RESEARCH ARTICLE

Experimental playback of natural gas compressor noise reduces incubation time and hatching success in two secondary cavity-nesting bird species

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ABSTRACT

Natural gas compressor stations emit loud, low-frequency noise that travels hundreds of meters into undisturbed habitat. We used experimental playback of natural gas compressor noise to determine whether and how noise influenced settlement decisions and reproductive output as well as when in the nesting cycle birds were most affected by compressor noise. We established 80 nest boxes to attract Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Tachycineta bicolor*) to locations where they had not previously nested and experimentally introduced shale gas compressor noise to half the boxes while the other 40 boxes served as controls. Our experimental design allowed us to control for the confounding effects of both physical changes to the environment associated with compressor stations as well as site tenacity or the tendency for birds to return to the specific locations where they had previously bred. We incorporated behavioral observations with video cameras placed within boxes to determine how changes in behavior might lead to any noted changes in fitness. Neither species demonstrated a preference for box type (quiet or noisy), and there was no difference in clutch size between box types. In both species, we observed a reduction in incubation time, hatching success, and fledging success (proportion of all eggs that fledged) between quiet and noisy boxes but no difference in provisioning rates. Nest success (probability of fledging at least one young; calculated from all nests that were initiated) was not affected by noise in either species suggesting that noise did not increase rates of either depredation or abandonment but instead negatively impacted fitness through reduced hatching and fledging success. Compressor noise caused behavioral changes that led to reduced reproductive success; for Eastern Bluebirds and Tree Swallows, gas infrastructure can create an equal-preference ecological trap where birds do not distinguish between lower and higher quality territories even when they incur fitness costs.

Keywords: anthropogenic noise, compressor station, Eastern Bluebird, hatching success, incubation behavior, natural gas, shale gas, *Sialia sialis*, *Tachycineta bicolor*, Tree Swallow

LAY SUMMARY

- Natural gas is one of the most rapidly growing global energy sources with shale gas resources in particular expected to experience continued expansion.
- We used experimental playback of natural gas compressor noise to expose nesting Eastern Bluebirds and Tree Swallows to compressor noise.
- Eastern Bluebirds and Tree Swallows nesting in noisy nest boxes spent less time incubating their eggs, had fewer eggs hatch, and produced fewer young than their neighbors nesting in quiet boxes.
- Although there was a direct fitness cost, birds did not preferentially select quiet boxes over noisy boxes, suggesting they do not recognize the reduction in habitat quality resulting from the noise.
- Because shale gas development often occurs in relatively undisturbed natural areas that provide important habitat for breeding birds, it is imperative that we develop plans to manage and mitigate noise. These practices will also benefit other wildlife and people.

El playback experimental del ruido de un compresor de gas natural reduce el tiempo de incubación y el éxito de eclosión en dos especies de aves que anidan en cavidades secundarias

RESUMEN

Las estaciones de compresión de gas natural emiten un ruido fuerte de baja frecuencia que viaja cientos de metros dentro del hábitat no disturbado. Usamos playback experimental de ruido de un compresor de gas natural para determinar si y cómo el ruido influenció las decisiones de asentamiento y el rendimiento reproductivo, y para determinar en qué

momento en el ciclo de anidación las aves fueron más afectadas por el ruido del compresor. Establecimos 80 cajas nido para atraer individuos de *Sialia sialis* y de *Tachycineta bicolor* a las localidades donde no habían anidado previamente e introdujimos experimentalmente el ruido del compresor de gas de esquisto a la mitad de las cajas mientras que las otras 40 cajas sirvieron como control. Nuestro diseño experimental nos permitió controlar los efectos de confusión tanto de los cambios físicos al ambiente asociados con las estaciones de compresión, como la tenacidad del sitio o la tendencia de las aves de regresar a las localidades específicas donde habían criado previamente. Incorporamos las observaciones de comportamiento usando cámaras de video ubicadas dentro de las cajas para determinar cómo los cambios en comportamiento podrían llevar a cualquier cambio observado en la aptitud biológica. Ninguna especie demostró una preferencia por el tipo de caja (silenciosa o ruidosa), y no hubo diferencias en el tamaño de la nidada entre los tipos de cajas. En ambas especies, observamos una reducción en el tiempo de incubación, en el éxito de eclosión y en el éxito de emplumamiento (proporción de todos los huevos que llegaron al emplumamiento) entre las cajas silenciosas y ruidosas, pero no hubo diferencias en las tasas de aprovisionamiento. El éxito de anidación (probabilidad de emplumar al menos un joven; calculada a partir de todos los nidos que fueron iniciados) no estuvo afectado por el ruido en ninguna de las especies, sugiriendo que el ruido no aumentó las tasas de depredación o abandono, pero en cambio impactó negativamente la adecuación biológica a través de la reducción en la eclosión y en el éxito de emplumamiento. El ruido del compresor causó cambios en el comportamiento que llevaron a una reducción del éxito reproductivo; para *S. sialis* y *T. bicolor*, la infraestructura de gas puede crear una trampa ecológica de igual preferencia donde las aves no distinguen entre territorios de menor o mayor calidad, incluso cuando incurren en costos de adecuación biológica.

