



SYMPOSIUM

Effects of Experimental Anthropogenic Noise Exposure on the Reproductive Success of Secondary Cavity Nesting Birds

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Synopsis Artificial nest boxes are critical nesting sites for secondary cavity-nesting birds; however, they are often placed near roadways and in urban areas that experience noise pollution and other human-caused stressors. Recent correlative studies document both negative and positive influences of noise pollution on reproductive success. Additionally, observational studies have not determined which stage of the breeding process is most vulnerable to noise pollution—settlement, incubation, and/or provisioning. Here, we controlled for possible effects from non-random settlement and eliminated potential effects of roadways, such as collisions and chemical and light pollution, by experimentally introducing traffic noise into nest boxes after clutch initiation in two secondary-cavity nesting bird species. We found no evidence for an influence of noise on clutch size, brood size, number of fledglings, or overall nest success in western bluebirds (*Sialia mexicana*). In contrast, we found that ash-throated flycatcher (*Myiarchus cinerascens*) nests exposed to noise had lower reproductive success than quiet nests due to higher rates of abandonment at the incubation stage. Our results match recent research demonstrating that ash-throated flycatchers avoid energy-sector noise in their nest placement and, when they do nest in noise, experience stress hormone dysregulation and fitness costs. The lack of a response among western bluebirds differs from reported declines in reproductive success due to exposure to energy-sector noise; however, the absence of a response matches the response seen in other species using an in-box noise playback experiment. These results suggest that in-box noise exposure experiments may be appropriate for assessing noise impacts at the nest, and through some pathways (e.g., direct effects of noise on nestlings), but do not capture other ways in which noise can negatively affect birds during the breeding season that may ultimately cause declines in fitness. Additionally, although manipulative experiments that examine the influence of a single anthropogenic stressor on a single life stage can help reveal causal pathways, urban and other human-dominated environments are characterized by many stressors and future studies should seek to understand how noise interacts with other stressors to impact birds and other wildlife. Finally, in light of mounting evidence demonstrating declines in reproductive success due to noise, our results suggest that nest box placement near roads may be counterproductive to efforts to bolster population densities of some species.

Introduction

Secondary-cavity nesting birds have experienced a decline in natural cavities due to habitat loss, forestry practices that target snags for removal, and interspecific competition with non-native species (Willner et al. 1983). This loss in nesting sites, which are a critical limiting resource, is correlated with, and thought to contribute to, ongoing declines in breeding populations (Zeleny 1976). Recent conservation efforts have attempted to increase their breeding

success and densities by supplementing natural cavities with nest boxes (Libois et al. 2012; Briskie et al. 2014). The addition of nest boxes on the landscape should, ostensibly, support larger populations of secondary-cavity nesting species. However, they are often placed along roadways, in recreational areas, urban or suburban backyards, or other areas characterized by high levels of human activity and associated stressors (Miller et al. 1998; Jackson et al. 2013). For example, nest boxes placed adjacent to roads or

in urban and suburban settings are exposed to considerable traffic noise and other sources of noise pollution, which could negatively affect the likelihood of a breeding pair to use the box or negatively influence the outcome of a nesting attempt (e.g. Halfwerk et al. 2011a; Kleist et al. 2017, 2018). Thus, it is important to know whether pairs breeding in boxes in noisy areas have similar reproductive success to those in less noisy areas. In other words, the question is whether nest box placement in noise-polluted areas, such as along roads and in/near urban areas, is a benefit or hindrance to reproductive success and, ultimately, population persistence for secondary-cavity nesting species.

