An experimental test of chronic traffic noise exposure on parental behaviour and reproduction in zebra finches

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Chronic traffic noise is increasingly recognised as a potential hazard to wildlife. Various songbird species, for example, have been shown to breed poorly in traffic noise exposed habitats. However, identifying whether noise is causal in this requires experimental approaches. We here tested whether experimental exposure to chronic traffic noise affected parental behaviour and reproductive success in offspring number and growth in an important model of avian development, the zebra finch (*Taeniopygia guttata*). In a counterbalanced repeated-measures design, breeding pairs experienced continuous playbacks of one of two types of highway noise that previous spatial choice tests had shown to be neutral (control) or aversive. We monitored offspring development and parental feeding rates and nest attendance. Parental nest attendance was positively correlated with feeding effort and was higher in the aversive than in the control sound treatment and this effect was more pronounced for parents attending larger broods. However, neither noise condition affected offspring number, growth or body mass. There was also an absence of an effect of noisy conditions on these reproductive parameters when we combined our data with two other comparable studies in the same species in a meta-analysis. We discuss whether the increased parental engagement is a potential compensatory strategy that alleviated direct noise effects on the chicks. However, impaired parent-offspring or within-pair communication could also have increased parents' nest attendance time. Future work is required to test these possible explanations and investigate potential long-term costs of increased parental engagement.

Keywords:
Traffic noise, parental care, zebra finch, fitness, experimental exposure

Introduction

Wildlife diversity and abundance decline near roads that expose animals to altered habitats, traffic hazard, chemical and noise pollution (Benítez-López et al., 2010; Newport et al., 2014; Bennett, 2017; Kunc & Schmidt, 2019). This negative association is especially well documented in birds (Reijnen et al., 1996; Bayne et al., 2008; Arévalo & Newhard, 2011; Herrera-Montes & Aide, 2011). Field data comparing noisy versus quiet sites within the same populations found, for example, noisy territories to be associated with lower pairing success in ovenbirds (*Seiurus aurocapilla*, Habib et al., 2007), lower hatching success in Western bluebirds (*Sialia mexicana*, Kleist et al., 2018), smaller brood sizes in great tits (*Parus major*, Halfwerk, et al., 2011b) and Eastern bluebirds (*Sialia sialis,* Kight et al., 2012) and reduced feeding and nestling growth in house sparrows *(Passer domesticus,* Schroeder et al., 2012).

These observations are suggestive of a causal relation between elevated noise levels and reduced breeding performance. However, the presence of roads also alters vegetation and food availability, increases pollution and the danger of physical impact of moving vehicles. Any of these factors directly alters habitat quality in ways that could also affect breeding success. A number of experimental noise exposure studies addressed these potential confounds by breaking correlations between parental and territory quality and noise by cross-fostering chicks or by experimentally altering noise levels in the field (Table 1). Such noise treatments were found to affect a number of physiological and behavioural parameters, for example leading to a suppressed immediate corticosterone response in breeding female tree swallows (*Tachycineta bicolor*, Injaian et al., 2018c), altered territory choices in great tits (Halfwerk et al., 2016) and tree swallows (Injaian et al., 2018), increased vigilance in house sparrows (Meillère et al., 2015), altered intra-pair communication in great tits (Halfwerk et al., 2011a) or parent-offspring interactions intree swallows (Leonard & Horn, 2012; Leonard et al., 2015).

These observed physiological and behavioural effects of noise exposure, surprisingly, are not associated with a clear pattern of knock-on effects on reproductive outcomes across studies (neither within nor between species). As listed in Table 1, some studies reported negative effects of noise exposure on clutch size (Injaian et al., 2018a), hatching and fledging success (Mulholland et al., 2018) and offspring body condition (Injaian et al., 2018a, 2018b, 2018c; Ferraro et al., 2020), while others reported an absence of effects (Meillère et al., 2015b; Angelier et al., 2016; Halfwerk et al., 2016; Injaian et al., 2019; Williams et al., 2021) or

even mixed effects (Ferraro et al., 2020; Pandit et al., 2021) for some of the same measurements. The overall picture suggests a sleigh of physiological and behavioural parameters to change if birds are exposed to anthropogenic noise, but rarely, if ever, an effect on the net outcome of reproduction during the experimental period. However, we should be careful to draw any final conclusion from this set of first-generation studies, often only investigating one breeding event and varying in methodology, type of noise stimuli, and study species, as they also revealed how difficult it is to manipulate noise condition as a single parameter in the field.

Added complications arise from the interactions between noise playbacks and other ecological factors, as noise playbacks in the field can affect organisms other than the study species. For example, noise can reduce arthropod abundance (Bunkley et al., 2017), which may contribute to habitat degradation for breeding birds. Species interactions could thus amplify, mask or confound potential effects of noise on breeding performance. For example, at and around North American gas extractions sites, avian predators avoided the noisiest areas near the sites, which is likely the reason for the observed improved breeding performance of their prey species at noisy sites compared to nearby control sites (Francis et al., 2009). These examples show that although many bird species avoid noise (McClure et al., 2013; Liu et al., 2020) others might not (Francis et al. 2009) and depending on context and species, field playback experiments could invertedly selectively sample bird species or individuals with higher noise tolerance and associated poorer breeding quality (Naguib et al., 2013; Patrick & Weimerskirch, 2014). Sampling can also be biased, if lower quality individuals are more likely to settle for breeding in the poorer quality habitats near roads (Injaian et al., 2018a).

Table 1: Experimental studies testing effects of anthropogenic noise on different measures related to avian reproduction: ↑ positive, ↓ and negative and = no effects. Empty cells indicate that the study did not report the corresponding parameter. For playback duration, C = continuous (> 3 days), P = periodical (several hours per day for > 3 days), T = temporary (several times, or < 3 days); For stimuli, W = white noise, B = brown noise, AL = long anthropogenic noise recording (>1 hour), AS = short anthropogenic noise recording (<1 hour).

Species	Playback duration	Stimuli	Clutch size	Hatching success	Body condition[1]	Growth rate	Fledging success	parental behaviour	Reference
Field: observational studies									
27 species			↓	↓			↓		Senzaki et al. 2020[2]
Great tit			=	=	=		=		Grunst et al. 2020
Parus major			↓	=	↓		=	= Laying date	Halfwerk et al. 2011b
Chestnut-collared longspur *Calcarius ornatus*			=				=	= Total visits = Provisioning	Ng et al. 2019
Ash-throated flycatcher *Myiarchus cinerascens*	No playback			=	↑↓				Kleist et al. 2018[3]
Mountain bluebird *Sialia currucoides*				=	↑↓				
Western bluebird *Sialia Mexicana*				↓	↑↓				
Eastern bluebird *Sialia sialis*			=	=	=	=	↓		Kight et al. 2012
House sparrow *Passer domesticus*			=	=	↓		↓	=Nest box use % =Incubation time ↓Total Visits	Schroeder et al. 2012
Gray flycatcher *Empidonax wrightii*							↑	= nest box use %	Francis et al. 2011
Field: playback studies									
Great tit	T	As						↑↓Provisioning	Grunst et al. 2021[4]
		W						↑Visiting latency =Total visits	Naguib et al. 2013
Blue tit *Cyanistes caeruleus*		As						↓Total visits =Time per visit	Lucass et al. 2016
Tree swallow *Tachycineta bicolor*		W						↓Provisioning calls =Provisioning	Leonard et al. 2015
Eastern bluebird	P	B			↑			↑↓Total visits	Pandit et al. 2021
Tree swallow		As			=				Injaian et al. 2019
		As	↓	=	↓		=	↓Laying date	Injaian et al. 2018a
		As	=	=	↓		=	=Total visits	Injaian et al. 2018b
		As			↓	↑	=	↓Total visits ↑Vigilance	Injaian et al. 2018c
House sparrow		As			=	=			Brischoux et al. 2017
		As			=	=	=		Angelier et al. 2016
		As	=					=Nest box use% =Laying date ↑Vigilance	Meillère et al. 2015a
		As	=	=	=	=	=	=Nest box use% =Laying date	Meillère et al. 2015b

