

# Anthropogenic noise is associated with reductions in the productivity of breeding Eastern Bluebirds (*Sialia sialis*)

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**Abstract.** Although previous studies have related variations in environmental noise levels with alterations in communication behaviors of birds, little work has investigated the potential long-term implications of living or breeding in noisy habitats. However, noise has the potential to reduce fitness, both directly (because it is a physiological stressor) and indirectly (by masking important vocalizations and/or leading to behavioral changes). Here, we quantified acoustic conditions in active breeding territories of male Eastern Bluebirds (*Sialia sialis*). Simultaneously, we measured four fitness indicators: cuckoldry rates, brood growth rate and condition, and number of fledglings produced (i.e., productivity). Increases in environmental noise tended to be associated with smaller brood sizes and were more strongly related to reductions in productivity. Although the mechanism responsible for these patterns is not yet clear, the breeding depression experienced by this otherwise disturbance-tolerant species indicates that anthropogenic noise may have damaging effects on individual fitness and, by extension, the persistence of populations in noisy habitats. We suggest that managers might protect avian residents from potentially harmful noise by keeping acoustically dominant anthropogenic habitat features as far as possible from favored songbird breeding habitats, limiting noisy human activities, and/or altering habitat structure in order to minimize the propagation of noise pollution.

**Key words:** anthropogenic disturbance; bioacoustics; breeding; Eastern Bluebird; fitness; noise; *Sialia sialis*; Williamsburg, Virginia, USA.

## INTRODUCTION

Anthropogenic activities can introduce significant noise pollution into the environment. The loudest noise pollution generally exceeds levels achieved by natural sources of noise, and may permeate the habitat to a greater degree. For example, noise levels in roadside forests may reach 98 dB at the edge nearest the road (5 m away) and remain at detectable levels several hundred meters into the trees (Arévalo and Newhard 2011). Further, the timing and pattern of human-made noise may be unpredictable and differ significantly from those found in nature (Warren et al. 2006, Barber et al. 2010, Pijanowski et al. 2011). Exposure to noise pollution has the potential to increase physiological stress levels in animals (Kight and Swaddle 2011), reduce foraging success (Siemers and Schaub 2011), alter species' behavioral time budgets (Quinn et al. 2006), mask

acoustic communication (Slabbekoorn and Peet 2003, Patricelli and Bickley 2006), and alter community structure (Francis et al. 2009, 2011b).

An increasing number of anthropogenic noise studies have shown that adult animals are remarkably flexible, over both the short and long term (Barber et al. 2010, Verzijden et al. 2010, Hanna et al. 2011), when it comes to responding to the presence of anthropogenic noise. For example, species of frog, fish, bird, and whale have all been shown to alter their vocalizations in order to reduce masking by anthropogenic noise (Sun and Narins 2005, Vasconcelos et al. 2007, Francis et al. 2011a, Hanna et al. 2011, Parks et al. 2011). European Robins (*Erithacus rubecula*) in noisy areas have been found to sing more at night, when it is quieter (Fuller et al. 2007), while mouse-eared bats (*Myotis myotis*) preferentially hunt in quieter habitats (Schaub et al. 2008). Thus, by altering how, when, and where they perform certain behaviors (i.e., their phenotypes), many animals appear capable of tolerating the presence of noise pollution.

Even among the most phenotypically plastic species, however, noise may have negative effects over the long term. A study in a Canadian population of Ovenbirds (*Seiurus aurocapillus*) found that older males claimed quieter territories and left noise-polluted sites to first-

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year breeders (Habib et al. 2007); as a result, the younger males suffered lower pairing success. Although there are several potential explanations for these patterns, they may indicate that females regard noisier territories as unattractive, are unable to hear the vocal displays of males residing in noise-polluted sites, or both. Even where pairs are formed, increases in ambient noise may be accompanied by waning female preferences for their pair-bonded mates, as found in an aviary study on Zebra Finches, *Taeniopygia guttata* (Swaddle and Page 2007). This may be caused by masking of pair-bond vocalizations between mates which, in the wild, could lead to higher levels of divorce between breeding attempts, as well as higher levels of cuckoldry within breeding attempts.