Traffic noise is a low frequency, chronic stimulus that has increased dramatically in recent decades (Barber et al. 2010). Songbirds, including secondary-cavity nesting birds, are considered especially vulnerable to this and other forms of anthropogenic noise pollution because of their reliance on vocal communication (Patricelli and Bickley 2006). Indeed, mounting evidence suggests that avian communities in areas exposed to anthropogenic noise are structured non-randomly based on vocal characteristics (e.g., Francis et al. 2011b; Proppe et al. 2013; Francis 2015). Additionally, recent evidence suggests that placing nest boxes in noise-polluted areas could decrease, rather than promote, nest success. For instance, correlations between anthropogenic noise and reduced reproductive success have been observed in eastern bluebirds (*Sialia sialis*; Kight et al. 2012), great tits (*Parus major*; Halfwerk et al. 2011a), and house sparrows (*Passer domesticus*; Schroeder et al. 2012). However, in these studies, effects from noise were not explicitly disentangled from effects of other disturbances that co-occur with elevated noise levels (e.g. traffic, habitat modifications, presence of people and pets, etc.). Additionally, another study found reproductive success increased for several species in noisy areas due to changes in nest predator activity (Francis et al. 2009). Besides these conflicting results, studies that report declines in reproduction in noisy environments (e.g. Halfwerk et al. 2011a; Kight et al. 2012) were not able to parse the mechanisms responsible for declines in reproduction and several non-mutually exclusive alternatives are possible. Noise may cause declines in reproduction during one or more stages of the breeding process. Prior to nesting, a female's ability to assess mate quality could be compromised by energetic masking of sexual signals (Halfwerk et al. 2011b). During incubation and provisioning, noise could alter parent or offspring stress hormone concentrations (Crino et al. 2013; Kleist et al. 2018) due to changes in perception of

predation risk via masking or distraction. Additionally, increases in vigilance coupled with declines in foraging have been observed in laboratory studies in birds (*Fringilla coelebs* and *Zonotrichia leucophrys*; Quinn et al. [2006] and Ware et al. [2015], respectively) and free-living mammals (*Cynomys leucurus*; Shannon et al. 2014). Similar trade-offs could exist for nesting birds, such as maintaining visual vigilance off the nest at the expense of incubation. During the nestling provisioning stage, noise can also interfere with parent-offspring communication at the nest (Leonard and Horn 2012), although it is unknown whether this results in any changes in reproductive success. Alternatively, birds may settle non-randomly across the landscape such that individuals in good condition settle in quiet environments and those in poor condition are forced to occupy territories in noisy areas—resulting in what appears to be a direct consequence of noise, but instead is an indirect effect caused by self-sorting of individuals according to the acoustic environment. For example, Habib et al. (2007) found that areas exposed to energy-sector noise had significantly more inexperienced male ovenbirds (*Seiurus auro-pilla*) defending territories than comparable quiet areas. Studies that can identify which stage of the breeding process is most susceptible to deleterious effects of noise may help us better understand the mechanisms by which noise can lead to reduced fitness.

In this study, we sought to determine whether traffic noise causes a decline in reproductive success by experimentally manipulating the acoustic environment of randomly assigned nests after nest-site selection and nest initiation. Importantly, this approach minimizes the possible effects of self-sorting with respect to noise and isolates the influence of noise at the nest on reproductive success. We hypothesized that chronic noise exposure induces critical behavioral changes during both the incubation and nestling provisioning stage. We predicted that individuals using nest boxes experimentally exposed to noise via playback systems (treatment nests) would experience lower reproductive success, reflected by fewer eggs, chicks, fledglings, and/or smaller nestlings, compared with individuals using nest boxes without noise exposure (control nests). We also expected that a smaller proportion of nest attempts exposed to experimental noise exposure would result in a successful outcome, defined as at least one fledgling leaving the nest, relative to nest attempts at control nests. Thus, our manipulative approach has the potential to identify whether noise at the nest affects reproductive success and

determine at what stage these effects appear to be most important.

Materials and methods

Study area and species

We studied wild populations of western bluebirds (*Sialia mexicana*) during the 2015 and 2017 breeding season and ash-throated flycatchers (*Myiarchus cinerascens*) during the 2015–2017 breeding seasons. Our nest box study system was established on California Polytechnic State University Lands and situated adjacent to campus in San Luis Obispo County on the central coast of California (Supplementary Fig. S1). Nest boxes measured 30×19×18.5 cm and were constructed from redwood boards. The study area is situated far from major roadways and experiences low levels of anthropogenic activities, including occasional university vehicles, recreational hikers, runners, and mountain bikers. The system consisted of 217 nest boxes placed roughly 60 m apart (mean = 61.66 ± 1.58 SE) across 4.8 km² of habitat consisting of open grasslands bordered by chaparral, and oak and riparian woodlands. Nest boxes were placed approximately 1 m above the ground on pre-existing fence lines ($n=200$) or posted on coast live oak (*Quercus agrifolia*) or California bay (*Umbellularia californica*) trees ($n=17$).