Palabras clave: comportamiento de incubación, estación de compresión, éxito de eclosión, gas de esquisto, gas natural, ruido antropogénic*o, Sialia sialis, Tachycineta bicolor*

INTRODUCTION

Natural gas is one of the most rapidly growing global energy sources and will account for an estimated 39% of U.S. energy production by 2050, with shale gas resources in particular expected to experience continued development in the coming decades (U.S. Energy Administration 2018). As shale gas development has expanded both nationally and globally, concern over ecological effects has increased (Brittingham et al. 2014). One source of concern is the increased levels of noise associated with natural gas compressor stations and its effects on birds and other wildlife (Bayne et al. 2008, Francis et al. 2009, 2011).

Compressor stations produce broadband noise that occurs continuously and is audible to birds as well as to humans and other wildlife. Compressor stations are necessary to pressurize gas for downstream transport, and they utilize large engines and cooling machinery that can generate chronic disturbance in the surrounding habitat (Habib et al. 2007, Francis et al. 2011, Kleist et al. 2018). Sound disturbance from compressor stations and associated energy development has been linked to a number of effects on birds throughout their life cycle including avoidance, reduced abundance and species richness, changes in age structure, changes in community interactions, increased stress levels, lower hatching success, and changes in behavior (Habib et al. 2007, Bayne et al. 2008, Francis, 2009, Kleist et al. 2018).

Despite important progress in understanding the effects of gas compressor noise, we still lack an understanding of the mechanisms by which noise affects the distribution and fitness of birds (Barber et al. 2010, Francis and Barber 2013). One problem has been that studies of compressor noise are frequently confounded with a number of other factors that must be controlled for if we are to fully understand how noise affects birds. A primary confounding variable is that the noise is usually also associated with many physical changes to the environment including changes in the vegetation, increases in impervious surfaces, and habitat fragmentation, making it difficult to isolate the effects of noise from other disturbances that are occurring simultaneously. Some researchers have been able to address this with experimental studies specifically designed to isolate noise effects from other associated sources of disturbance (Blickley et al. 2012, Cinto-MeJia et al. 2019).

However, even for experimental studies that isolate the effect of noise, the confounding effect of site tenacity is still a problem when comparing abundance and distribution of birds in response to noise. Numerous studies have shown that birds tend to return to the same territories where they previously bred (reviewed in the work of Zack and Stutchbury 1992). Thus, it may take multiple generations before changes in abundance or settlement patterns are noted even if the specific territory quality has changed. In addition, in order to understand why demographic changes occur, behavioral observations are required to sort out the potential causes.

The goal of this study was to investigate when in the nesting cycle birds are most affected by compressor noise using 2 model species and 1 standardized system of noise playback. To control for the confounding issues, we experimentally introduced compressor noise without associated changes to the physical environment. Because our study species were secondary cavity nesters, we were able to reduce the confounding issue associated with site tenacity by establishing nest boxes in fields where they had not previously occurred. To better understand the mechanism for any observed differences between birds nesting in noise-exposed and control boxes, we included behavioral

observations throughout the nesting cycle. We predicted that (1) birds would preferentially settle in quiet boxes over noise-exposed boxes; (2) birds in noisy boxes would expend less effort in incubating eggs and feeding young, resulting in lower hatching and fledging success; and (3) nest survival would be lower in noise-exposed boxes. Our predictions were based on results from other studies suggesting that noise can influence multiple aspects of breeding behavior (Kleist et al. 2017, 2018).