Cumulatively, these studies indicate that the presence of noise, especially noise that masks crucial vocalizations, could have negative effects on avian fitness. Despite this prediction, little research to date has explicitly investigated the potential fitness costs of breeding in noisy territories (but see Francis et al. 2009, 2011b, Halfwerk et al. 2011). To help bridge that gap, we examined a population of Eastern Bluebirds (*Sialia sialis*) nesting across an anthropogenic noise gradient. We hypothesized that male fitness would be lower in territories with higher levels of environmental noise in the frequency range used for bluebird communication; in other words, males whose songs and calls were more likely to be masked should have lower breeding success. To test this prediction, we quantified acoustic conditions in active bluebird territories across an anthropogenic noise gradient. Within each territory, we measured cuckoldry rates, clutch size, brood size, brood growth rates, brood condition, and total number of fledglings produced. We predicted that, in noisier breeding territories, cuckoldry rates would be higher, while clutch size, brood size, brood growth rates, brood condition, and total number of chicks fledged per nest would all be lower. We acknowledge that this study design is correlative; hence, we cannot tease apart the many putative environmental factors that could be associated with variation in anthropogenic noise. However, our investigation of an otherwise disturbance-tolerant species (Kight 2010) helped us minimize the effects of such confounding factors and focus more narrowly on the relationships between noise and bluebird reproductive parameters.

## MATERIALS AND METHODS

### *Study site and species description*

We studied wild populations of cavity-nesting Eastern Bluebirds during the 2007 and 2008 breeding seasons. We have collected data from these populations since 2002, taking advantage of the birds' willingness to occupy a network of wooden nest boxes distributed across an anthropogenic noise gradient in Williamsburg, Virginia, USA. The boxes are located at a variety of site types, including cemeteries, campuses, parks, recreation-

al facilities, and golf courses. Previous work indicates that measures of direct disturbance (i.e., traffic, pedestrians, bicyclists, dog walkers) within bluebird breeding territories are not related to the physical condition of nesting adults, availability of resources, offspring provisioning rates, or depredation rates (Kight 2005, Kight and Swaddle 2007, Hubbard 2008, Burdge 2009; J. P. Swaddle, *unpublished data*). Therefore, Eastern Bluebirds across this gradient appear to be fairly disturbance-tolerant; as a result, direct anthropogenic disturbance does not reliably explain fitness variation in this population (Kight 2005, Kight and Swaddle 2007). Hence, for this population, any relationship between noise and fitness is unlikely to be mediated solely by a correlation between noise and disturbance. Other information about the nest boxes and their placement has been provided in more detail elsewhere (Le Clerc et al. 2005, Cornell et al. 2011).

### *Evaluating environmental noise*

We recorded environmental noise at nest boxes ( $n = 34$ ) between 0700 and 1700 hours during the breeding seasons (March–August) of 2007–2009. Because preliminary analyses indicated that environmental noise conditions at our study sites were not greatly affected by time of day, time of season, or year (all  $P > 0.200$ ), we pooled all recordings collected throughout this study period into a single data set. Previous studies in this system have also found high inter-box consistency regardless of time of day, season, or year (Kight 2005, 2010, Kight and Swaddle 2007, Kight et al., *in press*).

All recordings were collected using a Sennheiser ME67 shotgun microphone (Wedemark, Germany) and a Marantz PMD660 solid-state recorder (Kanagawa, Japan). Prior to the start of data collection, we calibrated the microphone using a digital sound level meter so that all recordings could be adjusted to reflect “real-world” values. In each territory, the microphone was placed ~20 m from the nest box, positioned parallel with the ground at a height of ~1.5 m. Modeling our methods after Brumm (2004), we then collected recordings in each of the cardinal compass directions in order to obtain a noise sampling representative of the entire territory. We collected 45 seconds of ambient noise recording in each direction, for a total of three minutes from each site. Using Raven 1.3 acoustic analysis software (Cornell Laboratory of Ornithology, Ithaca, NY, USA), we extracted three 0.05-second clips from each direction, sampling at ~15-second intervals throughout the original recording. This methodology was used so that ambient noise recordings could easily be compared with those collected during a concurrent study on bluebird song and noise at the same territories (Kight 2010).

