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Traffic noise inhibits cognitive performance in a songbird

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Noise pollution is commonly associated with human environments and mounting evidence indicates that noise has a variety of negative effects on wildlife. Noise has also been linked to cognitive impairment in humans and because many animals use cognitively intensive processes to overcome environmental challenges, noise pollution has the potential to interfere with cognitive function in animals living in urban areas or near roads. We experimentally examined how road traffic noise impacts avian cognitive performance by testing adult zebra finches (*Taeniopygia guttata*) on a battery of foraging tasks in the presence or absence of traffic noise playback. Here, we show that traffic noise reduces cognitive performance, including inhibitory control, motor learning, spatial memory and social learning, but not associative colour learning. This study demonstrates a novel mechanism through which anthropogenic noise can impact animals, namely through cognitive interference, and suggests that noise pollution may have previously unconsidered consequences for animals.

1. Background

Increasing human populations have led to a pervasive rise in environmental sound, probably providing strong selection pressures on wildlife [1]. Sound can have direct impacts on animals, for example, by damaging auditory hair cells [2], but it can also have less obvious indirect impacts. Many animals use sound to transmit information and anthropogenic noise has been widely shown to negatively impact animal communication by masking important vocal signals, including sexual signals [3], begging calls [4] and alarm calls [5].

Recent research shows that the impacts of noise range beyond the direct auditory effects of sensory cell damage and signal masking, with noise pollution leading to a variety of non-auditory changes in animals' physiology [6], habitat use [7,8] and reproductive success [8]. Some of the most apparent indirect effects of noise are behavioural, for example, noise changes temporal patterns, spatial distributions, mate attraction, territory defence and decreases foraging efficiency owing to increased anti-predator behaviour [9].

In humans, increased noise levels have been associated with impairment of a variety of cognitive processes [6]. Much of this work focuses on noise pollution from airplanes [10]. For example, children attending school near airports tend to perform worse on cognitive assessments [11]. Road traffic noise is also pervasive across many landscapes [12], yet few studies have systematically examined the effects of traffic noise on cognitive performance [10].

It seems likely that anthropogenic noise pollution would have similar impacts on cognitive processes in other animal species, but this topic has been little studied [13]. Cheng *et al.* [14] showed significant cognitive impairment in mice following prolonged periods of continuous, high amplitude, white noise playback. In this experiment, the noise was presented at levels sufficient to produce oxidative damage in the brain, negatively impacting cognitive performance. We know little about how traffic noise impacts

cognition in real time or during shorter periods of exposure, more realistically simulating the roads that animals would encounter in nature. Noise could impair learning directly or could have indirect effects on cognitive performance by distracting animals from other tasks [15,16]. Noise also increases vigilance behaviour [17–19], probably further reducing attention to cognitively challenging tasks.

Birds are likely to be affected by noise pollution because of their highly developed brains [20] and reliance on cognitive processes for successfully navigating challenges in their environments [21]. We tested the impacts of road traffic noise on adult zebra finch (*Taeniopygia guttata*) cognitive performance using a battery of foraging tasks associated with different types of cognition. We tested inhibitory control [22] using a detour-reaching task based on Boogert *et al.* [23], and then used a lid-flipping protocol [24] to test motor learning, associative learning and spatial memory [25]. Last, we tested birds on a social learning task to assess social cognition [26]. Control birds completed these cognitive tasks under ambient laboratory conditions while experimental birds had traffic noise played at realistic sound levels during the trials. We predicted that if traffic noise impacts cognitive performance, finches exposed to noise should have lower scores compared with control birds not exposed to noise.

2. Methods

(a) Subjects and housing

We randomly selected adult male and female zebra finches from the Pacific University colony. Birds were maintained at 25°C and 40% humidity with full-spectrum daylight lighting on 12 : 12 h light : dark cycle. Birds were housed in wire home cages (47 cm length, 89 cm width, 44 cm height), in single sex groups of about eight individuals. Each cage contained newspaper bedding, wooden perches, water dishes, food dishes and cuttlefish bones. Finch seed and fresh water supplemented with vitamins were provided ad libitum.

During testing, all individual learning trials took place in test cages identical to home cages but split in half with an opaque divider, with one subject on each side. Each test cage had a water dish and wooden perch placed on one side of the cage, half-way up (22 cm) and diagonal to the front of the cage. During all trials, except the social learning experiment (see below), subjects were held in visual but not acoustic isolation from other birds undergoing testing. Subjects were deprived of food, but not water, for 2 h before trials to ensure they were motivated to participate.