METHODS

Study Site and Study Species

We conducted our study at Penn State's Russell E. Larson Agricultural Research Center (RELARC), outside State College, Pennsylvania. This site is ~2,000 acres of mixed farmland, pasture, wooded hedgerows, and small woodlots and is used for agricultural research and demonstration plots. Anthropogenic noise on the site is primarily limited to occasional mowing and farm vehicle traffic. We chose this site because it had expansive areas that did not have any nest boxes prior to our study. This enabled us to avoid legacy effects stemming from previous nest box occupancy or previous site familiarity, as birds using our nest boxes were likely new to the site. An onsite weather station provided temperature and other weather data.

We investigated the responses of Eastern Bluebirds (*Sialia sialis*) and Tree Swallows (*Tachycineta bicolor*) to experimental compressor noise at nest boxes. Both species are secondary cavity nesters that use nest boxes (Gowaty and Plissner 2020, Winkler et al. 2020). Eastern Bluebirds are found in Pennsylvania year-round and breed as early as April, sometimes continuing into late August, raising up to 3 broods per season (Gowaty and Plissner 2020). Tree Swallows are migrants, and most individuals arrive mid-March to early April. Tree Swallows breed through May and June and usually raise one brood (Winkler et al. 2020).

We captured adults of both species using mist nets and hand capture in the boxes and banded them with a USGS aluminum band (banding permit #23938). Only birds at nest boxes were captured. We attached a unique combination of 3 color bands to bluebirds for re-sighting purposes. We aged female Tree Swallows based on the proportion of plumage that was dull brown rather than iridescent, assigning individuals to second year (SY) or after second year (ASY) (Pyle 1997). We were able to age several females from video obtained during behavioral trials, so some individuals were aged even though they were not banded. Male Tree Swallows could not be aged reliably (Pyle 1997). Eastern Bluebird wing color and feather shape vary by age but differences can be subtle with older individuals having bluer plumage and more rounded feather tips (Pitts 1985, Pyle 1997). We photographed the wings of each Eastern

Bluebird captured and 5 banders independently aged each bird by plumage as either ASY or SY from the photos. We assigned an age to individuals when there was >60% agreement among the independent observers.

Nest Boxes and Experimental Design

We placed 80 nest boxes along unpaved roads and fields at RELARC in mid-March 2017 prior to the onset of the breeding season. All nest boxes were at least 400 m from a 2-lane paved road lightly traveled by passenger vehicles. Eastern Bluebirds and Tree Swallows use similar habitat and will compete for cavity space when cavities are limited. Therefore, we provided paired nest boxes to reduce competition (Parren 1994). We erected a total of 40 pairs of boxes ~100 m apart; a within-pair distance of ~2 m allowed both Tree Swallows and Eastern Bluebirds to nest at a given box site (Parren 1994). All nest boxes had a top-opening design and a small black wooden block resembling the cameras (see Section Behavioral Observations) used for behavioral observations. The wooden blocks were replaced with the cameras during behavioral trials.

Pairs of boxes were in lines with alternating pairs designated as control or treatment, resulting in 20 pairs of control boxes (quiet) alternating with 20 pairs of treatment boxes (noisy). Experimental compressor noise was introduced (see Section Sound Source) at treatment boxes shortly after boxes were installed and prior to bluebirds or Tree Swallows establishing territories. Playback systems were placed 1 m behind and centered between each set of treatment boxes. We placed plastic weather shelters over each speaker to prevent weather damage. We placed identical plastic weather shelters at pairs of control boxes to make pairs visually identical (i.e. every box pair had an identical black shelter regardless of whether it was a treatment or control pair).

Five randomly selected pairs of control boxes served as silent controls, with a silent noise file playing through the speakers. Silent files were comprised of a zero-wave file that produced no sound when the speaker was powered on to control for the presence of noise emanating from electrical components. These were included to ensure that any differences that we found between treatment and control boxes were due to the actual treatment sound and not due to the presence of undetected noise emanating from the electrical components.