We chose to focus our analysis on the 1–5 kHz frequency range only. This represents the greatest overlap between the bandwidth containing adult Eastern Bluebird vocalizations (which most commonly occur in

the 1.5–4 kHz range [Huntsman and Ritchison 2002, Kight 2010]) and terrestrial anthropogenic ambient noise (which is generally loudest in the 0.2–2 kHz range [Slabbekoorn and Peet 2003, Fernández-Juricic et al. 2005, Wood and Yezerinac 2006]). We admit that it would be necessary to measure the auditory capabilities of Eastern Bluebirds in order to predict most accurately which frequencies of anthropogenic noise bluebirds are more susceptible to. However, justification of both our technique and its underlying assumptions is provided by a recent study on Great Tits (*Parus major*), which found that the birds were most affected by noise pollution in the frequency range with the greatest overlap between their song and noise from human traffic (Halfwerk et al. 2011).

Prior to analysis, all clips were bandpass filtered between 1 and 5 kHz. Again using Raven software, we then measured three aspects of ambient noise: peak frequency (frequency with the maximum power), average root-mean-square (RMS) amplitude (a measure of the magnitude of the noise volume), and peak RMS amplitude (a measure of the magnitude of the loudest amplitude recorded over the duration of the clip). For each site, we averaged all 12 values (4 directions  $\times$  3 clips per direction) obtained for the acoustic noise variables in order to yield one average measure for each noise variable per territory. As frequency and amplitude characteristics of environmental noise are generally correlated, we entered our noise variables into a principal components analysis (PCA), which yielded a single principal component (PC) with an eigenvalue  $>1$ . This PC (hereafter called Sound PC) explained 65.4% of the variance and loaded negatively for peak frequency (loading factor =  $-0.294$ ) and positively for both amplitude measurements (both loading factors =  $0.969$ ). Thus, as Sound PC increased, ambient noises became louder and lower pitched.

It is important to note that, because we sampled along a noise gradient, our recordings include not only anthropogenic noises (e.g., cars, voices, air conditioners, sounds of recreational activities, construction, and landscaping equipment), but also some elements of more “natural” sources of noise (e.g., other animals, rustling leaves). However, the loudest areas were consistently those dominated by anthropogenic noise (e.g., a mean of 67.5 dB(A) at a box on a college campus bordered by a busy road), while the quietest habitats were those farthest from human disturbance (e.g., a mean of 38.9 dB(A) at a remote box in a quiet state park). Thus, while the following analyses refer to the effects of “environmental noise” on breeding, at our study sites this was generally synonymous with “anthropogenic noise.”

#### *Collection of demographic data and calculation of breeding metrics*

All active nests were monitored throughout the March–August breeding seasons of 2007 and 2008.

Methods for monitoring are described in greater detail elsewhere (Kight 2005, Le Clerc et al. 2005, Kight and Swaddle 2007). Briefly, we visited boxes weekly throughout the egg-laying period and then twice a week during the chick growth period. This allowed us to determine when each clutch was initiated (clutch initiation date, CID), how many eggs were laid, how many of those eggs hatched, and how many fledglings were produced (referred to henceforth as *productivity*). By measuring wing length and mass of each chick, we were also able to generate a growth index (residual of wing length against age, averaged per brood), and a body condition index (residual of mass against wing length, averaged per brood) (Kight and Swaddle 2007). Because of the methods used to calculate growth and condition, approximately half the broods will have negative values for both variables.

Each nestling received a U.S. Fish and Wildlife Service aluminum band, as well as a unique combination of color bands. Parents that were not already marked from previous years of research were captured and similarly banded during blood collection.

#### *Blood collection and paternity analysis*

When chicks were 10–14 days old, we collected blood samples using brachial venipuncture. Because Eastern Bluebirds often remove unhatched eggs and dead nestlings from their nests, we were only able to consistently obtain blood or tissue samples from live chicks. We caught parents using mist nets or trapdoors placed over the entrance hole to the box. When possible, we also collected blood samples from neighboring adults (e.g., potential extra-pair parents). Blood was collected into heparinized capillary tubes and then immediately transferred to QIAcard FTA spots (Qiagen, Hilden, Germany). These were allowed to dry completely and then were sealed into small multibarrier pouches (Qiagen) for storage at room temperature.

Blood samples were purified using one of two methods: QIAamp DNA Micro Kit (Qiagen) or Whatman FTA Purification Reagent (Whatman Limited, Maidstone, UK). Gene products from both methods were amplified according to previously established methods (Faircloth et al. 2006). We focused our genotyping efforts on six tetranucleotide microsatellite loci that had previously been shown to have high allelic variability in Eastern Bluebirds (Faircloth et al. 2006): Sialia8, Sialia11, Sialia24, Sialia27, Sialia36, and Sialia37. Prior to the study, we confirmed the validity of all primer sets for our population. We combined 0.25–0.5  $\mu$ L of each polymerase chain reaction (PCR) product with Rox 500 size standard and performed electrophoresis on an ABI 3130 Genetic Analyzer (Applied Biosystems, Foster City, California, USA). Alleles were binned by hand following visual inspection in GeneMapper 3.5 (Applied Biosystems).