(b) Noise treatment

Subjects from the finch colony were randomly assigned into the noise or control group for each type of foraging task (detour-reaching, lid-flipping and social learning), so that some individuals were used as control birds in one set of trials and treatment birds in another. We randomly allocated individuals to treatment or control groups without regard to their plumage colour; cognitive performance of domesticated zebra finches does not appear to vary among plumage varieties [27]. The control group completed trials in regular laboratory conditions, in which the ambient noise (including fans and noises from other individuals in the colony) was around 50 dB. We measured amplitude as L_{AFmax} (maximum sound pressure level, frequency weighting: A, time weighting: F; 20 µPA reference value) using a calibrated Cel-246 SPL meter at the location of the bird. For the experimental group, we used a Pignose Legendary 7–100 speaker (Pignose,

Las Vegas, NV, USA) to play one of four different traffic noise recordings during the trials. Details are provided in [5], but briefly, traffic recordings were made approximately 10 m from a rural two-lane highway in Germany with moderate levels of traffic and road noise using a Sennheiser ME66/K6 microphone and Marantz PMD660 digital recorder. Playback files were edited to create 30 s recordings of mostly constant noise using the 'Mix Paste' and 'Crossfade' functions in Adobe AUDITION 3.0 (Adobe Inc., San Jose, CA, USA). Recordings were presented at 70 dB at the location of the bird, which is realistic for birds living approximately 30 m from the road [5]. The same speaker was placed near the cage for the control birds, but no sound was played during control trials. Noise was played only during the time period relative to the relevant cognitive assessment for each type of task (test phase for individual tasks and demonstration phase for social tasks).

(c) Detour-reaching
(i) Task apparatus

We constructed a detour-reaching task (electronic supplementary material, figure S1) to measure inhibitory control [22] based on Boogert *et al.* [23] and Ashton *et al.* [25]. The task apparatuses consisted of clear vinyl tubing (3.8 cm length, 7.6 cm diameter) secured to wooden bases (12.7 cm length, 8.9 cm width, 1.3 cm height). We also constructed opaque apparatuses used for initial habituation and training [23] by wrapping light-blue laboratory tape around the clear cylinder.

(ii) General experimental procedures

The detour-reaching task protocol proceeded in three phases: habituation, training and testing, modelled after Boogert *et al.* [23]. Noise playback was only present during the final test phase of this sequence. All trials for each individual were completed within a single day. We gathered usable data (in which the bird interacted with the task in some form during the testing trial) from 42 birds with the detour-reaching protocol including 22 birds (12 females and 10 males) in the experimental group and 20 birds (11 females and nine males) in the control group.

(iii) Habituation

The habituation phase was used to reduce the subject's neophobia towards the novel task apparatus [23]. We baited an opaque apparatus by spreading a mixture of two tablespoons of shredded spinach and one-half a tablespoon millet seed evenly throughout the inside of the cylinder. We then placed the apparatus in a test cage and oriented it perpendicular to the perch. This orientation allowed a perched bird to view the bait inside the cylinder. A food dish containing seed was also provided so that the individual was not deprived of food if they failed to forage from the novel apparatus. We placed the food dish approximately 5 cm away from the open end of the cylinder on the opposite side from the perch. The placement of the food dish near the open end of the cylinder had two purposes: (i) to allow the bird to gain experience with approaching the apparatus, and (ii) to provide the foraging bird a closer view of the bait inside the cylinder. A subject was introduced to the cage for a 3 h habituation period, during which we left the room and remotely monitored its behaviour.

(iv) Training

The goal of the training phase was to reinforce subjects' learning that food could be obtained from the opaque cylinder, but only by reaching into the open ends of the cylinder with their beaks [23]. Training trials lasted a maximum of 15 min, or until the individual correctly foraged (detoured around to the open ends of the cylinder to retrieve the food). Each trial was followed by

a 2 min intermission before the next trial. We remained hidden behind a curtain and out of the sight of the birds during trials. We observed subjects' behaviour in real time via a video camera connected to a computer monitor behind the curtain. During each trial, we recorded whether or not a subject approached the apparatus (within 5 cm) and whether or not a subject correctly foraged on food within the apparatus. The task apparatus was initially baited in a way that the food spilled out of the cylinder from both ends to promote recognition and foraging. Once an individual correctly foraged from the apparatus, subsequent trials proceeded without any of the bait spilling out. Individuals that reached three successful trials in a row when the bait was not spilling out of the cylinder progressed to the test phase. There were 21 birds total (16 females and five males) that failed to approach the apparatus (within 5 cm) for three consecutive training trials, which were considered too neophobic or unmotivated and excluded from analysis because their learning score on the test phase would not accurately reflect their learning capacity [24]. All birds that completed the habituation and training phases were randomly and evenly divided into either the experimental noise group or the control group for testing.