Tree swallow	C	AL	=	=			=	=Provisioning ↓Incubation time	Williams et al. 2021
Eastern bluebird		AL	=	=			=	=Provisioning ↓Incubation time	Williams et al. 2021
Western bluebird		As	=	=	↓		↑	↑Incubation time	Ferraro et al. 2020
		As	=	=	=		=		Mulholland et al. 2018
Ash-throated flycatcher		As	=	↓	↑		↓		Mulholland et al. 2018
Blue tit		W						↑Nest box use%	Halfwerk et al. 2016
Great tit		W	=	=	=	=	=	↓Nest box use%	Halfwerk et al. 2016
White-crowned sparrow *Zonotrichia leucophrys*		As			+		=		Crino et al. 2013
Laboratory: playback studies									
Japanese quail *Coturnix japonica*	P	As			=				Flores et al. 2020
Domestic canary *Serinus canaria*		W	↓						Huet des Aunay et al. 2017[5]
Zebra finches		As	↑	↓	↓	↑	=		Potvin et al. 2015
Zebra finches	C	AL		=	↓	↑	=		Zollinger et al. 2020

Studies were found searching the Web of Science (using ALL=(nois* OR traffic) AND ALL=(bird* OR avian*) AND ALL=(reproduct* OR fitness)) and Google Scholar (using (nois*|traffic) AND (bird*|avian*) AND (reproduct*|fitness)). [1]:Body condition is either body size, mass or scaled mass; [2]: Birds in closed habitats decreased clutch size to noise exposure; [3]: Body condition nonlinearly correlated to noise and decreased beyond 70 dB(A); [4]: Provisioning was affected by the interaction among noise type, sex and exploration score. [5]: Canary male songs were played back simultaneously together with noise.

In contrast to field studies, playback experiments in the laboratory allow researchers to keep environmental factors constant to identify direct versus indirect effects of noise on reproductive success. Huet des Aunay et al. (2007) tested whether noise affected female investment (clutch size) in domestic canaries (*Serinus canaria*), a species where male songs are sufficient to stimulate egg laying even in the absence of a male (Kroodsma, 1976). Tested females were exposed to playbacks of male song and urban noise in two conditions: the noise was played in between or during songs, therefore exposing females to the same amount of overlapping (masking parts of the song spectrum) or non-overlapping noise. In comparison with the non-overlapping, the overlapping noise treatment decreased clutch sizes, suggesting that masking noise interfered with the stimulating function of male song on the female's reproductive system. This study did not directly measure the associated physiological changes, but other studies have shown that urban or traffic noise exposure can lead to e.g. increased levels of antioxidant glutathione (a potential marker of oxidative stress) in Japanese quail chicks (Flores et al., 2020), corticoid responses in tree swallows (Injaian et al., 2018c) and western bluebirds (Kleist et al., 2018), suppressed immune response to

phytohemagglutinin in zebra finches (Brumm et al., 2021), and shortened telomeres in tree swallows (Injaian et al., 2019), great tits (Grunst et al., 2020), house sparrows (Meillère et al., 2015b) and zebra finches (Dorado-Correa et al., 2018).

Notably, most studies to date focused on the effects of prolonged or chronic noise exposure on either parents *or* offspring, but rarely on both parents *and* offspring. Two such studies (Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020), however, have been conducted in zebra finches (*Taeniopygia guttata*), an important model for avian development (Griffith & Buchanan, 2010). Breeding pairs exposed to playbacks of urban park noise with edited-in vehicle sounds had an increased embryo mortality compared to a no-playback control group (Potvin & MacDougall-Shackleton, 2015). However, the overall breeding outcome (i.e. the number of fledglings) did not differ between the treatment and control group suggesting that the noise exposed birds initially had laid more eggs. A comparable study that also exposed breeding zebra finches either to traffic noise or to a control treatment without playback (Zollinger et al. 2020), found no treatment effects on the embryo mortality rate or the number of offspring. In both zebra finch studies (Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020), the offspring mass at early age was, however, negatively affected by the noise treatment. Early mass is an important predictor of adult condition in zebra finches (Buchanan et al., 2004; Krause et al., 2017), thus showing that the noise treatment had an effect on offspring development. There were no behavioural observations in these studies, so it is not clear whether the noise had a direct effect on chick development or that the effect was indirectly arising from altered parental behaviour. Experimental studies, monitoring both parental behaviour and chick development, could help to answer the question of whether negative noise impact is directly acting on chicks or indirectly via their parents.

The field of experimental noise exposure studies in birds is growing quickly but also still developing its paradigms as becomes apparent when comparing the type and duration of playbacks used across studies (see Table 1). Ideally, any experimental study should compare carefully selected noise stimuli to a suitable control treatment. Studies to date have tested a great array of different types of anthropogenic noise (or digitally synthesized forms of it) as stimuli but mostly compared a noise-exposed group to a control group not experiencing any playbacks. A no-playback group provides the clearest contrast to a playback group to demonstrate adverse effects of a noise stimulus. However, such a design cannot separate

noise specific effects from effects of experiencing a sudden change from a quiet to a noisy environment or from effects arising from hearing unknown, novel sounds.

We therefore designed a study to compare two types of highway noise, for which it had been previously shown that they were behaviourally neutral or aversive to adult zebra finches from our colony (Liu et al., 2020). Briefly, small groups of zebra finches were temporarily housed in two interconnected aviaries that differed in the presence and/or intensity of traffic noise playback. The birds could fly freely to express spatial preferences with respect to sound exposure levels. All birds selected for the current breeding experiment had been previously tested in this setup and were shown to have spatial preferences for a quiet aviary over one with high (but not moderate) intensity traffic noise. Based on these previous tests (Liu et al., 2020), we selected the aversive (high-intensity) traffic sound level as experimental treatment and the behaviourally neutral (not avoided, moderate-intensity) traffic sound level as control treatment for the current breeding experiment. In a fully balanced design with cross-over, each pair was allowed to breed twice: once while exposed to the aversive and once to the control traffic noise recordings. By monitoring parental behaviour, reproductive output and chick development, we aimed to investigate whether potential detrimental effects of chicks were co-occurring with altered parental behaviour or whether the noise altered parental behaviour but not the chicks' development and survival. We also conducted a post-hoc meta-analysis combining our data with two other published noise exposure breeding studies (Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020).

Materials and Method

Subjects and housing

The zebra finches used in this study originated from the breeding colony at Leiden University. Thirty breeding pairs (900 ± 60 days old) were established from a pool of birds that had participated in a noise avoidance test (Liu et al., 2020). The breeding experiment reported here started 142 days after the noise avoidance test. Birds were caught from single-sex aviaries (L x W x H: 2 x 2 x 2 m) and unrelated birds were randomly assigned to pairs and each pair was placed into one of 30 identical breeding cages (1 x 0.5 x 0.4 m), in one of two identical breeding rooms (3.65 x 3.05 x 3. m, for details see Figure 1). Every breeding cage had an opening (0.09 x 0.09 m) to hold a white plastic nest box drawer (0.11 x 0.09 x 0.09 m) in the top right corner of the cage.

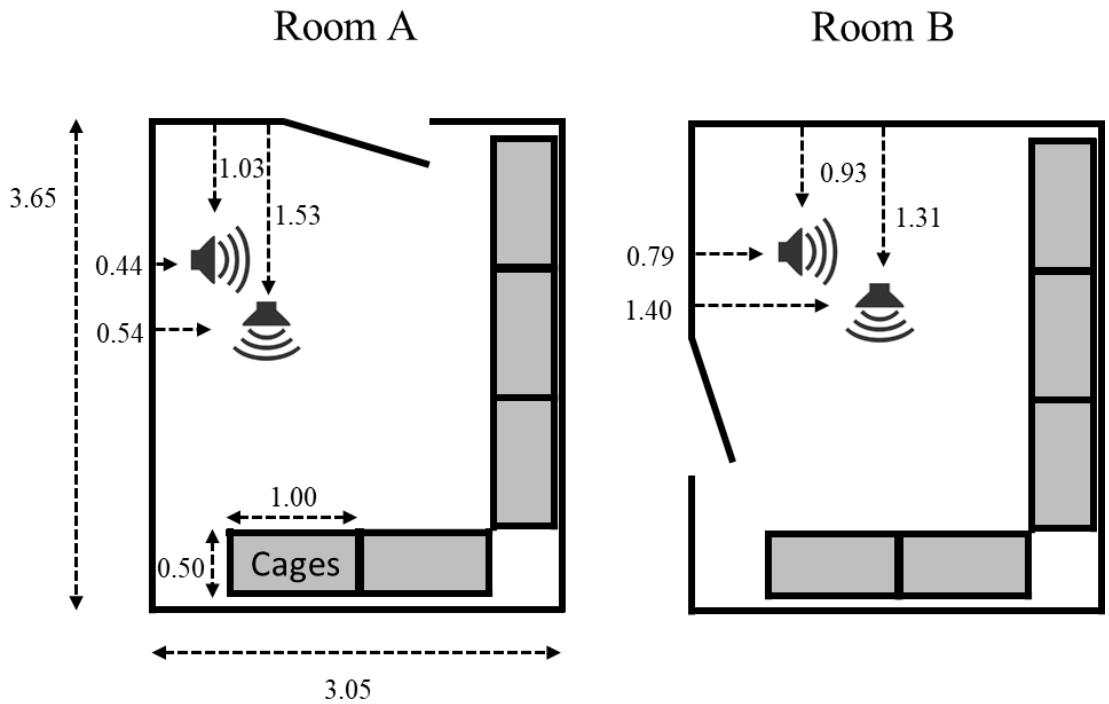


Figure 1: Top view of the two breeding rooms showing the location of the loudspeakers (speaker signs) and breeding cages (grey boxes). In each room, blocks of cages were stacked three rows high along two of the walls of the room. The cages in the lowest row were situated 0.6 m above the ground on supporting cabinets (1 x 0.5 x 0.6 m). All measurements are given in meters.