Sound Source

We obtained recordings of compressor noise using laboratory-grade measurement microphones calibrated to meet Type 1 precision specifications which are standard for high-quality field measurements (GRAS 40AE/26CG microphone and a Roland R44 4-channel WAV-file recorder). These recordings were taken at an

active compressor station over a 2-week period. The sound files we used for experimental playback were made up of five 1-hr recordings taken at various times and weather conditions. We played these 1-hr files on shuffle at each noisy box simultaneously. The sound was played at nests using Boss ATV20 speakers and an AGPTek mp3 player powered by 12V marine deep cycle batteries. Compressors generate considerable acoustic energy, with a large proportion of this energy occurring between 0 and 200 Hz and continuing on to ~10,000 kHz. The speakers used in our study had a nominally flat response from 45 Hz to 10,000 kHz, which allowed a large portion of the sound's power to be replicated. We also tested whether noise playback from these speakers was realistic by recording our reproduced sound and confirming that recordings had the same frequency-line structure as the actual compressor noise, and that the level achieved was representative of near-station compressor noise (Appendix Figure 2). Noise played continuously except while the speaker batteries charged overnight twice a week. We used an Extech 600 (C-weighting and slow) sound level meter to determine the average power of sound at nest boxes every 5 s for 3 hr at each noisy pair, 1.5 hr with the sound on and 1.5 hr with the sound off, alternating which state was recorded first. To obtain an example of how noise propagated in the immediate area, we took readings every 10 m from one noise-exposed box out to ~70 m. We found that once we measured beyond 40 m from the box, noise levels were not different from ambient levels, suggesting that introduced noise did not impact adjacent nest boxes. Introduced noise raised sound pressure levels by 29.1 ± 3.3 dB(C) over ambient, which resulted in an average power level of 84.3 ± 1.9 dB(C) immediately outside nest boxes. This is consistent with the power of compressor stations relatively near the source (Barber et al. 2010).

Monitoring, Settlement, and Measures of Reproduction

We checked all nest boxes every 1–3 days. A box was considered occupied when at least 1 egg was laid, using the date of first egg as the settlement date. The date of the first egg laid in the study was designated settlement day 1. Thus, settlement date is an indication of when a box was selected and was used to compare whether there was a preference between quiet or noisy boxes. We recorded the number of eggs or nestlings in each box at each visit. Both species typically lay 1 egg each day (Gowaty and Plissner 2020, Winkler et al. 2020). In cases where multiple eggs were present when the box was checked, we determined the date of first egg by backdating.

When an occupied nest was found empty, we assumed depredation, and cold eggs or dead nestlings indicated abandonment. Empty nests in which the nestlings were at day 16 or older were considered successful since Eastern Bluebirds are capable of flight by day 14 and fledge around day 19 (Gowaty and Plissner 2020). Tree Swallows typically fledge between day 18 and 22 (Winkler et al. 2020). We considered a nest successful if at least 1 young fledged from the nest.

In addition to overall nest success, we calculated a number of additional measures of reproductive output and success including clutch size, proportion of eggs that hatched (hatching success), proportion of young that fledged (fledging rate), as well as proportion of eggs that produced fledglings (fledging success). Hatching rates, fledging rates, and fledging success were restricted to nests where at least one young fledged from the nest in order to test for changes in egg viability and brood reduction separately from depredation or abandonment which was accounted for in measures of overall nest success.

Behavioral Observations

At each occupied nest, we conducted a single behavioral observation at 3 nest stages: (1) egg incubation, (2) young nestlings (day 4–7), and (3) older nestlings (day 9–11; Williams 2018, 2019). Each observation was 3-hr long, resulting in a total of 9 hr of footage per nest across the developmental period. We chose these ages because Eastern Bluebirds are typically able to regulate their body temperature without brooding by day 8 and Tree Swallows by day 9, so the females' provisioning budget changes after that time (Gowaty and Plissner 2020, Winkler et al. 2020). Observation periods took place from 0800 to 1100 hr EST each morning on days with no rain or excessive wind. We attached GoPro Hero4 Session cameras to the inside of the nest box at ~0730 hr, and we discarded video recorded before 0800 hr before analysis to allow time for birds to return to normal behavior.