(v) Testing
The goal of the test phase was to examine the effect of traffic noise on a zebra finch's ability to inhibit incorrect prepotent foraging responses [22]. Trials for the test phase proceeded similarly to the training phase, except now the apparatus was transparent instead of opaque and trials were shortened to 5 min, or until the bird reached the food. Task apparatuses were also now presented parallel to the perches so that the openings were on the sides relative to the birds' position, thereby decreasing the chances that they would initially approach the end of the task apparatus instead of the centre. Each bird received a total of four test trials, which were separated by 2 min intermissions. During each trial, we recorded whether an individual pecked at the side of the transparent cylinder (incorrect) and whether it detoured around to the open ends of the cylinder to retrieve the food (correct) [23]. A trial was considered to be a success if an individual detoured to the open ends of the cylinder to retrieve the food without first pecking at the side [23]. Detour-reaching task scores were the number of trials performed correctly on the test phase out of the four opportunities.

(d) Lid-flipping tasks
(i) Task apparatus
We constructed a lid-flipping task apparatus based on Boogert et al. [24] that was used to measure motor skill learning of a novel task, associative learning and spatial memory. The apparatus consisted of a wooden foraging grid ($20.5 \times 14 \times 1.3$ cm) containing two rows (spaced 4.4 cm apart) of five wells (1 cm deep and 1.5 cm wide) for a total of 10 wells on each block. The centre points of adjacent wells were spaced 3.3 cm apart. The lids were composed of blue plastic discs (2 cm diameter) with paper squares (2.7×2.7 cm) secured to the top of the lid. The four corners of the paper squares were folded upwards and acted as a handle for flipping the lids. The underside of the lids had felt bumpers (1.3 cm diameter, 0.2 cm high) which fitted exactly into the wells of the foraging grid. Lids weighed approximately 0.78 g.

(ii) Experimental procedures
Throughout all three cognitive tasks, wells were baited with about 0.15 g of shredded spinach and about 0.05 g of millet seed, both of which are preferred foods of zebra finches. We used both food sources to control for individual food preferences.

Over the course of several weeks, we led a group of four to six birds from the same home cage progressively through three different cognitive tasks (motor learning, colour association and spatial memory). Individuals were kept in visual isolation from one another during cognitive testing; however, groups were kept together outside of trials (i.e. during the night and early mornings). Keeping birds in groups of familiar individuals helped to decrease stress and neophobia.

(iii) Habituation
On the first day, we habituated a full group of 4–6 subjects (11 groups total) to the experimental apparatus. During habituation, the birds were exposed to regular laboratory conditions, including occasional cleaning and husbandry. Following the initial habituation period, each bird was tested singly in half of a test cage (see above for details) in visual isolation from other experimental subjects and the home cages. To reduce stress associated with isolation, all subjects were in view of two birds of the same sex, referred to as 'companion birds'. Companion birds were experimentally naive and were not used as subjects in subsequent trials.

Habituation was conducted in two stages, each lasting 5 h. For the first stage, we baited the foraging grid with spinach and placed it, without lids, into a test cage in the morning. The food dish was placed directly next to the baited grid to encourage birds to forage in close proximity to the grid. After 5 h, the birds progressed to the second stage of habituation. The grid was removed and restocked with spinach, this time with the lids added and arranged in level one difficulty (see below) before it was placed back in the cage next to the food dish. Five hours later habituation ended and the foraging grid and divider was removed from the test cage. The birds remained together overnight. Starting the next day, we began testing birds with the lid-flipping protocols, beginning with a basic lid-flipping task (motor learning) and then proceeding on to colour association (associative learning) and spatial memory trials after an individual passed the previous task.

(iv) Motor learning
The lid-flipping protocol was used to measure motor pattern learning of a novel foraging task and introduce a baseline skill used for subsequent cognitive assessments. For this task, birds underwent a learning protocol based on Boogert et al. [24] wherein subjects learnt to flip lids from the foraging grid to access a hidden food reward hidden in the wells (electronic supplementary material, figure S2A–D). The difficulty of the task increased across each of four stages of training. At level 1, the lids were position next to the wells. At level 2, the lids were positioned so that they covered half of the well. At level 3, the wells were fully covered by the lids completely hiding the food from view. Last, at level 4, the felt bumpers were fully fitted into the wells, requiring that individuals remove the lid from its well in order to access the food reward [24]. All lids used in this foraging task were the same light green colour.

Through repeated trials, each bird was led progressively through the increasingly difficult levels of the task [24]. Every trial had a duration of 15 min and we recorded the number of wells accessed by each bird during each trial. Like in Boogert et al. [24], each bird that managed to reach the bait in at least two of the wells during a single trial progressed onto the next level of difficulty for the subsequent trial. Failure to do so resulted in returning to the previous difficulty level on the next trial. During the 15 min break between trials, we removed and rebaited the foraging grids. For the experimental group, traffic noise was played during each trial but not during the breaks between trials. The learning criteria were that a bird successfully complete the most difficult level of the task (level 4) three times in a row.