Our study sites were spatially clustered in four distinct areas (e.g., York River, College of William and Mary

campus, central Williamsburg, Williamsburg Country Club), each separated by a minimum of 3.2 km (2 miles). Additionally, there is fairly high site fidelity among our population of Eastern Bluebirds (C. R. Kight, *unpublished data*). Thus, it was unsurprising that preliminary analyses with CERVUS v.3.0.3 (Marshall et al. 1998) and GENEPOP 4.0 (Raymond and Rousset 1995a, b) both indicated the presence of subpopulation structure across our samples. In other words, birds that lived in territories at one locality were more likely to be related to other birds from that locality than to breeders in other nesting sites. As a result, we examined each subpopulation separately when performing allele frequency calculations and conducting further paternity analyses.

Allele frequencies were established by CERVUS. In one of the subpopulations, one locus (11a) showed significant deviation ( $P = 0.0005$ ) from Hardy-Weinberg equilibrium; in another population, this was true of three loci (8a, 11a, 27a) (all  $P < 0.00004$ ). This likely stems from even greater population substructure than that used to group our samples here, nonrandom sampling of individuals, and/or small sample size (Faircloth et al. 2006). We used CERVUS to assign paternity across 43 nests laid in 34 nest boxes over the course of the study period. Because a preliminary analysis indicated possible egg-dumping, we conducted a parent-pair analysis rather than a straightforward paternity test. The list of candidate parents included all adults sampled within each subpopulation. Parameters were as follows: number of candidate mothers = 2, of which 50% were assumed to have been sampled; number of candidate fathers = 3, of which 67% were assumed to have been sampled; error rate = 0.036 (calculated from mother-offspring mismatches in our data set); confidence levels were 95% and 99%. The average exclusion probability across all nests was 98.5%.

Although we had originally attempted to genotype birds at all six focal loci, this was not always possible because insufficient quantities of blood were sampled from some individuals. Ultimately, we conducted paternity tests using all individuals that had been genotyped at a minimum of three loci (total  $n = 146$  chicks and 67 adults; mean number of loci = 5.20). Incomplete broods were examined for nine nests (20.9%). We have attempted to correct for this imbalance in our statistical analyses (see *Statistical analyses*). Cuckoldry rate was calculated as the number of extrapair young divided by the total number of nestlings.

#### *Statistical analyses*

To investigate the impacts of environmental noise on breeding success, we constructed general linear mixed-effects models using the lme4 package in R v2.13.1 (R Development Core Team 2005). We used stepwise deletion of nonsignificant fixed effects to obtain minimal adequate models (Pinheiro and Bates 2000, Crawley

2002). Independent models were created for each of six breeding metrics: cuckoldry rates, brood growth rates, brood condition, clutch size, brood size (a proportion indicating the number of eggs that hatched), and productivity (the absolute number of fledglings produced, rather than a proportion of the brood, because only two nests (4.7% of the total) experienced brood reduction). We obtained qualitatively similar results from our analyses if we substituted an information theoretic model selection process, and also if we combined reproductive metrics using a PCA and looked for associations between the resulting metrics and both environmental sound and breeding density.

Breeding density was included as a covariate in all models, as it is known to affect paternity in Eastern Bluebirds (Gowaty and Bridges 1991), and because it is often a correlate of noise (e.g., since birds in noisy urban areas are often at higher densities than conspecifics in quieter rural locations [Nemeth and Brumm 2009]). It was represented by a PC (Density PC) derived from a PCA on three factors: the number of boxes within a 400-m radius of the nest box, the number of boxes within an 800-m radius of the nest box, and the distance to the nearest box. The 400-m measurement reflects the number of potential extrapair mates and amount of competition for resources near the box. The 800-m measurement provides a better indication of a box's relative position within the breeding area (since boxes at the edge have fewer neighbors, while boxes in the middle have more); this helps take edge effects into consideration. We did not include data on bluebirds nesting in natural cavities because few, if any, exist at our sites. The PCA yielded a single PC with an eigenvalue  $> 1$ . The PC, which accounted for 61.4% of the variance, loaded highly for the number of boxes within both 400 m (loading factor = 0.952) and 800 m (loading factor = 0.859) of the focal box, but negatively for distance to nearest box (loading factor =  $-0.444$ ). Thus, increasing values of Density PC indicate increasing density of boxes both locally and across the entire site.