Sound stimuli

For the noise exposure during breeding, two 24-h recordings of highway traffic noise were chosen from a pool of field recordings that had been collected for our earlier study using SM1 sound meters (Wildlife Acoustics; details see Liu et al., 2020). Noise exposure studies generally compare traffic noise to no playbacks, but without information on birds' reactions to novel sounds, with such designs, any observed effect could also arise from the presence of a novel sound rather than from traffic noise *per se*. We thus used the results from a previous spatial avoidance test (Liu et al., 2020) to select a behaviourally neutral sound (moderate-intensity, far-distance traffic noise) as control and an aversive experimental treatment sound (high-intensity, near-distance traffic noise).

Briefly (details in Liu et al., 2020), the ‘near-distance’ and ‘far-distance’ recording had been recorded at 15 m (52.098504N, 4.439159E) and 300 m distance (52.103469N, 4.441135E) from the same highway (A4, between Amsterdam and Rotterdam in the Netherlands) during the same 24h interval. At both locations the sound meters had been placed in open landscape

at a height of ca. 0.8 m above the ground such that the microphone pointed across the open landscape towards the highway. Absolute sound pressure levels (SPL) of the first three minutes of each recording in the field were measured by a sound pressure meter (Pulsar Instruments Plc, Model 30, A weighted, reading LAT with an interval of 10 seconds) and then used later as reference to calculate the average sound levels per 30 seconds for the entire recordings (see details in Liu et al., 2020): Mean of all 30s blocks: near-distance: 68.7 ± 3.2 dB(A), far-distance: 52.8 ± 5.2 dB(A), re:20 µPa. For these recordings (and from another location) 30-minute-long sequences (extracted from recordings between 11 and 12 am) had been used in the noise avoidance behaviour tests (Liu et al., 2020) that involved the same birds now recruited as parents in the current study. Note that in these previous tests, the parental birds had not changed their behaviour or moved away from the far-distance (moderate level) highway noise, henceforth we selected and designated this moderate-intensity as behaviourally neutral control sound. In contrast, the high-intensity near-distance stimuli had been actively avoided and were thus selected as behaviourally aversive level for the current breeding experiment.

Traffic noise playbacks

Two loudspeakers (CB4500, Blaupunkt, Hildesheim, Germany) were positioned (details see Figure 1) in each breeding room opposite the breeding cages and playback levels were adjusted such that the sound level during playback was roughly the same in every breeding cage (aversive noise: cages 70.2 ± 0.5dB(A), empty nestboxes 68.5 ± 0.9dB(A); control noise: cages 51.5 ± 0.4dB(A), empty nestboxes 51.4 ± 0.6dB(A)), and equivalent to the levels at the recording location when measured with the same sound pressure meter. Because it has been hypothesized that nesting material might act as an insulator to ambient noise (Potvin, 2019), we also checked after the experiments whether sound levels were attenuated inside the nestboxes when they contained zebra finch nests. To do so, a set of the same type of nestbox (N = 18) with completed zebra finch nests inside were obtained from our regular laboratory breeding colony after chicks had left the nests. These nestboxes were then placed into the exact same cages used in this study. We found no measurable differences in sound levels inside these nestboxes with nest material compared to what we had measured before with empty nestboxes (aversive noise: 69.1 ± 1.1dB(A), control noise: 52.1 ± 0.4dB(A)).

Experimental breeding

All breeding pairs participated in two rounds of breeding while exposed to continuous traffic noise playback of the looped 24h recordings of either the aversive or the control traffic noise (see Figure 2). The pairs were moved into the breeding cages 3 days before the onset of the noise playback. From day 3 onwards, the volume of the playback increased daily (by 5 dB(A) for the aversive noise and 4 dB(A) for the control noise) for 14 days until the noise level inside the breeding cages had reached the same level as at the original recording sites. After another week, all pairs were provided with a nestbox, hay and coconut fibre to build nests.

All nestboxes could be opened from outside the cages and were checked daily by one of the experimenters (QL, EG and KF) to track the dates of egg laying and hatching. When a chick hatched, it was weighed and for each chick within a brood the down feathers were cut in an individual specific pattern (head, back, leg or one wing; see Adam et al., 2014 for details) that served as individual ID until the birds were old enough to receive a leg ring. All broods within a room were fully or partly cross-fostered at age 3.6 ± 1.7 days keeping brood sizes within the natural range but aiming (breeding synchrony permitting) for mostly small (2-3 chicks) or large broods (5-6 chicks) to test whether more vulnerable, low condition chicks from larger brood sizes (Naguib et al., 2004; Naguib & Gil, 2005) were more susceptible to chronic traffic noise exposure. Cross-fostering also spread siblings over as many broods as possible to break correlations between parental quality, brood size and offspring quality. The brood sizes before and after cross-fostering were not correlated (Spearman, $r_s = 0.21$, N = 43 broods, $p = 0.18$, pairs without offspring were excluded from this analysis). The age composition after the cross-fostering was ideally no more than a day between subsequent hatching dates, but because of asynchronous breeding this was up to two days in some nests resulting in a range of 0 -2 days and a mean of 1.1 +/- 0.2 days.

When the median age of a brood reached 11 days, chicks were banded with an orange plastic numbered ID-ring on their left leg. When individual chicks reached 65 days of age, they were moved from the breeding cages to participate in a noise avoidance test and then moved to single-sex aviaries (200 x 150 x 200 cm, 12 - 20 birds) in bird stock rooms without playbacks (ambient sound level without birds < 40 dB(A)). The parents remained in the breeding cages after all chicks had been moved from the room. Playback levels in both experimental rooms gradually faded out to ambient within one week. The breeding pairs were then given a two-week playback-free break before the noise playback procedure and a second breeding cycle

as described above started again. For this second breeding round, pairs remained in the same cages but the type of noise playback (aversive or neutral noise) was reversed between rooms.

Breeding outcomes

All breeding cages were checked daily after introduction of the nest boxes until all chicks had fledged or more than 40 days since the introduction of the nestboxes had passed without any chicks hatching. We counted the latency to the first egg (in days, counting from the day the nestboxes were provided), the clutch size (as number of eggs laid without a break longer than 3 days), and the number of successfully hatched chicks per pair per breeding round. In the first round, we weighed the clutch, but due to an unfortunate combination of personal and technical circumstances, the clutch weight was not assessed completely and reliably in the second round. However, in the second round, we had additionally weighed the chicks on their first day ('hatchling weight') when handling them for cutting their down feathers. While this measure will show some variation with respect to the number of hours since hatching, the measure should still detect systematic differences at the group level and we therefore report this measure to compare reproductive output among the groups in the second round before cross-fostering started. In addition, in both rounds, individual offspring weight was measured when chicks were 11, 65 and 120 days old. Weight measures were taken as follows: For weighing the very young chicks (at 1 and 11 days), the experimenter prepared a temporary replacement nest with hay and coconut fibres and put this on the weighing dish of a digital balance (Sartorius, BL600, Göttingen, Germany +/- 0.1g). The balance was reset to zero before adding the chick to the dummy nest. To transfer the chick to the dummy nest, the experimenter inserted a partition in the middle of the cage at a moment when both parents were on the side without the nestbox. This created temporarily two compartments, one containing the parents and the other the nestbox. The nestbox could now be swiftly removed from the cage by opening the nestbox drawer. Chicks were identified by their down feather cuts and each chick scheduled for weighing was quickly transferred to the dummy nest on the balance and immediately afterwards returned to its own nestbox. If a brood was also scheduled to be filmed on the same day, the video recording always preceded the weighing. At 65 days, individual juvenile birds were caught from their cages with a net and put in a bag to be weighed on the same balance before being moved to two connected aviaries (2 x 2 x 2 m) to participate in a noise avoidance tests, that was part of a series of tests continuing into adulthood (Liu et al in prep) and were then moved in with other same-age, same-sex young birds (N = 30-40) to be housed in a group aviaries (1/2 x 2 x 2 m). At 120 days, individual

283 birds were caught with a net from their aviary and briefly put in a bag to be weighed on the
284 same balance before participating in a noise avoidance test.