Once a bird successfully did so, the grid was removed and the testing day ended. Birds who failed to complete the task by the end of the day were presented with the same task the following day starting at the same level in which they left off until the bird successfully met the learning criterion.

Each bird received a learning score equal to the number of trials necessary for it to demonstrate learning of the task (i.e. the first trial of the three consecutive solves, when it first demonstrated the ability to solve the task). Birds that continued to participate in trials, but nonetheless failed to achieve criterion after 60 trials, were given 60 as a learning score. Trials in which birds did not interact with or approach within 5 cm of the foraging grid did not affect the bird's learning score to ensure that an individuals' learning score did not inadvertently incorporate neophobia. Neophobia was measured independently of learning by counting the number of trials in which a bird failed to approach within 5 cm of the apparatus. We compared learning scores and neophobia for control birds with those exposed to experimental traffic noise. In total, we calculated learning scores for 18 birds (nine females and nine males) in the control condition and 19 birds (10 females and nine males) in the experimental noise condition.

(v) Associative learning

After each bird completed the lid-flipping protocol described above, it moved on to associative colour learning (electronic supplementary material, figure S2E). The goal of this task was to learn to discriminate between different colours of lids to determine which wells contain the food reward. Similar to Ashton et al. [25], the lid colour was changed from the previously used green to light and dark blue. We used different shades of the same colour rather than distinct colours to minimize the effects of any existing colour biases [28]. Light blue or dark blue was randomly assigned as the rewarded colour [25].

Trials lasted for 5 min in duration with 10–20 min between trials. The subjects were presented with the foraging grid with all the lids fitted securely into the wells, similar to the final level in the motor task. Using a random number generator, we randomly chose four of the wells to be baited and covered by the appropriate coloured lid, with the other six covered with non-rewarded coloured lids. For each trial, we remotely watched the first two lid-flips for each bird and recorded whether they were baited (correct colour lid) or unbaited (incorrect colour lid). The task was considered to be solved when the bird correctly flipped both the first and second lids on three consecutive trials. We tested a total of 16 birds in the control treatment (nine males and seven females) and 16 birds in the traffic noise treatment (seven males and nine females). As with motor learning, we played traffic noise only during the experimental trials and assessed the performance of each individual on the colour association task by calculating its learning score.

(vi) Spatial memory

After completing associative learning, a bird moved on to a spatial memory task (electronic supplementary material, figure S2F), modified from Ashton et al. [25]. In this task, lid colour was changed to purple to help distinguish this task from the previous ones. The four corners of the grid were covered by the purple lids, with one corner randomly chosen to be the baited well for each individual. Trials were again 5 min in duration with 10–20 min breaks. For each trial, the first lid flipped was recorded and if it was baited (correct corner), the trial counted as a success. Once a bird achieved three successful trials in a row, it was considered to have learned the spatial task and assigned a learning score. For spatial memory, we tested a total of 11 individuals (six males and five females) in the control group and 14 individuals (six males and eight females) in the traffic noise group. As above, traffic

noise was only played while each bird interacted with the foraging apparatus and non-participation was not counted against a bird's learning score.

(e) Social learning
(i) General task apparatus

We tested whether social learning was impacted by traffic noise using a string-pulling task that was novel for all of the birds. The task involved pulling out twine knots to access food hidden within wooden blocks (electronic supplementary material, figure S3). We created two versions of the task (horizontal and vertical) and tested whether birds would learn by observing trained individuals solve the task and copy the same version that was demonstrated. Feeding apparatuses were $2.54 \times 2.54 \times 18.5$ cm long, with three 2 cm wells drilled on one side each to a depth of 1.2 cm and spaced 6 cm apart. Perches were added, either on the adjacent side (horizontal tasks) or on the same side, 3 cm below each well (vertical tasks). Because task colour influences the likelihood that zebra finches will copy the foraging preference of demonstrators [29,30], all of the foraging apparatuses were the same colour (unpainted wood) with yellow tape to help make the wells more visible to the birds.

(ii) Training

Six zebra finches that had previously completed all lid-flipping tests were chosen to be trained as demonstrators, with three trained on the vertical and three on the horizontal feeders. During training, the birds were housed in a large home cage, with an opaque divider visually separating the two groups.

We used a shaping procedure to train the demonstrators, beginning with 24 h of habituation to three uncovered apparatuses, with a spinach/millet mixture replenished in each well every 3–4 h. As above, we placed the regular food dishes near the apparatuses to entice them to interact with the new objects. Each group of demonstrators were initially trained to forage only on horizontal or vertical apparatuses. The horizontal apparatuses were placed on the bottom of the cage at least 4 cm apart. The vertical apparatuses were placed about 7–10 cm above the bottom of the cage, attached to one of the walls using a binder clip, with at least a 4 cm between feeders. Birds were allowed 5 min to forage before we removed and rebaited the feeders, with 5 min breaks between training sessions.