Data collection and field monitoring

Nest box monitoring began in early March and continued until mid-July each year. We monitored nest boxes for nesting material or nesting activity about every 3 days and always at least twice a week. Complete nests were checked daily for clutch initiation. After the first egg was laid, active nests were monitored every 2–3 days, with the exception of one critical period: nearing the end of incubation stage (day of hatch) we monitored nests daily. Nestlings were banded and measured on day 12 of the nestling stage (i.e., 12 days after the first egg to hatch per nest) to diminish the possibility of force-fledging and to standardize measurements across all nests. We continued to monitor nests throughout the nestling provisioning stages at least every 3 days. Nests were considered successful if one or more chicks successfully fledged, or were missing from the box on or near the expected fledge date and there were no obvious signs of depredation or abandonment.

Nest box manipulation

We exposed 26 western bluebird nests to experimental traffic noise and included 32 nests as controls during the 2015 and 2017 breeding seasons

($n=58$). Additionally, we exposed 10 ash-throated flycatcher nests to experimental traffic noise and used 12 nests as controls across the three breeding seasons ($n=22$). Nest treatments were assigned such that the first active nest of the season was randomly assigned to either a treatment or control, but then subsequent nests' assignments alternated to minimize differences in clutch initiation dates (CIDs) among the treatment and control nests. This method was used due to known declines in clutch size with CIDs (Siikamaki 1998). Experimental treatments were usually (92% of nests) implemented on the clutch initiation day (i.e., day the female laid the first egg of the clutch). For occasions in which active nests were discovered on the second egg-laying day ($n=8$, western bluebird only), they were assigned control boxes. Additionally, all second nesting attempts ($n=8$, western bluebird only) were given the opposite treatment received from the first nesting attempt. Nests were assumed to be second nesting attempts if a new nest was discovered in the same nest box within days of the failure or success of the first nest ($n=3$). For nests in previously unoccupied boxes that had visible fledglings at or near the nest box ($n=5$), we used two criteria to deduce the parents: (1) Location/proximity to a nest box that recently successfully fledged young and (2) Timing, as second-attempt nest building often started near the end of the nestling stage.

Treatment boxes contained one of two kinds of playback systems: (1) a Satechi SD mini portable pocket speaker mp3 player attached via a USB cord to an external battery pack (IntoCircuit Power Bank) and (2) a STORMp3 player/speaker. Both systems were fixed to the nest box roof with zip-ties attached to cable holders. Despite several successful earlier laboratory trials with the Satechi system, in 2015 several units failed to remain playing continuously in the field when the internal battery lost power (~5 h) or external battery pack turned off (~5–24 h), and had to be manually reset daily. The initial nests (western bluebird nests only, $n=8$) that were exposed to this intermittent treatment were switched to the continual playback system (STORMp3) by the time the incubation stage began (i.e., before the final egg was laid). In control boxes, we installed wooden blocks (5.08×10.16×15.24 cm) containing electrical wire and tape drilled into the roof of the nest box to account for the potential influence of a novel object in the nest box.

For each species, treatment nests received a randomly assigned unique playback file to provide a range of acoustic conditions that characterize busy highways. There may be relatively small changes in

sound levels across a 24-h period for many busy roads (see Fig. 3 in Halfwerk et al. 2011a) because the average vehicle is slower when vehicle density is high and, thus, produces less noise than at night when vehicle density is lower. To simulate exposure to relatively constant traffic noise levels we recorded traffic noise on local highways during morning hours (i.e. 7 am to 10 am) between October 2014 and May 2015 using Roland R05 recorders at a distance of 10 m from the roadway, which is within the range of distances of many fence lines bordering roadways on which nest boxes are placed (T. I. Mulholland, personal observation). Following preliminary analysis of playback speaker reproduction of recordings made at 10 m from roadways, we also made recordings at 20 m from roadways at many of these locations because speaker reproduction of recordings at 10 m better reflected acoustic conditions at 20 m from roadways (see the “Results” section). Recordings made at 10 m averaged 200 ± 16 SEs and were looped continuously. Recording amplitudes were standardized to the same peak power in Raven Pro 1.5 to control for the influence of especially high amplitude acoustic events. Prior to standardization, a 5 s fade in and fade out was added to each recording to control for rapid onset and falloff of noise levels, which have the potential to elicit startle responses in animals (reviewed in Francis and Barber 2013). We then standardize the playback stimulus in each box to approximately 65 dB(A) at 10 cm, an amplitude known to result in behavioral changes in other studies (reviewed in Shannon et al. 2016) and lasted throughout the entire nesting period. Batteries were changed every 2–3 days during monitoring visits to ensure continuous exposure to the noise. Time-weighted sound levels (A-weighted L_{eq} , fast response, re. 20 μ Pa), which reflects the mean sound level over the period of measurement, were taken from within each nest box for 5 min after initial treatment instillation and following each battery change to standardize experimental playback sound levels using either a Larson-Davis 824 or 831 Sound Level Meter, or, on rare occasions, a MicWi436 measurement kit paired with an iPhone using the SPLnFFT application, which has been shown to be equivalent to a type 2 sound level meter (Kardous and Shaw 2014). We also monitored control nests every 2–3 days and measured ambient noise levels using the same equipment. In 2015, immediately after each nest fledged or failed, we recorded sound levels in the box for approximately 1 h using Roland R05 recorders. This was necessary for qualitative comparisons of spectral profiles of the received experimental stimuli to the original recordings of traffic noise.