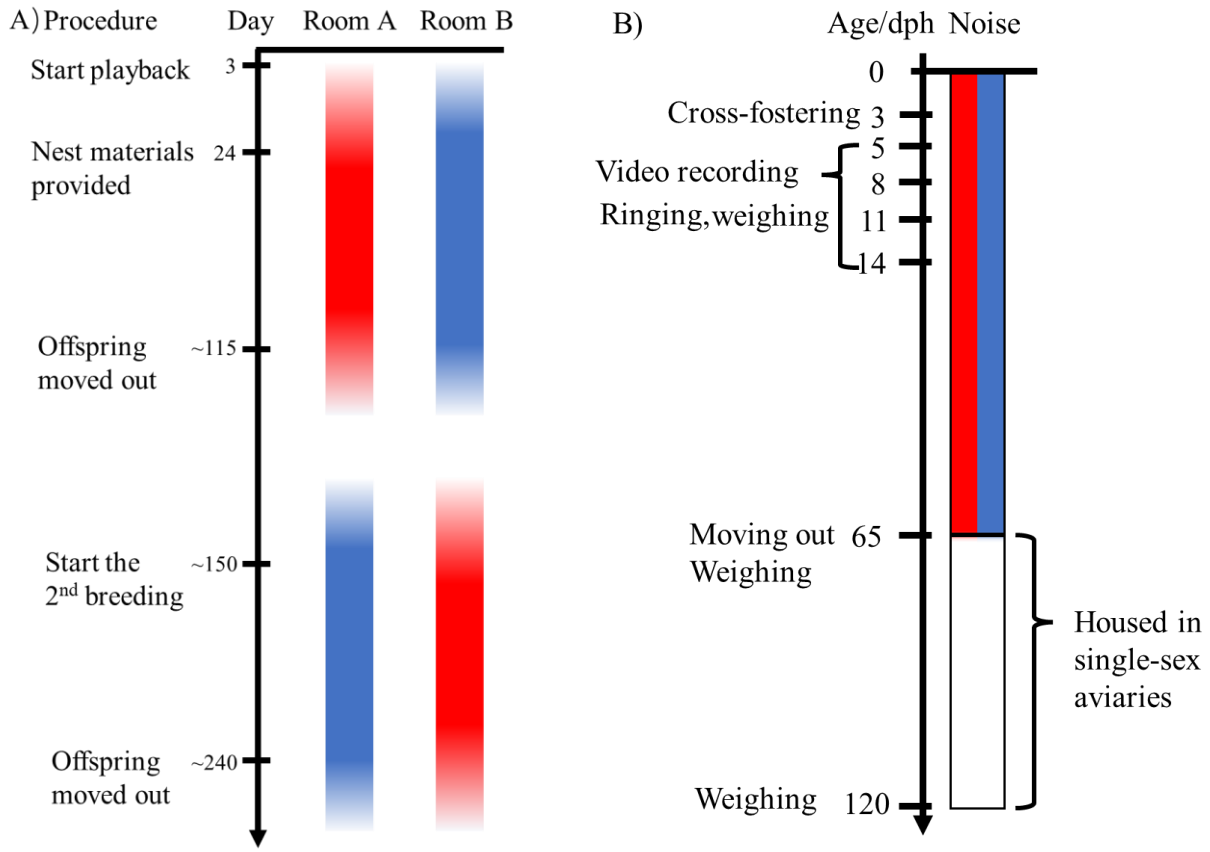


Figure 2: **Schematic view of the timeline of the breeding procedure (a) and experimental procedure (b).** Colour (red = aversive, blue = control) indicates the noise type and the colour gradient indicates the relative intensity of the noise playback compared to the peak level. a) Y-axis shows the days since the start of the experiment. b) Y-axis shows offspring age (in days post hatching) in relation to the reported procedures.

285

286 *Video recording of parental behaviour*

287 During the first breeding round, when the pairs had hatchlings and the median age of a brood
288 reached 5, 8, 11 or 14 days, a camera (Panasonic HC-v500, Osaka, Japan/ JVC, Everio HDD,
289 Kanagawa, Japan/ JVC quad, Kanagawa, Japan) was placed in the middle of the room to
290 simultaneously film all focal cages from the front. These videos were later used to score nest
291 attendance of the parents. To validate whether nest attendance predicted feeding events, in-
292 nest cameras (GoPro HERO 3+, GoPro, California, United States) that could be fixed under
293 the roof of the nestbox were used to record inside the nest. To prevent a neophobia response
294 to the in-nest cameras during filming, dummy cameras (a black cardboard dummy imitating
295 the GoPro HERO 3+) had been attached to all nestboxes from day 1 onwards. These were
296 replaced with real cameras only on the day of filming and returned afterwards. On the

recording day, an experimenter (QL, EG or KF) first slowly approached the cage, and then used an opaque plastic divider to divide the cage in two compartments, taking care to have the pair on one side and the nest on the other. Then, the experimenter opened the nestbox drawer, replaced the dummy with a real, already switched on camera, returned the nestbox and removed the inserted partition. Upon leaving the room, the experimenter switched on the room camera to film all focal cages from the front. Fifty-five minutes later, the room camera was switched off and in-nest cameras were replaced with dummy cameras. For the second breeding round, when nest attendance had been validated to predict feeding events (see below), only nest attendance was assessed (filming the breeding pairs with chicks with the room camera). To keep procedures identical to the first breeding round, the experimenter nonetheless repeated the movements of placing and removing the in-nest cameras at the beginning and at the end of the recording.

Video scoring

For all video recordings, the first 5 min were excluded from analyses to make sure birds had enough time to resume normal activities after the disturbance. Recordings were then analysed with the observers blinded to the treatment from the start of the 6th to the end of the 55th minute to have equally long sequences of 50 min for all recordings. Recordings were scored in BORIS video analysis software (Friard & Gamba, 2016, v.6.1.6). From the room camera recordings, we measured the duration of individual parents' nest visits by marking the time of all instances from when a bird entered the nestbox (= both legs inside) to when the bird left the nestbox (= both legs outside). Male and female parents could be told apart by their differences in plumage. The cumulative time each parent spent in the nestbox could then be obtained by adding up the duration of all the nest visits per recording. This cumulative time was labelled as 'nest attendance'. We also calculated a pair's 'combined nest attendance' during the recorded period by adding up the total time each parent spent in the nestbox.

In addition, we scored individual feeding events from the recordings of the in-nest cameras used in the first breeding round. Each instance where a parent inserted at least part of its beak into a chick's mouth was counted as a feeding event. Videos were scored at least by one experimenter (EG) blinded with respect to the treatments. We firstly established inter- and intra-experimenter fidelity in scoring: two observers (QL and EG) separately scored the same five videos and their scores were highly similar (intraclass correlation coefficient = 0.99). EG also checked her own intra-observer repeatability by rescoring the first three videos after

having finished all videos. The initial and later scores of these videos were highly consistent (intraclass correlation coefficient = 0.99).

Statistical analyses

Reproductive parameters

To test if noise exposure affected reproductive investment, we created generalised mixed linear models in R (package glmmTMB in R 3.5.3) with the following response variables: 1) latency to the first egg; 2) clutch size; 3) successfully hatched chicks; 4) the number of unhatched eggs. The playback type (aversive/neutral), breeding round (1 or 2, ordered categorical) and their interaction were fixed effects. Biological parent IDs were random intercepts. Effects of the two noise treatments on pairs' breeding behaviour and performance, were tested with linear models with clutch weight (round 1) and hatchling weight (round 2) as the response variable and playback type as fixed effect. For each measurement, we created two models, first including all pairs and then repeating the analyses with excluding the pairs that had not laid any eggs. To test if the 11, 65 and 120 day old offspring weights were affected by noise treatment, we created a linear mixed model with offspring weight as the response variable. Playback type and age of the offspring (11/65/120) were both set as categorical variable (because three time points are not sufficient for modelling linearity) and breeding round were fixed effects. Brood size (1-6) was a covariate. We also included the interactions among playback type, age and brood size in this model. Bird IDs and social parent IDs were treated as random intercepts.