After the subjects learned to feed from the uncovered wells, the twine knots were introduced to create the motor task necessary to access the hidden food reward. Once all of the birds successfully removed knots to access food during three consecutive sessions, we added three apparatuses of the non-trained orientation. To ensure that demonstrators did not inadvertently learn to forage on the incorrect orientation, we glued the twine so that the birds could not pull the knots out. Once demonstrators had learned to ignore the incorrect orientation tasks, we added traffic noise playback. This was done to reduce the chance that noise playback during the treatment trials would inhibit successful demonstrations. Subjects not being used for a given day of experimental trials were reinforced with their respective tasks.

(iii) Experimental trials

We tested observers singly, with two demonstrators for each trial. Because the sex of observers and demonstrators can influence the degree of copying in zebra finches [29,31,32], we used only female finches as both observers and demonstrators for all trials. The afternoon before the trial, we randomly selected two demonstrators and one observer and placed them in the right and left parts of a testing cage ($45 \times 76 \times 45$ cm) separated by a wire divider to maintain visual and acoustic contact.
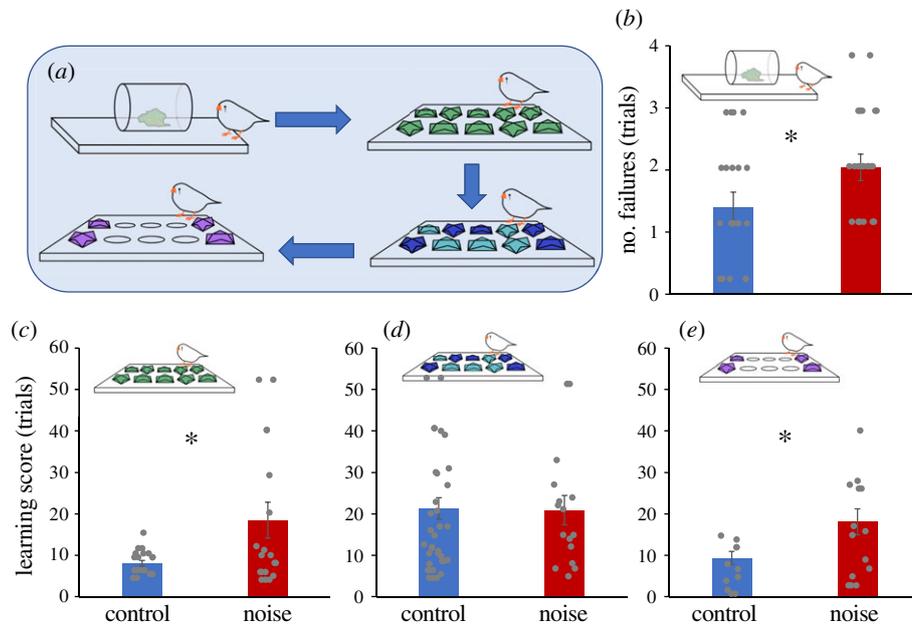
Figure 1. Traffic noise reduces performance on several different individual cognitive tasks. (*a*) Each bird was tested sequentially on four cognitive tasks, either in a relatively quiet laboratory or with experimental traffic noise playback. Traffic noise decreased performance on (*b*) detour-reaching, (*c*) motor learning and (*e*) spatial memory, but not on (*d*) colour association, and asterisks indicate statistically significant differences (*p* < 0.05). (Online version in colour.)

The treatment (noise or control) and orientation (horizontal versus vertical) for each trial was randomly determined.

Birds were moved from the home room to a quiet testing room in the morning and allowed to acclimate to the new room for 1.5 h. After acclimation, food was removed for another 1.5 h. An opaque partition prevented the subject from viewing the foraging tasks prior to the demonstration. Two foraging apparatuses of each orientation (horizontal and vertical) were introduced into the demonstrator side of the cage, with each well covered by twine knots. The correct orientation was baited with spinach and millet seeds and the incorrect orientation had the knots glued to prevent incorrect demonstrations.

The demonstration began when the opaque partition was removed and lasted for 10 min. Observers could visually and vocally interact with the demonstrators through the wire partition (electronic supplementary material, figure S3). Demonstrators in both treatment groups had similar performance levels, measured by the number of wells correctly foraged during a demonstration (mean ± s.e.: 5.5 ± 0.30 (control) versus 5.1 ± 0.35 (noise); *t*-test: $t_{18} = 1.05$, $p = 0.31$, $d = 0.38$). After the demonstration, the opaque partition was replaced and the apparatuses and demonstrator birds were removed. Demonstrators were moved to another adjacent cage and used as 'social companions' as described for previous tasks. The foraging apparatuses were then baited and replaced in the same locations, with all wells of both orientations (horizontal and vertical) baited and covered with knots. The trial began when the partitions were removed, and the observer was given 30 min to interact with the apparatuses. Trials were repeated until the subject foraged from at least one of the apparatus wells, with one additional demonstration and test phase necessary for four birds in each test group.