Morphological measurements and banding

Because we predicted that experimental traffic noise would negatively affect nestling development, we measured three standard morphological measurements on day 12 of the nestling stage. Tarsus length (mm) and unflattened wing chord (mm) were measured to 0.1 mm precision using a standard wing ruler or caliper. Mass (g) was measured using a spring scale (Avinet, Pesola 50 g) to the 0.1 g precision. Prior to taking these measurements, we banded all nestlings with standard US Geological Survey aluminum bands.

Data analysis

To verify sound levels were higher in treatment nests than control nests, we used two-sample *t*-tests. To determine the effects of treatment on reproductive success, we evaluated evidence for an influence of the experimental noise treatment on several relevant response variables in both western bluebirds and ash-throated flycatchers: nest success, clutch size, number of hatchlings, number of fledglings, nestling mass, wing chord length, and tarsus length. We used linear mixed effect models (LMM) and generalized linear mixed effect models (GLMM) with binomial (logit link), Gamma (log link), or Poisson error (log link) for all models. We used Gamma rather than Poisson error for count data when residuals from models with Poisson error were over (>1.4) or under (<0.75) dispersed. In addition to testing the effect of the traffic noise treatment on response variables, in all models we included CID, which was centered and scaled to improve model convergence. For models of brood size, we also included clutch size as a predictor. We modeled number of fledglings with and without brood size as a predictor, which provides insights on changes in reproductive outcomes during the nestling stage independent of those during the incubation stage. Brood size was also included in models evaluating nestling measurements. We included year as a random effect in all models and, for LMMs pertaining to nestling measurements, we included Box ID as a random effect to account for the non-independence among nestlings in the same nest. For models involving nestling measurements, we verified residuals error met model assumptions by examining residual distributions with histograms and QQ plots, and transformed response variables by either cubing (western bluebird wing chord and mass) or squaring (western bluebird tarsus) when necessary. Additionally, because nests received different playback systems in 2015, in a preliminary analysis we explored whether system type

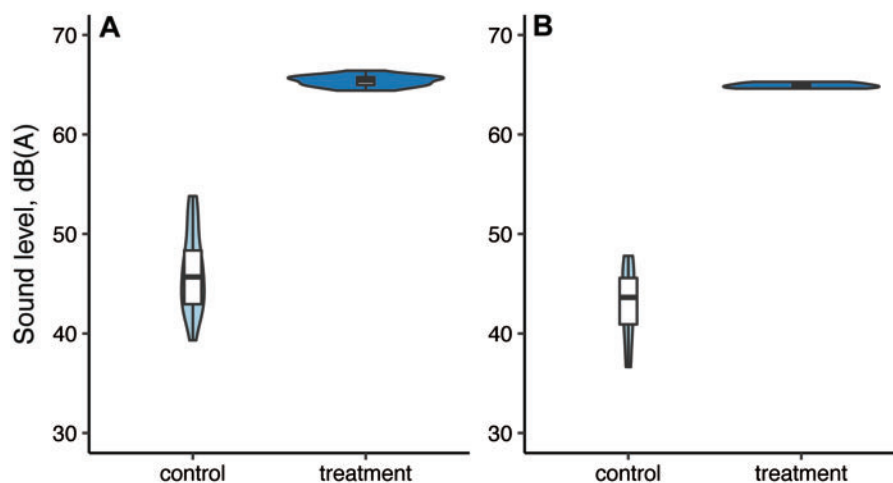


Fig. 1. Average sound levels (dB(A)) in control versus treatment boxes for western bluebirds (A) and ash-throated flycatchers (B). (A) Control average $L_{eq}=46.19 \pm 3.99$ SE dB(A) at 10 cm, Treatment average $L_{eq}=65.38 \pm 0.55$ SE dB(A). (B) Control average $L_{eq}=42.99 \pm 1.67$ SE, Treatment average $L_{eq}=64.91 \pm 0.11$ SE. Boxplots show the median and quartiles and whiskers denote 1.5 times the interquartile range. Violin outlines illustrate kernel probability density, i.e., the width of the shaded area represents the proportion of the data located there.