As single studies with relatively small sample sizes might produce spurious results (Cooper et al., 2019), we also performed a meta-analysis combining our results on hatching failure (unhatched eggs or embryo mortality) and offspring mass with the data from two other similar studies in which zebra finches were also raised under chronic anthropogenic noise exposure (Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020). These two and our study measured mostly the same parameters (hatching success, fledging success, chick mass at different stages) but treatment effects on hatching failure differed between studies, and was either the total number of unhatched eggs (our study) or embryo mortality (Potvin & MacDougall-Shackleton, 2015 and Zollinger et al., 2020). The effect size of noise on offspring mass was calculated by fitting three linear mixed model models of offspring mass (same variables as the overall offspring mass model except for the age of the offspring), one model per age. To calculate the effect size of these models, 'effectsize' function (method =

'refit', robust = TRUE) from the R package 'effectsize' (version 0.4.1, Ben-Shachar et al., 2020) was used. We then combined the effect sizes from our and the two aforementioned studies. Since both studies used a Bayesian framework, we directly took their reported 'mean effect' for embryo mortality and offspring mass as treatment effect and calculated the accompanying standard error using the following formula: (upper limit of CI – lower limit of CI)/3.92. With the effect sizes from three studies obtained, a meta-analysis was performed on hatching failure and offspring mass. First for each development stage (hatchlings, fledglings and subadults and adults) then combining all development stages. Function 'metagen' (random-effects model, Hedges' g, other settings are default) from the R package 'meta' (version 4.15-1, Schwarzer, 2007; Balduzzi et al., 2019) was used to perform all meta-analyses.

Parental behaviour

We tested if the sex of the parent affected the nest attendance using a linear mixed model. Nest attendance was the response variable, the sex of the parent (female/male), breeding round (first/second) and the playback type (aversive/control) fixed effects, brood size (1-6) and brood median age (5, 8, 11, 14) covariates. We also added the interactions between the playback type and 1) sex, 2) brood size, 3) brood median age to the model. Social parent IDs were treated as random intercepts. This analysis was repeated, using the same approach and the same factors (without the factor parental sex) for the combined nest attendance.

To test if combined nest attendance predicted feeding events, we created another generalised linear mixed model using data from the first breeding round where we had measured both parental attendance and had scored parental feeding activity using the in-nest videos. The total of the feeding events was the response variable, the scaled (mean = 0, SD = 1 after scaling) combined nest attendance was the explanatory variable, the noise playback a fixed effect, brood size and brood median age covariates and social parent IDs random intercepts. We also included the interactions between playback type and 1) brood size and 2) brood median age in this model.

Model selection

For all models, whenever an interaction term was not significant, we then compared the full model with a novel model keeping all previous factors but excluding the interaction term(s). If the novel model was significantly better in explaining the data, we treated the novel model

399 as the best model. The report of the models with rejected terms can be found in
400 supplementary data (Tables S2-S4).
401
402 **Results**
403 *Reproductive outcomes*
404 The majority of pairs (23/30) laid eggs in both breeding rounds (for details, see Table S1).
405 Six pairs only laid eggs in one breeding round: of these four pairs were in the control noise
406 and two pairs were in the aversive noise. One pair did not lay eggs at all. Among pairs that
407 had eggs, 13 pairs successfully hatched offspring in both breeding rounds, six pairs only had
408 offspring in the control noise, four pairs only had offspring in the aversive noise and another
409 four pairs did not have any offspring in any noise. The latency to the first egg, clutch size, the
410 number of successfully hatched chicks and the number of unhatched eggs did not differ
411 between the two noise treatments or breeding rounds (see Figure 3a-e, Table 2, for rejected
412 interactions, see Table S2). Clutch weights in the first round were not affected by playback
413 treatment, and this held both for the sample including or excluding the pairs that had not
414 produced a clutch (see Table S5). Likewise, in the second round, total hatchling weight per
415 brood was not affected by playback type including or excluding the pairs that had not laid any
416 eggs (see Table S5)
417

Table 2: Results of the generalised linear mixed model analyses of breeding outcomes: a) latency to the first egg, b) clutch size, c) successfully hatched chicks and d) number of unhatched eggs.

Effects	χ^2	**p-value**
a) Latency to the first egg		
Noise	0.02	0.89
Round	2.00	0.16
b) Clutch size		
Noise	0.10	0.81
Round	1.00	0.32
c) Successfully hatched chicks		
Noise	1.25	0.26
Round	1.25	0.26
d) Number of unhatched eggs		
Noise	0.62	0.43
Round	0.08	0.78

Marginal and conditional R^2 for the models are a) 0.04 and 0.06, b) 0.01 and 0.35, c) 0.02 and 0.65, d) 0.01 and 0.43. Biological parents' IDs were treated as random intercepts. The rejected interaction terms from these models can be found in Table S2.

418

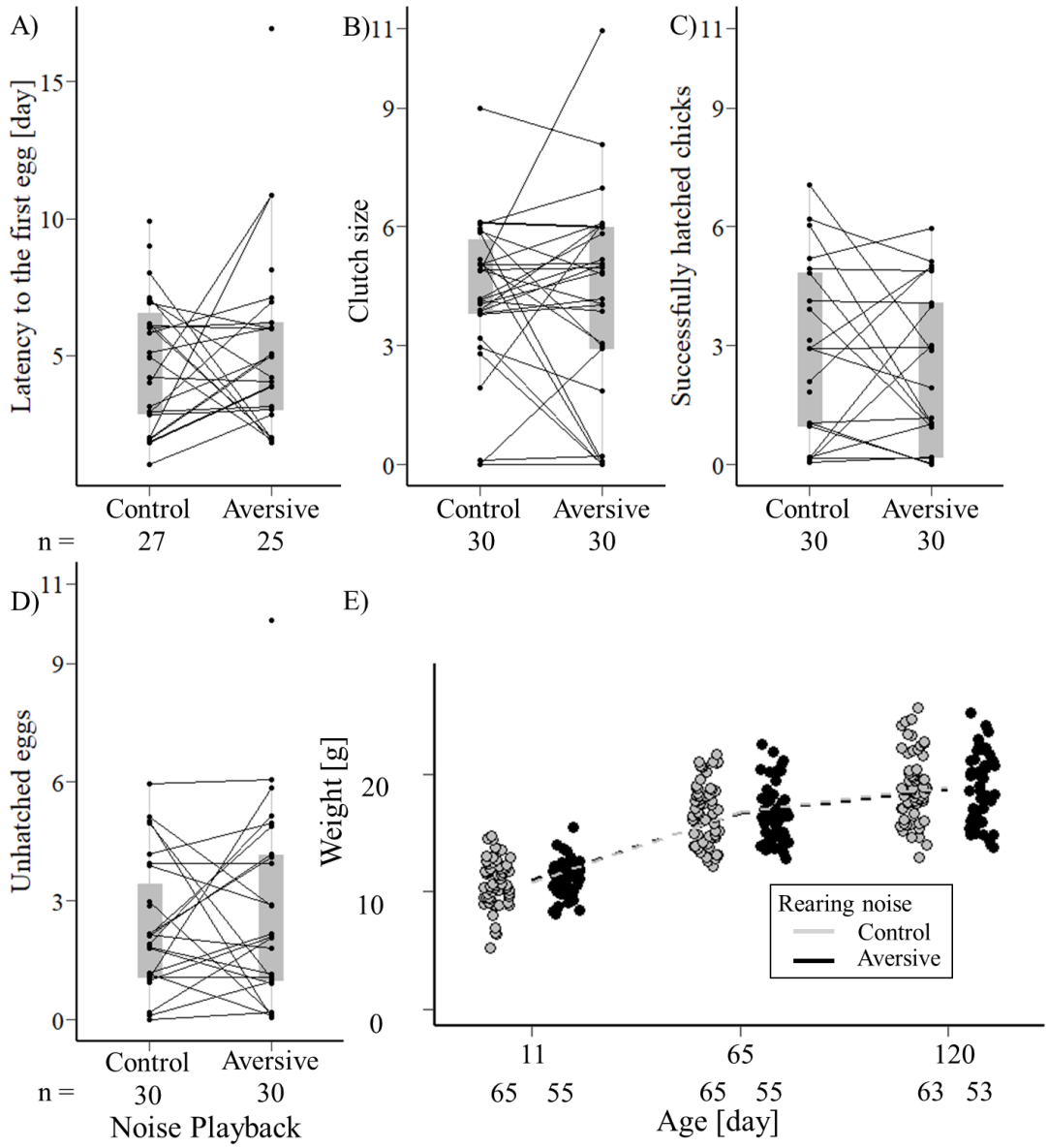


Figure 3: **Reproductive outcomes during continuous exposure to the high intensity aversive or control level traffic noise.** a) Latency to the first egg, b) cluth size, c) successfully hatched chicks, d) number of unhatched eggs. Each dot represents one pair during one breeding event (statistical details see Table 1). Two dots connected by lines belong to the same pair and show the two values obtained in each of the two breeding rounds. Grey overlayed boxplots give the median, 1st and 3rd quartile per treatment group. Details on individual pairs' breeding outcomes can be found in Table S1. e) Offspring mass at 11, 65 and 120 days. Each dot represents a single bird (statistical details see Table 2). For visualisation, overlapping data were randomly and horizontally jittered.