Box identity, nested within site identity, was included as a random factor in all analyses to help account for possible spatial autocorrelation of data. CID was also included as a random factor because Eastern Bluebird reproductive success has been found to vary seasonally, both across the species' range (Cooper et al. 2006) and within our study population (J. P. Swaddle, *unpublished data*). Finally, when examining the effects of environmental noise on cuckoldry rates, "proportion sampled" was also included as a control variable. This allowed us to include in the analysis broods that were incompletely sampled due to hatching failure, nestling mortality, or an insufficient blood sample.

Where necessary, data entered into PCAs were transformed to conform to model assumptions; the analyses themselves were performed in SPSS v16.0 (SPSS 2008).



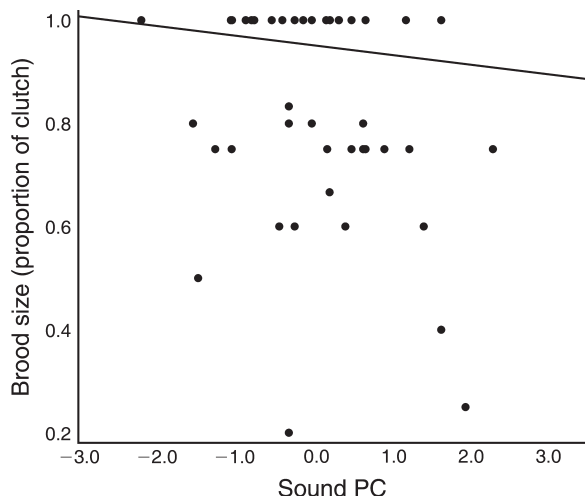


FIG. 1. A visualization of the weak negative relationship between Sound PC (environmental noise) and brood size (as a proportion of clutch size). Sound PC, which explained 65.4% of the variance in our data, loaded negatively for peak frequency (loading factor = -0.294) and positively for both RMS (root-mean-square) amplitude and peak RMS amplitude (both loading factors = 0.969). Thus, larger PC values reflect lower-pitched, louder environmental noise. For all figures, the straight lines are regression lines between the environmental variables, and the metrics of breeding success.

RESULTS

All but 2 of the 43 Eastern Bluebird nesting attempts successfully fledged young. One failure occurred at a nest box placed alongside an athletic field; it appeared that an athlete or ball had collided with the box, causing parental abandonment after the nest and its contents fell to the ground. The other failure occurred at a box located next to a long rural road leading into a state park; the adults abandoned their two-week-old chicks for reasons we could not discern.

Models including breeding density, environmental noise, and the interaction between these two variables did not adequately explain variations in cuckoldry rates (all  $\chi^2_1 < 2.18$ ; all  $P > 0.140$ ), brood growth rates (all  $\chi^2_1 < 3.06$ , all  $P > 0.300$ ), brood condition (all  $\chi^2_1 < 0.614$ ,  $P > 0.433$ ), or clutch size (all  $\chi^2_1 < 2.41$ ; all  $P > 0.120$ ). However, we did note that there was a trend toward decreasing brood size at higher levels of environmental noise ( $\chi^2_1 = 3.061$ ,  $P = 0.080$ ; Fig. 1).

The minimal adequate model explaining variation in nest productivity (number of fledglings) included only Sound PC, which was negatively related to productivity ( $\chi^2_1 = 4.54$ ,  $P = 0.033$ ; Fig. 2). Although Density PC (breeding density) was not included in the minimal adequate model describing variations in productivity, there was a trend toward a positive relationship between these two variables ( $\chi^2_1 = 3.37$ ,  $P = 0.066$ ; Fig. 3).