We quantified the amount of time each female spent on the nest during the 3-hr incubation observation period by analyzing videos manually with Behavioral Observation Research Interactive Software (BORIS, Friard and Gamba 2016). We defined incubation as the female sitting on the nest with her body in contact with the eggs. Eastern Bluebirds and Tree Swallows typically incubate for ~14 days, beginning when the last egg has been laid (Gowaty and Plissner 2020, Winkler et al. 2020), so we recorded incubation behavior ~7 days after the final egg was laid to prevent overlapping with hatching or recording behavior in boxes where incubation had not yet occurred.

We quantified the number of feeding visits during the younger and older observation periods by analyzing video observations manually in BORIS. We defined feeding as the transfer of a food item from the parent to a nestling.

We recorded data as feedings per hour in order to compensate for slight variation in trial lengths due to equipment failure or weather.

Statistical Analyses

We analyzed data on settlement and box use, clutch size, hatching and fledging success, and incubation and feeding rates in R 3.5.1 (R Core Team 2018) with treatment (control or noisy), species (Eastern Bluebird [EABL], Tree Swallow [TRES]), and female age (SY and ASY) included in the models. We included female age in the models but did not include the age of males since we were unable to age any of the male Tree Swallows. Means are presented ± 1 standard deviation. Results are presented with the regression coefficient and *P* value as well as with predicted values derived from the models for both species in noisy and control boxes. Predicted values were obtained using function *predict{stats}* in R. For all generalized linear models (GLMs), we tested for model fit by using the residual deviance to perform a goodness of fit test for the overall model.

Silent controls were used primarily as a qualitative check to ensure that differences noted between control and treatment boxes were due to the treatment sound and not due to other sounds associated with the speakers. In preliminary analyses, we analyzed the data with and without silent controls and with the silent controls as a third group. The significance or lack of a treatment effect did not change when they were excluded, and due to the small number of silent control boxes, they were not designed to be a third treatment group. For clarity and to increase the sample size of control boxes, silent controls were combined with controls for all analyses. In cases where we did find a difference between noisy and control boxes, we repeated the analyses with silent controls included as a third group and show these results also.

Settlement and box use. We looked at settlement and box use in a number of different ways. We report the total number of boxes by treatment type by species for all nesting attempts. To look specifically at initial settlement patterns, we restricted our analysis to first nesting attempts in order to avoid confounding effects associated with box reuse. We used a chi-squared contingency test to determine if nest box use was independent of noise status (e.g., control or treatment). We used Fisher's exact test of independence to determine if nest box use differed between treatment groups for different age classes of birds.

We tested whether the date a nest box was settled differed between control and treatment boxes using Poisson regression for count data with a GLM function (family Poisson log link). The response variable was the study day on which the first egg was present in the nest box. We restricted our analysis to first attempts so we could look specifically at initial settlement. We included treatment, species, and female age as factors. We hypothesized that even if box use did not differ between treatment types, control boxes might be settled before treatment boxes.

Clutch size, hatching, and fledging. To determine the effect of noise on clutch size, we used Poisson regression for count data with a GLM function (family Poisson log link). The response variable was the maximum number of eggs laid during a nesting attempt; and treatment, species, and female age were included in the model. To determine how noise affected hatching and fledging success, we analyzed hatching success (proportion of eggs that hatched), fledging rate (proportion of young that fledged), and fledging success (proportion of eggs that fledged) using a binomial family GLM with a logit-link function. The response variable for each nesting attempt was the number successful (e.g., hatched, fledged) and the number that failed. The model results allow us to predict the probability of hatching, fledging, etc. For this test, we only used nests in which at least one egg hatched to test for changes in egg viability or brood size rather than considering depredation or abandonment.

Daily nest survival. We calculated daily nest survival rates using the nest survival model in program MARK 8.2 (White and Burnham 1999, Dinsmore et al. 2002). Two failures in Eastern Bluebirds and one failure in Tree Swallows were human-caused and were excluded from the analysis. Our data met the assumptions of the nest survival model including that nests were correctly aged when found and nest fate was correctly determined (Dinsmore et al. 2002). We assume the data met the other assumptions including that nest checks did not influence survival, nest fates were independent of one another, and homogeneity of daily nest survival rates (Dinsmore et al. 2002). In addition, all control and treatment nests were treated identically in terms of frequency of nest checks. A nest was considered successful if at least 1 young fledged from the nest.