Offspring mass at the age of 11, 65 and 120 days old decreased with brood size but not in relation to playback type (see Figure 3f, Table 3) and there were no significant interactions between these terms (for rejected interactions, see Table S3).

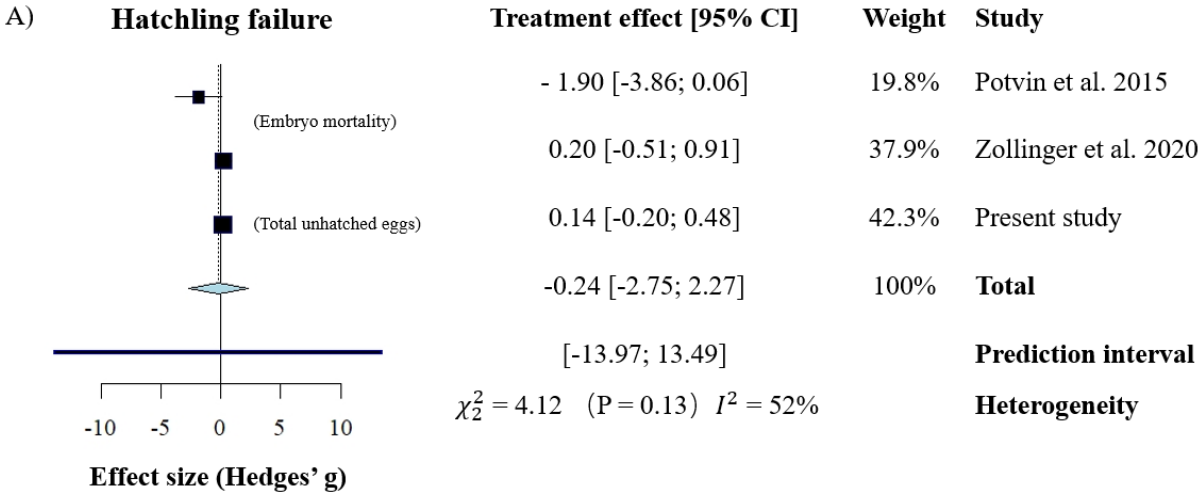
Table 3: Results of linear mixed model analyses of offspring weight at 11, 65 and 120 days.

Effects	Estimate	Std.Error	χ^2	P value
Noise			0.41	0.52
Age			**1489.43**	**<0.001**
Round			3.10	0.08
Brood size	*-0.48*	*0.14*	**11.35**	**< 0.001**

Marginal and conditional R^2 for the model are 0.70 and 0.84. Social parents' IDs and bird ID were treated as random intercepts. The rejected interaction terms from this model can be found in Table S3.

Meta-analysis: Effect of sound exposure on zebra finch breeding outcomes

To date, the present and two other studies (Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020) have investigated the effect of noise exposure on breeding success in zebra finches. Combining the results in one meta-analysis shows no overall effect of chronic exposure to anthropogenic noise on hatching failure (effect size [95% CI] = -0.24 [-2.75, 2.27]) in zebra finches (Figure 4). Similarly, there was no effect of noise exposure on offspring mass (Figure 4): at the combined developmental stages (-0.17 [-0.40, 0.07]) or any of developmental stages when analysed separately: hatchling (-0.39 [-1.18, 0.40]), fledgling (- 0.04 [-0.53, 0.45]) subadult and adult (- 0.09 [-0.42, 0.34]).



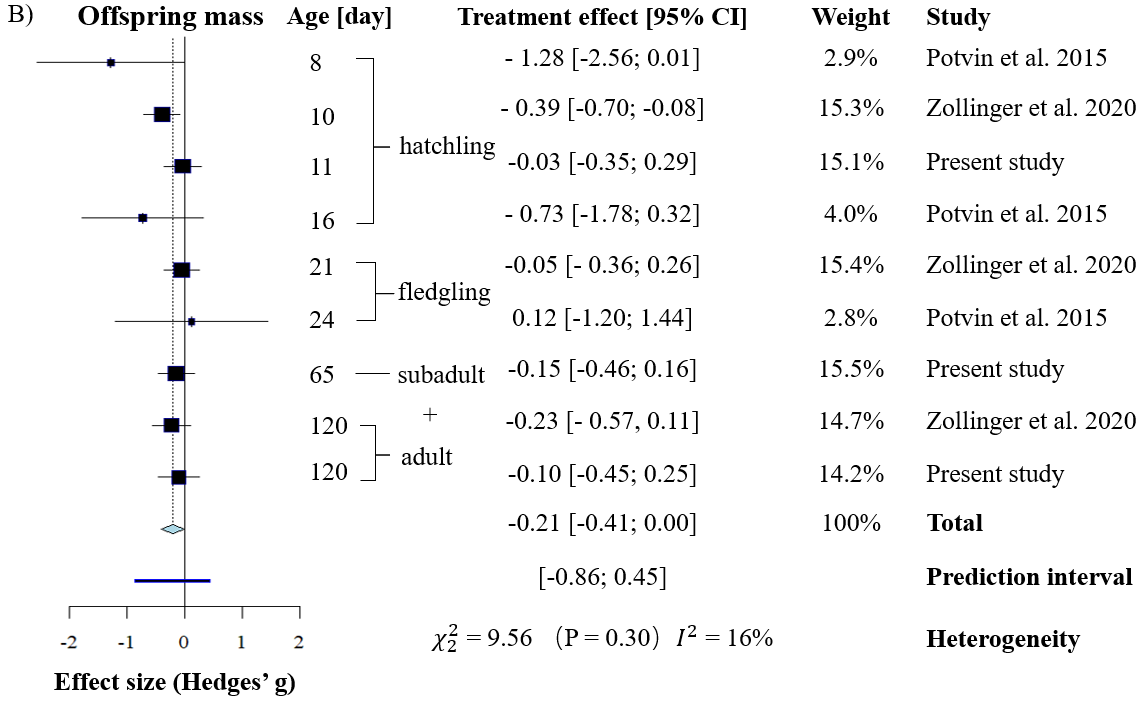


Figure 4: Forest plot of the effect sizes from a meta-analysis testing the effect of traffic noise exposure on a) hatching failure and b) offspring mass. Squares in the forest plot give the treatment effect with 95% confidence intervals. Negative values mean negative effects from noise exposure. The size of the squares reflects the weight of the data in the meta-analysis. The dashed line indicates the total treatment effects.

In terms of parental behaviour, both males and females spent more time attending the nest when exposed to the aversive noise (effect size [95% CI] = 0.40 [0.19, 0.62]). Nest attendance was overall negatively associated with brood size and brood median age. Males spent overall less time attending nests than females (Table 4a). Following analyses that combined data from both sexes of the same pair showed the same result in terms of effects of noise, brood size and brood median age (Table 4b, Figure 5). However, noise exposure did not affect the overall number of combined nest visits (Table 4c). The rejected interaction terms from aforementioned models can be found in Table S4.