DISCUSSION

We show that higher levels of environmental noise in the bandwidth used for Eastern Bluebird communica-

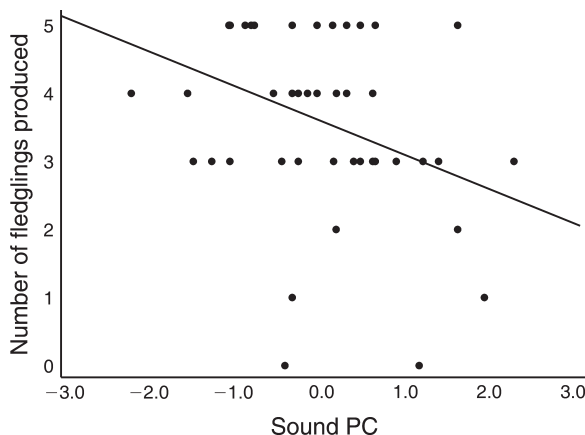


FIG. 2. A visualization of the negative relationship between Sound PC (environmental noise) and number of fledglings produced per nest. Sound PC loaded negatively for peak frequency (loading factor = -0.294) and positively for both RMS amplitude and peak RMS amplitude (both loading factors = 0.969) and explained 65.4% of the variance in our data. Larger PC values reflect lower-pitched, louder, ambient noise conditions.

tion are associated with reductions in productivity and, to some extent, brood size. However, we did not find any associations of environmental noise with clutch size, brood growth rates, brood condition, or cuckoldry rates. Bluebirds in our study area have previously been shown to be fairly tolerant of both direct anthropogenic disturbance and human habitat modifications, such that neither of these factors appears to explain variations in fitness metrics in our system (Kight 2005, Kight and

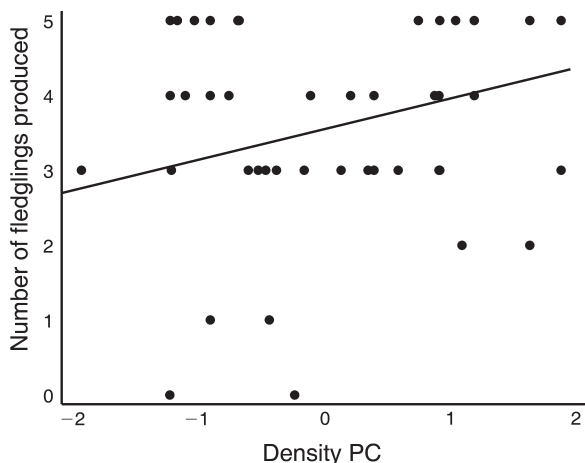


FIG. 3. A visualization of the weak positive relationship between Density PC (breeding density) and number of fledglings produced per nest. Density PC, which accounted for 61.4% of the variance in our data, loaded positively for the number of boxes within both 400 m (loading factor = 0.952) and 800 m (loading factor = 0.859) of the focal box, and negatively for distance to the nearest box (loading factor = -0.444). Larger values indicate higher box densities, both locally and across the entire site.

Swaddle 2007). Thus, we feel reasonably confident that the noise regimes themselves, rather than a related environmental variable for which they act as a proxy, are associated with the depression in productivity reported here.

Although the only statistically significant relationship was the association between noise levels and productivity ( $P = 0.033$ ), there was a trend for bluebirds in noisier habitats to have smaller broods ( $P = 0.080$ ), despite producing clutches that are similar in size to those laid in quieter areas ( $P = 0.182$ ). The mechanisms responsible for these trends may be physiological, behavioral, or some combination of the two. For instance, extreme noise is known to cause DNA damage (e.g., Frenzilli et al. 2004), which could cause females in loud environments to produce a higher number of infertile eggs. Noise might also have direct negative effects on developing avian embryos, as has been seen in fish (Banner and Hyatt 1973). Stress responses to loud and unpredictable noise regimes can suppress immune function (e.g., Van Raaij et al. 1996), which may increase chick die-off as a result of infection or, if their parents become ill, reduced parental care. Since noise pollution can cause increases in vigilance (Quinn et al. 2006), induce startle responses, and affect overall behavioral time budgets (as reviewed in Kight 2010), our results might also be explained by altered incubation and/or parental care behaviors in noise-exposed habitats; these possibilities are not mutually exclusive. In order to explore these and other possible mechanisms, and to understand their long-term implications, it will be necessary to conduct integrative studies that combine molecular techniques with behavioral observations, ecological measurements, and population-level analyses. However, our study does provide positive evidence that bluebird fitness is being compromised at stages between egg hatching and chick fledging, which is useful not only in proposing mechanisms for how noise affects breeding birds, but also in developing possible methods of sound management: We know that the birds will be particularly sensitive to noise during this (approximately) two-week time period.