was informative in explaining nest outcomes, which it did not (not shown). All statistical analyses were performed in R 3.2.2. We used the lme4 package (Bates et al. 2015) for all mixed effect models.

Results

Experimental noise exposure

Sound levels for western bluebird and ash-throated flycatcher treatment nest boxes were significantly louder than control boxes (bluebirds: $t = -21.26$, $df = 19.92$, $P < 0.001$; flycatchers: $t = -13.11$, $df = 5.04$, $P < 0.001$, Fig. 1). Power spectra of the original recordings versus the received playback stimuli within the box show that our playback systems elevated sound levels across the spectral range most audible to birds (i.e., 0.5–10 kHz; Dooling and Popper 2007, Fig. 2). In general, received playback stimuli had less energy at these frequencies than the original recordings that were 10 m from roadways, but were often higher than typical of noise spectral profiles at twice that distance (i.e., 20 m).

Western bluebirds

The noise treatment did not influence western bluebird clutch or brood size, number of fledglings, overall success, or chick body mass, tarsus length, or wing chord length (Tables 1 and 2; Fig. 3). However, nests initiated earlier in the season tended to have larger clutch sizes, clutch size was a positive predictor of brood size, and brood size was a positive predictor of number of fledglings.

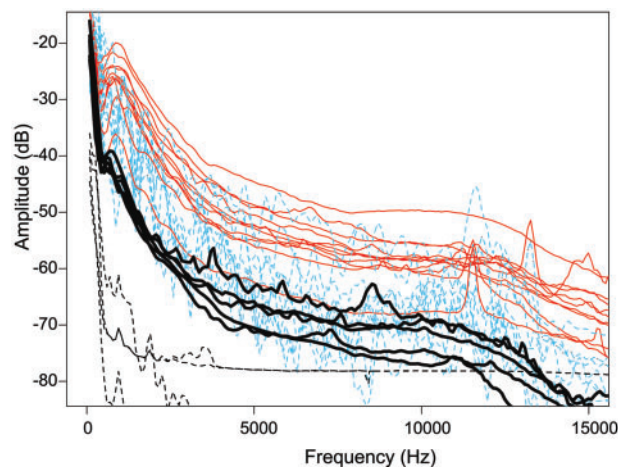


Fig. 2 Power spectra of original traffic recordings taken 10 m from the road (thin solid lines (red online) $n = 11$), playback (StorMp3 system) of original traffic recordings within the nest box (thick dashed lines (light blue online), $n = 11$), traffic recordings taken 20 m from the road at original locations (thick solid lines (black online), $n = 5$), and recordings made inside quiet control boxes (thin dashed lines (black online), $n = 4$).

Ash-throated flycatchers

For ash-throated flycatchers, clutch size did not differ between noise treated and control boxes; however, brood size was much smaller in noise-treated boxes than quiet control boxes (Table 3 and Fig. 3), due to high rates of nest abandonment during the incubation stage relative to control boxes. Accounting for the smaller brood size in treatment nests demonstrated that there were not any additional effects of treatment on number of fledglings

Table 1 GLMM model effects and 95% confidence intervals (95% CI) explaining western bluebird clutch size, brood size (number of hatchlings), number of fledglings, and success

Model	Effect	95% CI	
Clutch size Gamma (log link) error			
Treatment	0.030	-0.050	0.110
CID, scaled	-0.040	-0.070	-0.010
Brood size controlling for clutch size Poisson error			
Treatment	0.096	-0.168	0.359
Clutch size	0.298	0.104	0.492
CID, scaled	0.022	-0.119	0.162
Fledglings controlling for brood size Poisson error			
Treatment	0.068	-0.213	0.349
Brood size	0.356	0.216	0.495
CID, scaled	-0.005	-0.151	0.142
Fledgling without controlling for brood size Poisson error			
Treatment	0.121	-0.160	0.401
CID, scaled	-0.062	-0.205	0.080
Success binomial error			
Treatment	1.201	-0.470	2.872
CID, scaled	-0.168	-0.894	0.558

Notes: All models included Year and Box ID as random effects. Strong effects indicated in bold.