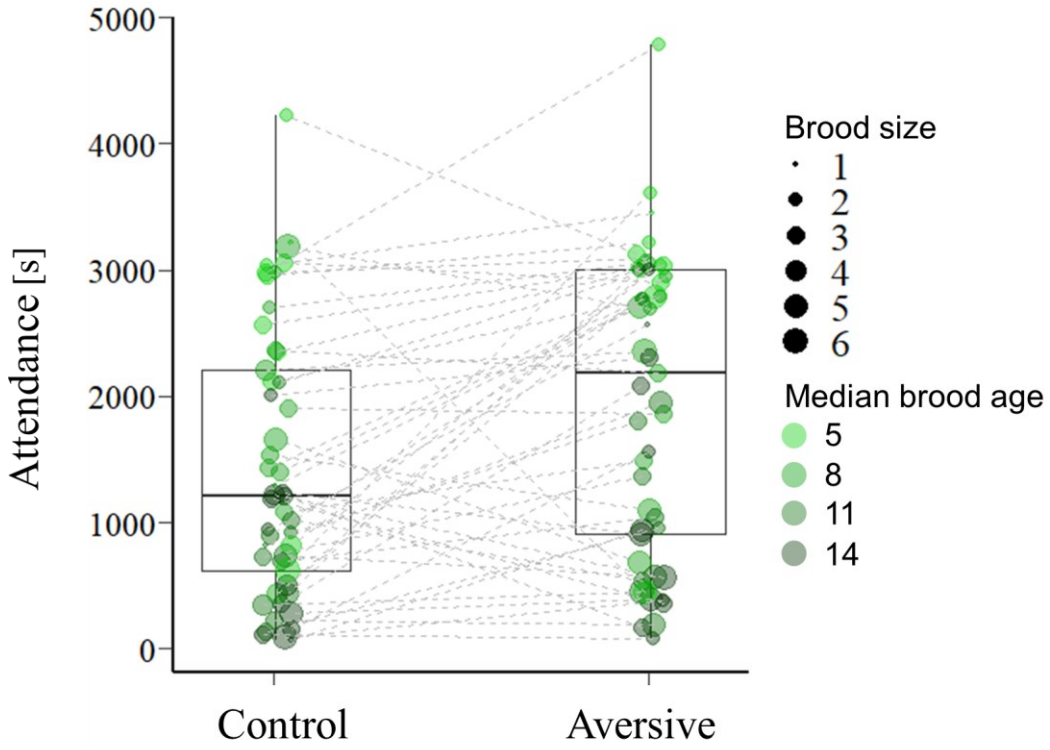


Figure 5: Parents' nest attendance during chronic noise exposure. Connected dots show the time parents were observed in the nest during breeding events during control or aversive noise playback. Each dot shows the total time parents spent in the nest during a 55min continuous sampling period (data extracted by blinded video analyses). The size and colour saturation of the dots code for the brood size and median brood age. Dots that are connected by lines show the same breeding pair's behaviour during either the aversive or control noise exposure at the same median brood age. Data are from N = 2 x 49 median-brood-age paired videos from 13 pairs that had chicks in both breeding rounds. Dot size increases with brood sizes and dot colour symbolizes median brood age.

Table 4: Results of generalised linear mixed model analyses of parental behaviour during the two different noise treatments. The first three models tested if a) nest attendance per parent, b) combined nest attendance and c) combined nest visits were affected by the playback type, breeding round, brood size and brood median age. Model d) tested if parents combined nest attendance, noise treatment and brood size predicted feeding events. Models shown are the best fitting models (for rejected terms see tables S4).

Effects	**Estimate**	**Std.Error**	**χ^2**	**P value**
a) Nest attendance per parent				
Sex			**11.11**	**< 0.001**
Noise			**11.00**	**< 0.001**
Round			0.11	0.75
Brood size	*-0.07*	*0.01*	**53.86**	**< 0.001**
Brood median age	*-0.03*	*0.00*	**82.90**	**< 0.001**
b) Combined nest attendance				
Noise			**13.38**	**< 0.001**
Round			0.05	0.82
Brood size	*-0.06*	*0.01*	**54.39**	**< 0.001**
Brood median age	*-0.03*	*0.00*	**103.75**	**< 0.001**

c) Combined nest visits				
Noise			0.33	0.56
Round			**9.67**	**0.002**
Brood size	-0.05	0.04	1.67	0.20
Brood median age	0.00	0.02	0.02	0.88
d) Feeding events (only measured in the first round)				
Nest attendance	*0.07*	*0.03*	**4.67**	**0.03**
Noise			1.50	0.22
Brood size	***0.56***	***0.13***	**15.81**	**<0.001**
Brood median age	*-0.08*	*0.01*	**116.00**	**< 0.001**
Noise * brood size			**6.02**	**0.01**

Marginal and conditional R^2 for the models are a) 0.36 and 0.36, b) 0.56 and 0.57, c) 0.08 and 0.10, d) 0.61 and 0.98. Social parents' IDs were treated as random intercepts. The rejected interaction terms from these models can be found in Table S4.

The analyses of the in-nest video recordings showed that combined nest attendance of both parents predicted the total feeding events (Figure 6, Table 4d). Besides, the parents fed the chicks more often if the brood was younger. The significant interaction between brood size and playback type showed that when exposed to the aversive noise, the parents with larger brood increased their feeding rate more than the parents with smaller brood (Table 4d and Figure 6).

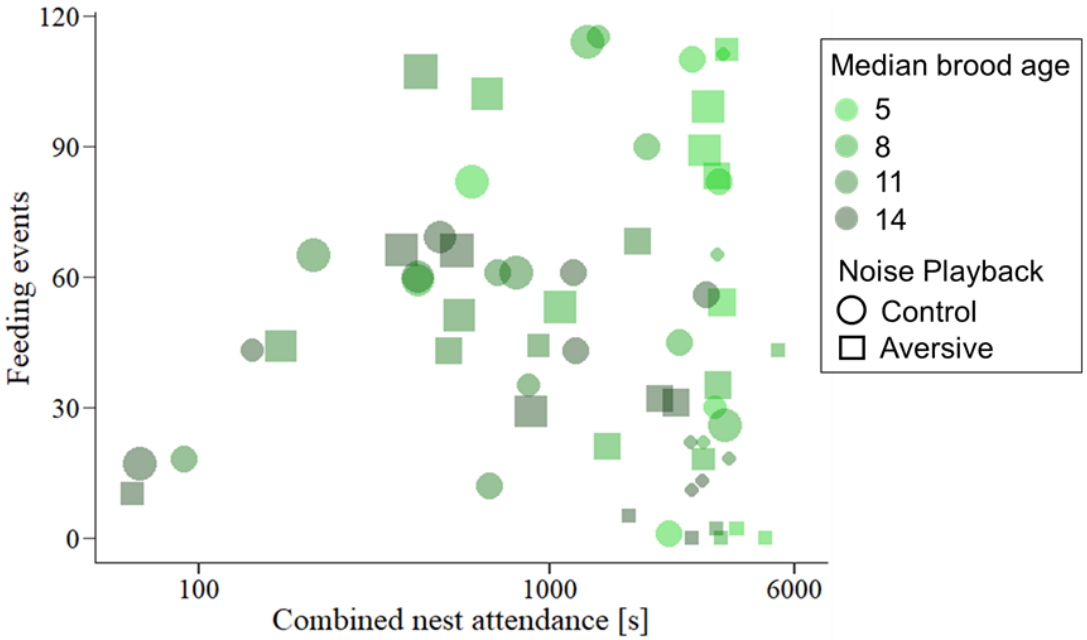


Figure 6: Combined nest attendance (the total time spent by the male and female in the nest) is positively correlated with feeding events. The x-axis is plotted on a logarithmic scale. Each symbol represents the data from one video recording (N = 66) of one pair during the first breeding round exposed to either control (circle) or aversive (rectangle) noise. Dot size increases with brood size (1-6) and dot colour symbolizes median brood age.

Discussion

The different traffic noise exposure conditions in our study affected parental behaviour, but the type of noise treatment had no significant impact on reproductive output. In both breeding rounds, parents spent more time attending the nest when exposed to the high intensity, aversive noise compared to moderate intensity control noise. Feeding rate, which was positively correlated with nest attendance, was higher in larger broods and more so if parents were exposed to the aversive than the control noise. While the parental behaviour changed according to noise treatment in both replicate groups there were no significant effects of the noise treatment on any of the measurements on chick growth or survival. There was no effect from the noise treatments on chick mass, but in line with previous reports in this species, chick mass was affected by brood size. Our meta-analysis of the combined data sets of our and two other similar zebra finch exposure studies, showed no overall effect from traffic noise exposure on hatching failure or offspring mass.