It is interesting to compare our results with those of the only other published study, to our knowledge, that has examined associations between environmental noise and measures of breeding success in a cavity-nesting bird species. In a study on Great Tits breeding in The Netherlands, Halfwerk et al. (2011) found that birds in noisier environments laid smaller clutches and produced fewer fledglings. As was also observed in our own study site (C. R. Kight and J. P. Swaddle, *unpublished data*), these variations in breeding success were not associated with the condition of adults. Thus, the reduction in productivity is not likely driven by overt differences in the phenotypic condition of the parents, but rather by fluctuations in the acoustic environment.

Although the studies have similar end results, a smaller number of fledglings produced in noisier areas,

they appear to stem from alterations at different life stages (e.g., between egg hatching and chick fledging for the bluebirds, but at egg laying for the Great Tits). Perhaps these reproductive differences were caused, at least in part, by the generally louder noise levels across the tit nesting sites compared with those recorded at our bluebird nestbox locations (minimum to maximum for tit study = 46.5 to 67.8 dB sound production level SPL (A); for bluebird study = 38.9 to 67.5 dB SPL (A)). It is also important to consider the effects of differences in habitat structure, source of noise, and pattern of noise pollution; while the tit study was conducted near a motorway where the predominant source of noise was traffic (Halfwerk et al. 2011), the bluebirds nested not just near roads, but also at campuses, cemeteries, parks, and golf courses. In future work, it will be important to investigate whether, and how much, variations in these habitat characteristics influence the relationships between noise and breeding success in different species.

Overall, tits and bluebirds have a number of life history traits in common, including the use of cavities for nesting, tolerance of anthropogenic disturbance (Gowaty and Plissner 1998, Maklakov et al. 2011), and use of vocalizations within the frequency range dominated by anthropogenic noise (Kight 2010, Halfwerk et al. 2011). Despite this number of similarities, and the shared loss of productivity in noisy areas, we propose that the mechanism driving reductions in fledging numbers differs for these two species, indicating that it may be difficult to extrapolate results across taxa (Francis et al. 2011a). Likewise, researchers should be cautious about applying results for secondary cavity-nesters, such as bluebirds and tits, to open-cup nesters. The latter, without any sound-attenuating walls around them (Swaddle et al., *in press*), may be more exposed to noise, but may also benefit more from a potential release from nest predation (Francis et al. 2009, 2011b). If variations in species' vocal responses to anthropogenic noise are any indication of the range of reproductive responses we can expect in noise-exposed birds, then the breeding success of even very closely related species may be differentially impacted by similar ambient environments (Francis et al. 2011a). From a conservation perspective, one of the most important avenues of future research will be identifying natural history characteristics that make species (or even individuals, implying that there may be capacity for adaptive responses of populations to noise) particularly susceptible to reduced reproductive success in noisy habitats.

Cumulatively, our results suggest that bluebird boxes placed in quieter habitats will experience greater reproductive output. More generally, our work indicates that breeding success can be altered by habitat factors associated with anthropogenic activities. This is an important step forward in understanding not only how humans affect the health and persistence of wild populations, but also what can be done to mitigate these impacts. We propose that population productivity

could be maintained by efforts that seek to reduce noise in songbird breeding habitats by placing acoustically dominant features (e.g., roads, machinery) farther from nesting areas, limiting noise production during particularly sensitive periods of breeding cycles (as indicated in our study), and/or abating current noise by altering habitat structure (e.g., introducing sound-absorbing structures such as partial sound walls and dense vegetation, removing highly sound-reflective surfaces, or even rerouting traffic) (Kight and Swaddle 2011). However, it is important to note that bird-friendly practices may have negative effects on other taxa (e.g., sound walls may limit movements of mammals and amphibians if not accompanied by other mitigation measures such as tunnels under roads), so it will be important for managers to assess the appropriateness of particular techniques for certain habitats prior to implementing them. We advocate a holistic view of management but emphasize that sound mitigation should be a factor within the collective decision-making process.

In the future, noise research will be greatly improved by experimental approaches. For instance, manipulations of habitat structure, food availability, and both the source and location of noise will all help elucidate how and why sound impacts reproductive parameters. In particular, we recommend that further experimental research focuses on the effects of anthropogenic sounds on eggs and nestlings, as individuals at these ages cannot simply flee noisy habitats (Swaddle et al., *in press*). Hence, a shift from adult to early life stages would be constructive in further understanding how noise pollution impacts bird populations.

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