During noise trials, pre-recorded traffic noise was played, as described above. The noise was played only during the demonstration phase because we were primarily interested in whether social learning, rather than recall of previously learned information, would be impacted by anthropogenic noise. Demonstrations and trials were recorded to video and observed in real time through a monitor. For each trial, we measured the latency to approach the task apparatus, latency to forage and whether the orientation of the first foraging attempt (horizontal

versus vertical) matched the demonstrated orientation. For this task, we had 10 individuals in the control and 10 individuals in the noise treatment.

(f) Statistical analysis

For each of the individual learning tasks (detour-reaching, motor learning, associative learning and spatial memory), we calculated each subject's learning score, as described above. To assess neophobia, we also calculated the number of trials in which a bird failed to approach within 5 cm for each of the learning tasks. To determine whether learning performance or neophobia differed between the control and experimental noise groups, we performed unpaired *t*-tests. Motor learning and spatial learning data did not meet the homogeneity of variances assumption, so for these, we used a *t*-test corrected for unequal variances. To assess whether individual differences in cognitive ability influenced results across tasks, we conducted the Spearman rank correlation analysis.

For the social learning task, we used *t*-tests to assess variation in latencies, and compared whether the first foraging attempt matched the demonstration using a likelihood ratio χ^2 test. All statistics reported are two-tailed and were computed in SPSS v. 26. To ensure that there were no unconscious biases in video scoring, a second blinded observer scored a subset of 10 anonymized videos for each task (50 videos total), resulting in 100% identical scores between the two observers.

3. Results

(a) Individual cognition

Traffic noise playback impacted performance on several different measures of cognition in zebra finches (figure 1). Inhibitory control significantly decreased in birds exposed to traffic noise (mean ± s.e.: 1.86 ± 0.20 successful trials) compared with control birds (2.6 ± 0.245; $t_{40} = 2.34$; $p = 0.024$; Cohen's $d = 0.29$). We observed a similar effect of traffic noise playback on motor learning ($t_{35} = 2.31$; $p = 0.029$, $d = 0.77$), with birds exposed to traffic noise taking significantly
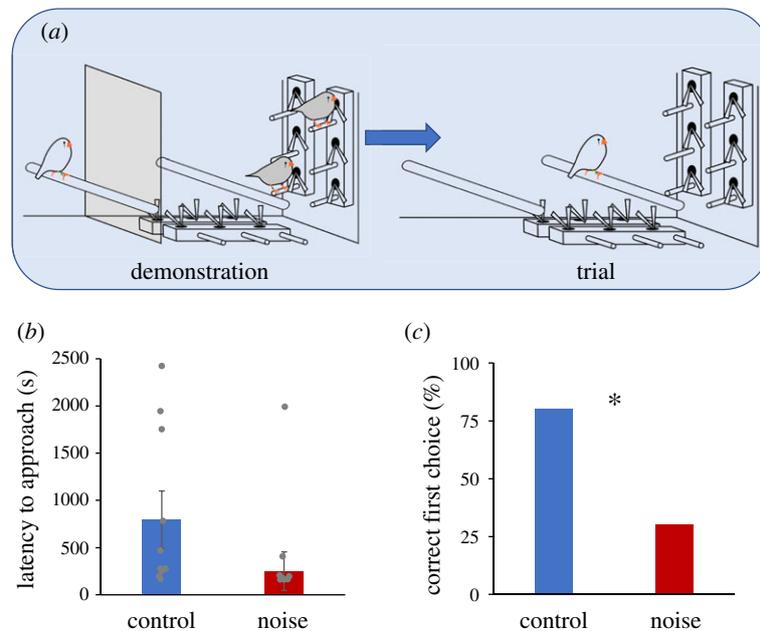
Figure 2. Social learning is impacted by traffic noise. (a) Birds were exposed to a novel knot-pulling foraging task with two options (horizontal or vertical feeders) following observing two trained birds (shown as grey individuals) demonstrate one of the two options. Traffic noise playback during the demonstration did not affect (b) neophobia, as illustrated by the latency to approach the task. However, it did (c) decrease the likelihood of copying the demonstrated option, and asterisks indicate statistically significant differences ($p < 0.05$). (Online version in colour.)

more trials (18.47 ± 4.34 trials) to learn the lid-flipping task compared with control birds (8.06 ± 0.698). The latency to learn to associate a colour with a food reward was not affected by traffic noise playback ($t_{34} = 0.085$; $p = 0.93$; $d = 0.03$), with noise-exposed birds (20.9 ± 3.54 trials) having similar learning scores with control birds (21.3 ± 2.59). Spatial memory was significantly decreased by traffic noise playback ($t_{23} = 2.27$; $p = 0.023$; $d = 1.0$), with birds exposed to traffic noise taking more trials (18.07 ± 3.14 trials) to learn the location of the baited well than did control birds (9.36 ± 1.57). We observed no effect of sex or sex–treatment interactions for any of the individual cognitive tasks ($p > 0.05$; electronic supplementary material, table S1).