The impacts of noise exposure on parental behaviour are in line with other studies reporting behavioural effects of noise on zebra finches fitness-relevant contexts, such as mate choice, intra-pair communication, vigilance, foraging and learning about new food sources (Swaddle & Page, 2007; Villain et al., 2016; Evans et al., 2018; Liu et al., 2020; Corbani et al., 2021; Osbrink et al., 2021). Against this backdrop, the absence of an effect on reproductive success and offspring condition seems at first surprising and also to differ from the findings of an earlier, comparable noise exposure study in zebra finches (Potvin & MacDougall-Shackleton 2015) where traffic noise exposure led to more nesting attempts, delayed egg laying dates, and a higher embryo mortality rate than pairs in a control group breeding without noise exposure. However, our meta-analysis, combining the data of all three noise exposure studies in zebra finches to date, showed no overall effect from traffic noise exposure on embryo mortality or offspring mass. This suggests that the findings of the individual studies that differed in the direction or presence of effects might have arisen from low power of individual studies (see the 'weight' in Figure 4). This interpretation seems more likely than that the differences were caused by the different playback protocols, as our data (two types of noise) and the data from one of the two studies using a noise versus silence treatment (Zollinger et al. 2020) both showed an absence of effects on measures of reproductive failure.

In contrast to the absence of an effect on the reproductive output parameters the noise clearly affected the behaviour of the parents: the aversive noise exposure increased nest attendance

overall (effect size [95% CI] = 0.40 [0.19, 0.62]) and increased feeding rates of parents with a larger brood in particular. Unfortunately, there are no data on parental behaviour in the other two studies, but our findings are unlikely to be spurious as the birds were tested in a paired-measures design, and the change in nest attendance showed a substantial effect size. This suggests that, although the reproductive outcome was not affected, parents exposed to the aversive high intensity noise might have put in extra efforts during chick rearing. It seems that (at least in the relatively benign environment of the laboratory), parents might be able to buffer some direct negative impacts of noise. This observation should be replicated first in other studies/populations, but such an interpretation is in line with the absence of an effect on chick biometrical measures in our study or the observations that initial lower weight in noise exposed chicks disappeared later on in the other two experimental noise exposure studies in this species (Potvin & MacDougall-Shackleton, 2015; Zollinger et al., 2020). The increased time and feeding investment adds to a list of other behavioural effects of noise in this species: pair bond erosion (Swaddle & Page, 2007), intrapair communication changes (Villain et al., 2016), increased vigilance (Evans et al., 2018) and inhibited cognitive performance (Osbrink et al., 2021).

The absence of an effect on reproductive success in benign laboratory conditions that offer abundant food, near constant climate and no predation risk is not necessarily in contrast with negative effects on breeding behaviour reported in field studies on other species (Naguib, 2013; Leonard et al., 2015; Lucass et al., 2016). The general picture arising from these studies is an overall negative effect of high noise levels on both parental visit rates and offspring condition, likely due to interference by noise on parent-offspring (Leonard & Horn, 2012; Schroeder et al., 2012) or parent-parent communication (Villain et al., 2016). For example, young blue tits beg more during playback of heterospecific sound than during species-specific calls or silence (Lessells et al., 2011) and continuous white noise increases begging in tree swallows (Leonard et al. 2015), which could be an explanation for why we saw the parents increase their nest attendance time. However, noise can also mask chick begging, so if parents do not hear begging calls well, or if chicks do not respond to parents arriving with food by begging (Leonard & Horn, 2012), feeding rates go down, which will cause a negative impact on chick growth. This will be much more pronounced in the field where parents have to work harder to find food, face additional impacts from roads (pollution) and increase their vigilance in noisy habitat (McIntyre et al., 2014; Meillère et al., 2015a). These complications could burden breeding parents and limit how much resource they would

divert to mitigate the effects of noise on their chicks. Such differences between field and laboratory conditions and also between species could explain why we did not find the reduced nest visits that had been observed in house sparrows in the field (Schroeder et al., 2012). It may also be that masking effects on communication have a different, probably larger impact on birds in real-world situations, compared to zebra finches in laboratory housing in small cages, with close proximity between all birds.

Additionally, zebra finches are opportunistic breeders originating from semi-arid zones with unpredictable food supplies and they are quite resilient to environmental challenges like extreme temperatures and nutritional stress (reviewed by Griffith et al., 2021). For example, the average egg mass and fledgling rate in zebra finches is not easily affected by variation in quality of their food (Griffith et al., 2021). This suggests that zebra finches are perhaps also less susceptible to potential detrimental effects of chronic traffic noise exposure than other species. Seasonal breeders, for example, rely on other environmental and intrapair cues than life-long opportunistic breeders. However, other aspects of zebra finch biology point to potential vulnerability to noise: synchronisation of breeding activity (Waas et al., 2005; Brandl et al., 2019) and parental communication (Villain et al., 2016) are all mediated by vocal communication (calls and singing), while zebra finch vocalisations carry only short distance compared to many other songbirds (Loning et al., 2021).

With so many effects on the behaviour of breeding birds of different species, the absence of short-term effects of experimental noise exposure experiments on reproductive success needs to be interpreted with caution: an absence of short-term effects is not predictive of potential long-term consequences (Santos & Nakagawa, 2012; Williams, 2018) and effects of chronic noise exposure might become apparent only later in life. For example, even in the absence of measurable differences in mass and in aspects of song performance known to be condition-dependent in noise-reared chicks when compared with control chicks at 120 dph (Zollinger et al., 2020; Liu et al., 2021), birds at the same age from these cohorts differed from control birds in telomere attrition rate, which has been linked to life expectancy (Dorado-Correa et al., 2018). We did not measure changes in physiology in either parents or offspring and we, therefore, cannot dismiss or exclude impacts that have been reported in quite a few studies (Injaian et al., 2018c; Kleist et al., 2018; Flores et al., 2020; Walthers & Barber, 2020; Zollinger et al., 2020).

In our study, reproductive success was unaffected, but birds attended their nests longer and fed their offspring more often in the high intensity, aversive noise condition than in the control condition. These results are in line with the parental compensation hypothesis that posits that parents may flexibly adjust their parental care to more demanding circumstances and thus buffering negative environmental impacts (Rehling et al., 2012; Vitousek et al., 2017). Increased nest attendance (and feeding rate) may have compensated direct negative effects (see also Pandit et al., 2021 for a similar result in bluebirds). Leonard et al., (2015) also found that insect-eating tree swallow parents fed their chicks more often with elevated noise levels, although this appeared not sufficient to prevent a detrimental impact of noise on offspring body condition in this species (Injaian et al., 2018b). Detrimental effects of white noise on immune responses in tree swallows was only found among light nestlings in large broods (Obomsawin et al., 2021). This, like our results, suggests that large broods may be particularly vulnerable to noise impacts and parents might need extra parental care to compensate the detrimental effects of noise. There are also congruent data on seed-eating species: in white-crowned sparrows, paternal nest attendance and feeding rate were found to be higher for nests closer to a road (Crino et al., 2011). Since our setting allowed us to exclude confounding factors like food availability and parental quality, the combined results from our study and these other field studies support that traffic noise affects parents and that increased feeding rates could be one way to mitigate negative effects of noise.

Another, not mutually exclusive explanation for the increased nest attendance may be that the communication between the zebra finch parents was undermined by the noisy conditions. There is evidence that zebra finch pairs use duet-like vocal exchanges to coordinate the parental behaviour (Boucaud et al., 2016, 2017) and that the level of coordination predicts fitness (Mariette & Griffith, 2012, 2015). Noise from wind for example, has been shown to structurally change their duets and spatial proximity (Villain et al., 2016). It is therefore possible that traffic noise exposure in our experiment affected vocal communication and made the birds stay longer at the nest due to interrupted duty relief. Similarly, interrupted communication between parents and offspring (Leonard et al., 2015) may also have increased nest attendance time. However, although zebra finch vocalizations are relatively soft compared to other songbirds (Loning et al., 2021), masking is still less likely for the current captive, close proximity conditions in the small-cage environment of our experiment.

In conclusion, we found further evidence for noise-related effects on bird breeding behaviour. Aversive, high-intensity, traffic noise changed how often zebra finch parents fed and for how long they attended their nestlings, even under benign laboratory conditions. In line with other studies in zebra finches and confirmed by a meta-analysis, we observed no negative impact on reproductive outcomes during the experiment. Future studies are required to test whether this is due to the flexibility of this nomadic and opportunistic breeder or whether benign conditions in captive breeding colonies buffer noise impact, or whether there are long-term costs to the altered parental behaviour. However, parental behaviour clearly changed during the high intensity noise treatment and is suggestive for a compensatory strategy and this warrants attention to further reveal short- and long-term impact of noisy conditions on individual fitness and population consequences.

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