn, H., Kluk, K., & de Kort, S. R. (2019). Aircraft sound exposure leads to song frequency decline and elevated aggression in wild chiffchaffs. *Journal of Animal Ecology, 88*(11), 1720–1731. https://doi.org/10.1111/1365-2656.13059

Wright, A. J., Hatch, L. T., Aguilar Soto, N., Kakuschke, A., Baldwin, A. L., Lusseau, D., Bateson, M., Beale, C. M., Martineau, D., Clark, C., Romero, L. M., Weilgart, L. S., Deak, T., Wintle, B. A., Edwards, E. F., Notarbartolo di Sciara, G., Fernández, A., Godhino, A., & Martin, V. (2007). Anthropogenic noise as a stressor in animals: A multidisciplinary perspective. *International Journal of Comparative Psychology, 20*, 250–273. https://doi.org/10.1016/j.socscimed.2010.01.002

Zollinger, S. A., Dorado-Correa, A., Goymann, W., Forstmeier, W., Knief, U., Bastidas-Urrutia, A. M., & Brumm, H. (2019). Traffic noise exposure depresses plasma corticosterone and delays offspring growth in breeding zebra finches. *Conservation Physiology, 7*(1), 1–15. https://doi.org/10.1093/conphys/coz056

Appendix

Table A1
Australian magpie site details

Site	Individuals	No. of locations	Average sound level (dBA)
AA*	1	2	40.2
AN	1	2	51.0
BB	1	2	54.6
CA	2	3	46.3
CC	1	2	48.1
CP	1	2	46.7
DR	1	2	50.5
ET	1	2	48.3
FH	1	2	56.9
FT	3	2	53.7
HP	3	3	49.9
LB	1	2	46.3
LH*	4	3	45.2
LS*	2	3	56.1
PH*	2	3	64.9
PP	2	3	48.6
RE	3	2	46.7
RP*	5	4	54.9
SE*	2	2	57.5
SF$^+$	1	2	48.6
SL$^+$	1	2	50.3
TT	2	2	53.7
TV$^+$	3	3	41.1
WH	1	2	41.1
XF	1	2	41.0

Site codes, number of individuals tested at each site, number of locations at which sound levels were recorded and the overall sound level at each site averaged over a weekday (24 h) and weekend (24 h) day. An asterisk denotes a site where a nestling sound level recording was taken; a plus sign denotes a single bird was tested twice at the site (only association and reversal learning).

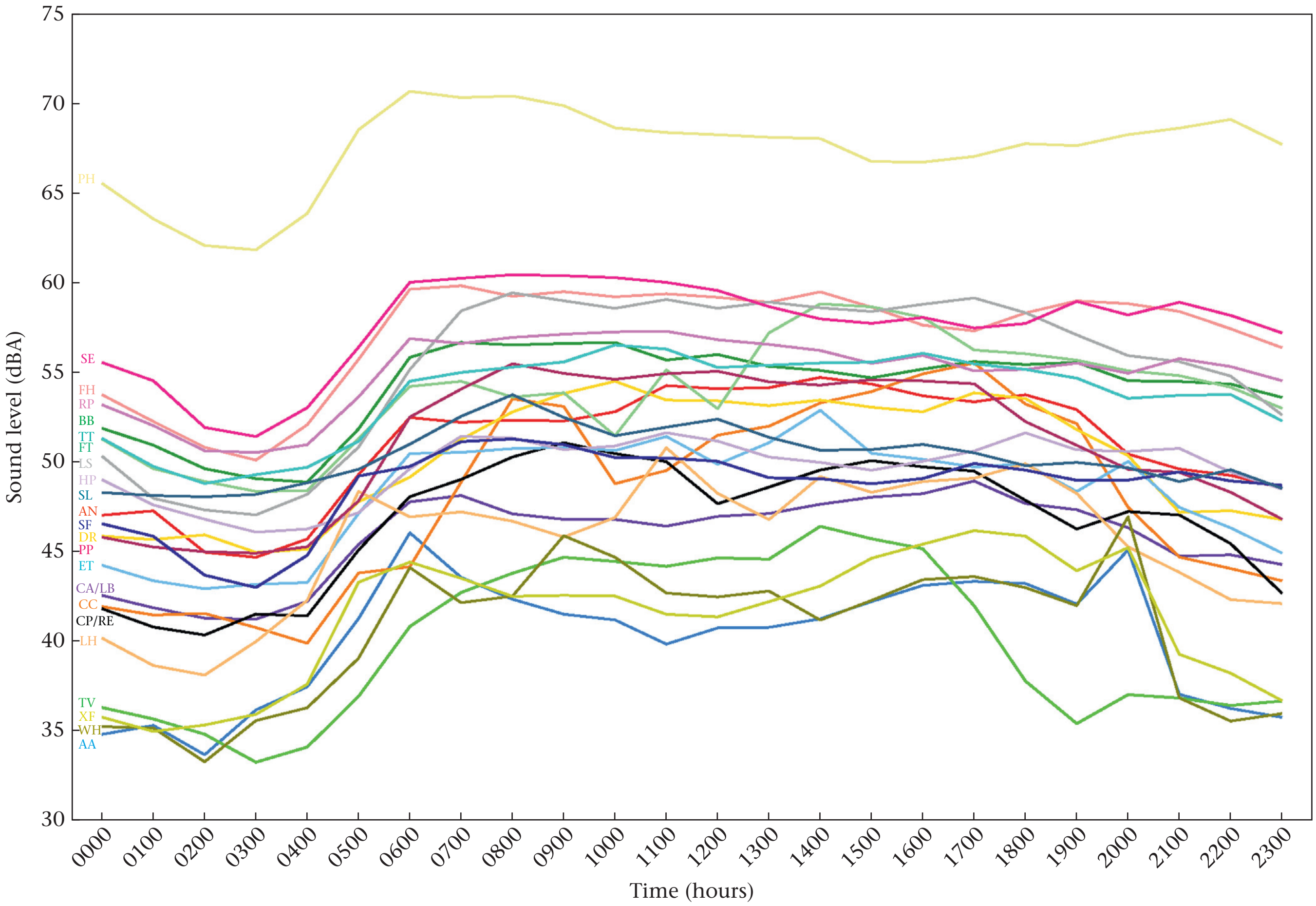


Figure A1. Hourly sound levels (dBA) at each site (magpie territory), averaged over a weekday (24 h) and weekend (24 h) day. For each site, average hourly sound levels are labelled with the designated site code and uniquely coloured. Two site codes listed for a single line indicates sites were adjacent and the same recordings were used.