Table 2 LMM model effects and 95% confidence intervals (95% CI) explaining western bluebird nestling body mass (g), wing chord length (mm), and tarsus length (mm)

Model	Effect	95% CI	
Mass³			
Treatment	-352.000	-2287.830	1583.747
Brood size	-554.800	-1658.678	549.009
CID, scaled	-892.700	-1843.973	58.633
Tarsus²			
Treatment	-9.734	-35.785	16.317
Brood size	18.007	3.199	32.814
CID, scaled	-35.037	-48.350	-21.724
Wing Chord³			
Treatment	-5040.000	-13,521.070	70,202.497
Brood size	2245.000	-2723.989	3441.059
CID, scaled	2641.000	-4354.271	3826.009

Notes: All models included Year and Nest ID as a random effect. Strong effects indicated in bold.

(Table 3). Irrespective of brood size, treatment nests successfully fledged fewer chicks than control nests (Fig. 3). Ash-throated flycatcher chicks in treatment boxes were no different from those in control boxes

Table 3 GLMM model effects and 95% confidence intervals (95% CI) explaining ash-throated flycatcher clutch size, brood size (number of hatchlings), number of fledglings, and success

Model	Effect	95% CI	
Clutch size Gamma (log link) error			
Treatment	-0.037	-0.115	0.039
CID, scaled	-0.035	-0.081	0.011
Brood size Poisson error			
Treatment	-0.528	-1.067	-0.001
Clutch size	0.296	-0.336	0.928
CID, scaled	-0.003	-0.282	0.276
Fledglings controlling for brood size Gamma (log link) error			
Treatment	-0.099	-0.699	0.501
Brood size	0.716	0.359	1.073
CID, scaled	0.101	-0.167	0.369
Fledglings Gamma (log link) error			
Treatment	-0.745	-1.328	-0.156
CID, scaled	0.048	-0.262	0.358
Success binomial error			
Treatment	-1.007	-2.847	2.355
CID, scaled	0.326	-0.683	1.335

Notes: All models included Year as a random effect. Strong effects indicated in bold.

with respect to tarsus and wing chord length. However, chicks in noise-treated boxes were heavier than those in control boxes (Table 4 and Fig. 3), even when controlling for brood size. Finally, there was no evidence that treatment nests were less successful in fledging at least one chick from the nest than control nests (Table 3).

Discussion

The expanding human population and our accompanying transportation networks pose several threats to wildlife. Noise pollution has recently been associated with changes in animal behavior (Quinn et al. 2006; Leonard and Horn 2012), physiology (Crino et al. 2013; Kleist et al. 2018), and reproductive success (Halfwerk et al. 2011a; Kight et al. 2012; Kleist et al. 2018). However, we do not fully understand which stages of the breeding process are most sensitive to disruption by noise. Here, using our manipulative approach, our study demonstrates that noise at the nest appears to have no apparent fitness consequences for western bluebirds. For ash-throated flycatchers, however, we found evidence that noise at the nest may have a direct negative effect on reproductive success.