We compared models for daily nest survival rate that included species (EABL, TRES), treatment (noisy or quiet), and female age (SY, ASY) and ranked them by Akaike information criterion (AIC_c) value (Akaike 1974). We selected the model with the lowest AIC_c value as the best and that any within 2 AIC_c points were competitive (Burnham and Anderson 2001). We show nest survival for an average 37-day nesting period (e.g., 4 days egg laying, 14 days incubation, and 19 days nestlings).

Incubation rates. We analyzed incubation rates using binomial family GLMs with a logit-link and produced Figure 1 using the package *ggplot2* (Wickham 2016). The response variable for each 3-hr trial was the total number of minutes the female spent on the nest and the total number spent off the nest. In addition to treatment, species, and age, we included mean temperature during the
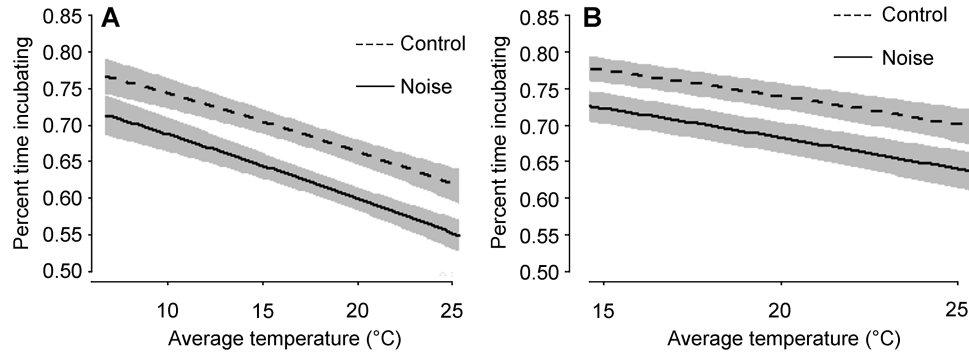
FIGURE 1. Proportion of 3-hr observation period that females in control and noisy (exposed to shale gas compressor noise) nest boxes spent incubating vs. average temperature (°C) for (A) Eastern Bluebirds ($n = 33$) and (B) Tree Swallows ($n = 18$). Shaded areas represent 95% confidence intervals.

trial since incubation rates are known to vary with temperature (Conway and Martin 2000), and we wanted to control for different temperatures across the trials. One Tree Swallow data point was excluded from analysis because we determined that the female had likely delayed incubation so the results did not reflect her actual incubation rates; the observation was well outside the range of other observations in the study (45 min of incubation compared to an average of 132 ± 18 min across other trials) and the eggs took ~3 weeks to hatch rather than 2.

Feeding rates. We analyzed feeding rates using Poisson regression for count data with a GLM function (family Poisson log link). Our response variable was the number of feedings per nestling per hour. We included treatment, species, and female age in the model and modeled data for young nestlings (day 4–7) and older nestlings (day 9–11) separately.

RESULTS

Eastern Bluebirds and Tree Swallows built 59 nests in 41 nest boxes throughout the 2017 season with 18 boxes used twice. They nested in 21 control boxes (including the 5 silent controls) and 20 noisy boxes. Eastern Bluebirds had 38 nests including 18 first attempts and 20 second or third attempts. Tree swallows had 21 nests, 20 first attempts, and 1 renest. We banded 34 Eastern Bluebirds (18 females and 16 males) and aged 30 of the adults (15 females, 15 males). We banded 20 Tree Swallows and aged 20 adult females, 13 in the hand and the remainder from video footage.

Settlement

There was no difference in the number of boxes selected by treatment type (control or noisy) by either Eastern Bluebirds or Tree Swallows (Table 1). Settlement patterns did not differ significantly between age classes and treatment for Eastern Bluebird males (Fisher's exact test,

$P = 0.59$), bluebird females (Fisher's exact test, $P = 1.0$), or Tree Swallow females (Fisher's exact test, $P = 0.18$). In addition, date of settlement did not differ significantly by treatment (GLM, $\beta_{Noise} = 0.075$, $P = 0.31$) but did differ by species (GLM, $\beta_{Species\_TRES} = 1.08$, $P < 0.0001$) and age (GLM, $\beta_{Age\_SY} = 0.31$, $P < 0.0001$). Tree Swallows nested later than bluebirds, and second-year birds nested later than older adults.