Traffic noise did not significantly increase neophobia for the detour-reaching task (t-test $t_{40} = 0.75$, $p = 0.46$; $d = 0.29$), with nearly all birds participating in all of the four trials, both for control (mean ±s.e.: $96 \pm 4\%$) and noise-exposed birds ($92 \pm 4\%$). By contrast, birds exposed to traffic noise had generally higher levels of neophobia for all of the lid-flipping-based tasks. In the motor task, birds in the control group had higher participation rates (mean $\pm$ s.e.: $99 \pm 0.6\%$) than those exposed to noise ($93 \pm 2\%$; t-test $t_{35} = 2.74$, $p = 0.012$; $d = 0.88$). The same pattern existed for the colour association ($t_{30} = 3.64$; $p = 0.002$; $d = 1.28$) and spatial memory ($t_{23} = 2.04$; $p = 0.058$; $d = 0.83$) tasks, with higher participation of control birds compared with those exposed to traffic noise ($99 \pm 0.2\%$ versus $81 \pm 5\%$ for colour association and $97 \pm 2\%$ versus $85 \pm 5\%$ for spatial memory). We observed no effect of sex or sex–treatment interactions on neophobia ($p > 0.05$; electronic supplementary material, table S2).

Individual cognitive performance scores were not strongly correlated among different tasks (Spearman ranks: $r_s = 0.02$–0.08; electronic supplementary material, table S3). By contrast, individual neophobia levels were more consistent between tasks ($r_s = 0.16$–0.68; electronic supplementary material, table S3). Neophobia was significantly correlated

with cognitive performance only for motor learning ($r_s = -0.60$, $p < 0.001$).

(b) Social learning
Birds exposed to traffic noise playback during the social foraging demonstration were less likely to copy the demonstrator (figure 2). While 80% of the control birds' initial forages were with the demonstrated option (horizontal or vertical), only 30% of the birds experiencing noise playback initially foraged from the demonstrated option (likelihood ratio test, $n = 20$, $p = 0.036$; Yule's $Q = 0.81$) Although there was a clear difference in copying, this did not seem to be owing to differences in neophobia or motivation between groups; we found no difference between groups in latency to approach the foraging tasks ($t_{18} = 1.48$, $p = 0.156$; $d = 0.66$) or initiate foraging ($t_{18} = 0.75$, $p = 0.463$; $d = 0.54$).

4. Discussion
We tested the prediction that zebra finches exposed to recordings of traffic noise would have less success on cognitive tasks than control birds and found evidence that traffic noise negatively impacted inhibitory control, motor learning, spatial memory and social learning. We found no effect of traffic noise on colour association learning. Each of these cognitive impacts could translate to negative indirect effects on animals living near roads.

The detour-reaching task measured inhibitory control, a skill which is useful for maintaining attention required to solve a problem [33]. Inhibitory control is related to brain size [22] with diminished inhibitory control correlated with inflexibility, which has been argued to have a negative impact on planning, problem-solving and judgement [34]. Additionally, inhibitory control underlies other types of learning [35] and is linked to general behavioural flexibility [36], which is important for adaptive responses to changing

environments. An increase in roads could lead both to rapid environmental changes and also simultaneously diminish a bird's ability to respond to those changes by negatively impacting inhibitory control.

Noise also negatively impacted several measures of cognitive performance assessed using variations of a lid-flipping task. The initial learning of this task served as an indicator of learning novel motor skills and object manipulation [24], both of which would be critical skills for effective and efficient foraging in the wild. Spatial memory is important for remembering the locations of food sources, territory boundaries and potential mates, so the observed reduction in performance could negatively affect wild animals. Recent work has demonstrated that cognitive performance on these types of tasks can relate to measures of fitness in wild animals [21,25]. Thus, traffic noise could potentially affect fitness, mediated by reduced cognitive performance.