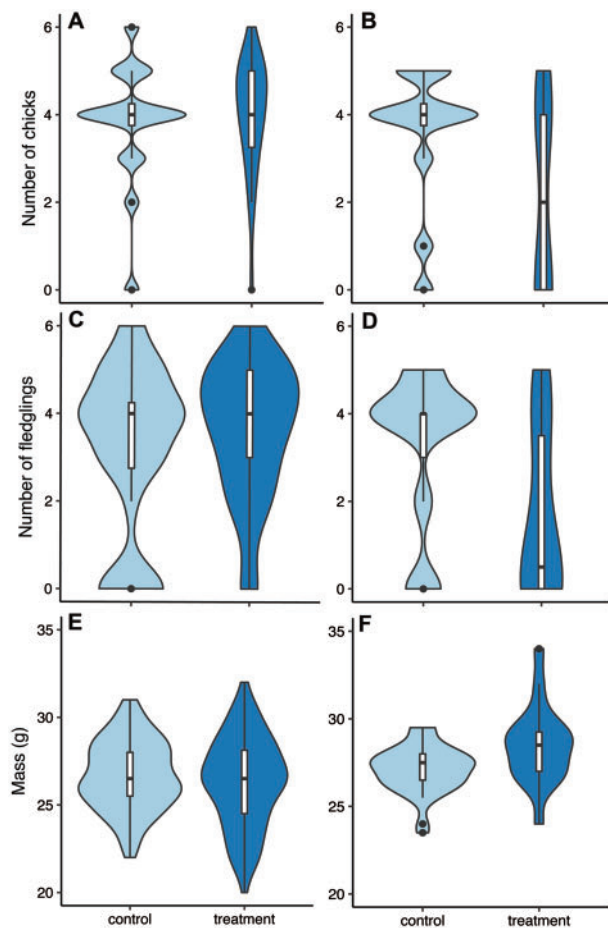


Fig. 3 Western bluebirds and ash-throated flycatchers were influenced differently by the experimental traffic noise exposure. The number of successfully hatched chicks did not differ between treatment and control boxes for (A) western bluebirds, but (B) ash-throated flycatcher nests in noise-treated nest boxes had fewer chicks than in control boxes. Similarly, number of chicks to successfully fledged did not differ between noise-treated boxes and control nests for (C) western bluebirds, but (D) ash-throated flycatcher nests exposed to traffic noise fledged fewer young. Body mass of chicks did not differ between treatment and control boxes for (E) western bluebirds, but (F) ash-throated flycatcher chicks in treatment nests were heavier than those in control boxes, even after controlling for brood size. Boxplot and violin outlines are as in Fig. 1.

Ash-throated flycatchers exposed to chronic traffic noise produced significantly fewer chicks and fledglings compared with those in control boxes. The difference appears to be driven by nest abandonment during incubation. In contrast, western bluebirds experienced no influence of treatment on nest success. Because we minimized the possible influence of self-sorting with respect to noise, these results provide partial support for a direct influence of noise at the nest on avian reproductive success. A similar direct effect of noise on reproductive performance may explain previous results of decreased success for

Table 4 LMM model effects and 95% confidence intervals (95% CI) explaining ash-throated flycatcher nestling body mass (g), wing chord length (mm), and tarsus length (mm)

Model	Effect	95% CI	
Mass			
Treatment	1.741	0.535	2.947
Brood size	-0.218	-0.981	0.546
CID, scaled	0.337	-0.226	0.900
Wing chord			
Treatment	0.524	-1.985	3.034
Brood size	0.521	-0.887	1.930
CID, scaled	0.169	-0.981	1.320
Tarsus			
Treatment	0.721	-0.058	1.500
Brood size	0.192	-0.295	0.679
CID, scaled	-0.184	-0.570	0.202

Notes: All models included Year and Nest ID as a random effect. Strong effects indicated in bold.

individuals breeding in noisy habitats. However, it remains possible that the reduced reproductive success documented in great tits (Halfwerk et al. 2011a) and eastern bluebirds (Kight et al. 2012) could be the result of non-random distributions of individuals across landscape. However, in the only known test of self-sorting with respect to noise, Kleist et al. (2018) found no evidence that western bluebird, mountain bluebird (*Sialia currucoides*) or ash-throated flycatcher female morphological measures vary systematically with respect to energy sector noise in New Mexico, USA.

Ash-throated flycatcher nests exposed to traffic noise produced heavier chicks, even when controlling for brood size. This may be the result of individual variation in personality types within the population, such that noise-exposed individuals that did not abandon the nest during incubation are less influenced by noise. Personality type has been shown to influence nest box provisioning rates in wild, breeding great tits, with more exploratory parents being less affected by noise than their more shy counterparts (Naguib et al. 2013). Future work should endeavor to link personality types to behavior in varying acoustic environments to determine whether personality may account for variation in fitness in response to noise exposure.

Outwardly, the different responses to noise among ash-throated flycatchers and western bluebirds align with recent evidence of their responses to this pollutant during breeding site selection and establishment. Kleist et al. (2017), working in a region

heavily developed by natural gas extraction activities in NW New Mexico, found that western bluebird settlement patterns were uninfluenced by energy-sector noise, but that ash-throated flycatchers avoided areas characterized by noise in their settlement. However, follow up research by Kleist et al. (2018) suggests that even though western bluebirds appear not to avoid noise in their nest site selection, they experience stress hormone dysfunction, greater hatching failure, and changes to chick body condition (i.e., feather development and body size) in areas exposed to higher noise levels. That Kleist et al. (2018) documented reproductive consequences linked to noise exposure for western bluebirds and we did not suggests that exposure away from the nest, or before clutch initiation, may be important for fully comprehending noise impacts in this species (see below).

Our results, and those of Kleist et al. (2017, 2018), suggesting that ash-throated flycatchers are noise sensitive improve upon earlier evidence that ash-throated flycatcher occupancy is unrelated to energy-sector noise (Francis et al. 2011a). In their study, Francis et al. (2011a) measured ash-throated flycatcher occupancy using point count surveys, whereas Kleist et al. (2017, 2018) measured nest box occupancy, stress hormones, and reproductive success. Two recent studies suggest that male birds occupying noisy territories have lower pairing success than those in less noisy locations (Habib et al. 2007; Gross et al. 2010). Thus, it is possible that territorial establishment among male ash-throated flycatchers is unrelated to noise, but that subsequent steps in the breeding process, such as mate attraction and hatching rate, are negatively influenced by noise pollution. This work underscores the need for measuring multiple response variables to fully understand the costs, or lack thereof, of breeding in noisy environments. Thus, future efforts should not only determine how individual densities or abundance vary with noise exposure, but simultaneously quantify pairing success to help tease apart which stages of breeding process are most sensitive and why.

Why our in-box treatments did not reveal fitness costs similar to those documented by Kleist et al. (2018) could reflect different sensitivities by the populations in California and New Mexico, or the context of noise exposure in the present study restricted to nest boxes. In support of the latter, Halfwerk et al. (2016) used a similar in-box noise exposure experiment and found no influence of noise on reproductive success in great tits, which conflicts with previous work in this species documenting large

reproductive consequences for birds exposed to actual traffic noise (Halfwerk et al. 2011a). Thus, context and the spatial and temporal extent of noise exposure may be key to understanding conflicting results for great tits, western bluebirds, and other species. Indeed, Ellison et al. (2012) suggested that animal responses to noise, or lack thereof, are rarely understandable unless the context of the animal is understood. That is, noise may only be problematic for animals engaged in particular behaviors, in particular locations or those at sensitive life stages. Although our in-box noise exposures allowed us to control for the possibility of individuals self-sorting across the landscape and to determine what degree noise exposure at the nest during incubation, brooding, and provisioning influences reproduction, this approach cannot gauge the influence of noise on pre-settlement stages (settlement patterns, mate choice), which may be equally or more vulnerable to noise pollution than post-settlement stages. Additionally, noise away from the nest and across the territory, where acoustic cues are used in many other facets of birds' daily lives, such as to passively survey for predators or aide in hunting prey, could be equally or more important than noise levels at the nest. In support of this possibility, Kleist et al. (2017) found evidence that the presence or absence of energy-sector noise across the landscape had a strong influence on the number of active nests for mountain bluebirds and ash-throated flycatchers in NW New Mexico, but that sound levels at individual nest boxes had a minor influence on occupancy patterns for ash-throated flycatchers and no influence on occupancy patterns in mountain bluebirds. Thus, when viewed in the context of other studies, our experimental design of in-box playback systems likely does not capture the myriad ways in which noise can affect birds in real landscapes. We therefore caution researchers interested in using in-box manipulative playbacks to consider the limited scope of exposure when drawing conclusions from their studies.

Finally, urban environments are complex and noise represents only one of the many environmental axes that can influence fitness. Experiments, such as ours, that isolate the influence of a single stressor to particular contexts are important for sorting among the many possible pathways by which human activities affect wildlife. Nevertheless, birds and other wildlife live in multi-stressor worlds and sensory stimuli such as noise, light, and other anthropogenic environmental changes often co-occur (Halfwerk and Slabbekoorn 2015; Swaddle et al. 2015). Future efforts must seek to understand how these stressors

interact. Lastly, although our study suggests that sensitivity to noise can vary across, and possibly within, species, it adds to the growing evidence suggesting that exposure to traffic noise has negative consequences for avian reproduction. For efforts intended to bolster populations of secondary-cavity nesting birds in urban and nonurban environments, nest boxes should not be placed near roadways; although convenient for humans, the cost to breeding birds may be too high.

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Supplementary data

Supplementary data are available at *ICB* online.

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