While traffic noise clearly impacted many measures of individual cognition, we did not find an effect on colour association. Given that both groups ultimately learned to associate the correct colour with a food reward, it seems unlikely that birds could not discriminate between the two shades of blue used in this task. Further, while recent research has shown that zebra finches can treat continuous colour variations as categories [37], the two variants of blue used in this study varied not only in hue but also brightness and saturation making discrimination by zebra finches possible (P. A. Green 2020, personal communication). We, therefore, do not think it likely that the lack of difference between experimental groups was owing to perceptual issues. The impacts of noise on inhibitory control (discussed above) could have knock on effects on learning and these effects can vary by type of learning [33]. While we do not know the mechanism, our data suggest that colour association is affected differently than other cognitive measures. The ability to discriminate between colours is advantageous to many animal species [38], with colour variations related, for example, to mate quality. As we found no effect of noise on colour-associative learning, it seems that these aspects of behaviour would be less impeded by traffic noise.

Individual performance was not highly repeatable across the battery of different cognitive tasks used in this study. While some avian work has shown individuals to have repeatable cognitive performance across different tasks [39], other studies suggest that cognitive performance is more task-specific, or modular [23]. We found strong individual effects on neophobia, but not on performance across different cognitive tasks, suggesting more modular cognition. While noise is clearly the most important factor explaining average cognitive performance rates, our study suggests the intriguing possibility that noise pollution could differentially affect performance on different types of cognitive tasks for different individuals.

Social learning was also negatively affected by traffic noise, with fewer birds copying the demonstrated option when noise was present. Social learning is a powerful method for animals to rapidly learn about novel environments [26]. In this task, the traffic noise exposure occurred during the demonstration—the phase in which learning took place—but not during the testing phase, suggesting that noise either made birds choose to avoid copying the demonstrator, perhaps because they negatively associated the stress from noise with the demonstrator [40,41], or that noise inhibited learning, perhaps owing to distraction [15–19]. In social foragers, such as zebra finches, not being able to effectively copy the foraging behaviour of other individuals could result in missed foraging opportunities, potentially reducing fitness. Our data indicate that animals living in areas that are exposed to traffic noise would not be able to rely as heavily on copying other individuals. Although we found a strong effect of noise on the experimental subjects, it is important to note that the demonstrators continued to perform at a high level despite traffic noise playback. This suggests that while traffic noise clearly inhibits learning, it might not have as strong of an effect on the recall of previously learned skills.

The negative impacts of noise on cognitive performance could be owing to direct inhibition of learning or indirect effects of reduced attention towards the learning tasks because of distraction [15–19]. Our performance scores only included trials where the bird interacted with the foraging task, thus removing trials in which birds were obviously distracted from the task. We also found, with the exception of the motor learning task, little relationship between performance and neophobia scores within individuals. However, it is possible that noise caused lower levels of distraction during trials in which the birds did interact with the tasks. While we have documented clear effects on cognitive performance, we are not able to tease apart the exact mechanisms underlying this change in performance at this stage.

In addition to its effects on cognitive performance, traffic noise also impacted neophobia across many of the different tasks used in this study. Object neophobia is a 'personality' trait, and is repeatable within individuals [42]. Our results suggest that the addition of traffic noise can increase neophobia, further confirming that neophobia can be situationally plastic [42]. Recent work indicates that other aspects of personality, for example, boldness level, affect how different individuals adapt their behaviour to chronic noise [43]. While we observed increased neophobia in individuals exposed to traffic noise in nearly all of the individual learning tasks, we did not find the same effect in the social learning trials. Zebra finches are highly gregarious and have heightened neophobia when isolated [44], so the social context could have helped reduce the impacts of noise on neophobia in the social learning trials. While it is often adaptive for animals to be more cautious when exposed to loud sounds [42], in human-dominated environments where traffic noise is pervasive, high levels of neophobia could actually be detrimental.

Our findings could also be relevant to animals living in urban areas, which often feature high levels of traffic and other types of anthropogenic noises. Urban areas provide new opportunities for animals that can adjust to rapidly changing environments [45]. Animals with highly developed cognitive abilities, including big brains and high levels of learning, innovation and problem-solving, are particularly successful in urban environments [46]. Yet, we have shown here that anthropogenic noise reduces the ability of animals to perform cognitively challenging tasks, suggesting that noise associated with urban areas may in turn impact one of the key traits that helped promote animal success in these environments. Further, increased neophobia owing to noise pollution could decrease an animal's ability to successfully exploit novel food sources and adapt to changing environments [35,46]. While we have demonstrated the degree to which new sources of anthropogenic noise can impact animal cognition in a species that typically resides outside of urban areas, it is possible that urban specialist species have

evolved adaptations to mitigate these effects and future work should examine whether their cognitive processing responds similarly to noise pollution.

Our data indicate that traffic noise can impair multiple aspects of cognitive performance in songbirds and provide a novel mechanism by which noise could negatively impact animals exposed to noise pollution. Future work should examine how these cognitive effects impact individual fitness and population dynamics.

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