Clutch Size, Incubation, and Hatching

Clutch size did not differ significantly between noisy and control boxes (GLM, $\beta_{Noise} = 0.025$, $P = 0.86$), between species (GLM, $\beta_{Species\_TRES} = 0.20$, $P = 0.14$), or between age classes (GLM, $\beta_{Age\_SY} = -0.08$, $P = 0.55$). Average clutch size in Eastern Bluebirds was 3.9 ± 1.2 eggs in control boxes and 4.3 ± 0.6 eggs in noisy boxes. Average clutch size in Tree Swallows was 5.1 ± 0.7 in control boxes and 5.2 ± 1.0 eggs in noisy boxes.

Incubation rates differed with treatment (GLM, $\beta_{Noise} = -0.34$, $P < 0.001$), temperature (GLM, $\beta_{Temp} = -0.03$, $P < 0.001$), and species (GLM, $\beta_{Species\_TRES} = 0.36$, $P < 0.001$), but not with age (GLM, $\beta_{Age\_SY} = -0.01$, $P = 0.77$). Incubation rates were lower in noisy boxes for both bluebirds and Tree Swallows across a range of temperatures (Figure 1). In addition, incubation rates were lower for bluebirds than Tree Swallows, and as commonly occurs, rates declined as temperatures increased (Figure 1). At 15°C predicted incubation rates for bluebirds were 0.70 in control boxes and 0.64 in noisy boxes while Tree Swallow incubation rates dropped from 0.77 in control boxes to 0.72 in noisy boxes (Figure 1). When silent controls were included as a separate group, the significance of the results did not change (GLM, $\beta_{Noise} = -1.3$, $P < 0.001$; GLM, $\beta_{Temp} = -0.03$, $P < 0.001$; GLM, $\beta_{Species\_TRES} = 0.33$; $P < 0.001$, GLM, $\beta_{Age\_SY} = -0.03$, $P = 0.56$), and incubation rates were higher in silent controls (GLM, $\beta_{Silent} = 0.383$, $P < 0.001$).

For both species, the noise had a negative effect on hatching success. In nests where at least 1 egg hatched,

TABLE 1. Box settlement by 22 Eastern Bluebird pairs and 20 Tree Swallow pairs at 40 control and 40 noisy (exposed to compressor noise) nest boxes.[a]

| | Box type | | | |
Species	Control[b]	Noisy	χ^2	P
Eastern Bluebird	9 (2)	9	0	1
Tree Swallow	11 (3)	9	0.2	0.65
Combined	20 (5)	18	0.10	0.74

[a] Data are restricted to first nesting attempts.
[b] Silent controls are in parentheses () and included in the total.

hatching success differed significantly between noisy and control boxes (GLM, β_{Noise} = −1.65, P = 0.005) but not between species (GLM, $\beta_{Species\_TRES}$ = 0.59, P = 0.26) or age class (GLM, β_{Age_SY} = −0.36, P = 0.47). The predicted probability of a bluebird egg hatching was 0.95 (0.5 failure) in a control box and 0.80 (0.20 failure) in a noisy box. For Tree Swallows, the probability of an egg in a control box hatching was 0.97 (0.03 failure) and 0.88 (0.12 failure) in a noisy box. The significance of results did not change when silent controls were included as a third treatment group. Hatching success was lower in noisy boxes (GLM, β_{Noise} = −2.11, P = 0.006) but not in silent controls (GLM, β_{Silent} = −1.41, P = 0.18).

Provisioning Rates, Fledging, and Nest Success

There were no significant differences in provisioning rates (food delivered per nestling) between noisy and control boxes in either nests with younger (GLM, β_{Noise} = 0.0002, P = 1.0) or older nestlings (GLM, β_{Noise} = 0.135, P = 0.37). Feeding rates were higher for Tree Swallows than Eastern Bluebirds in nests with young (GLM, $\beta_{Species\_TRES}$ = 0.359, P = 0.04) and older nestlings (GLM, $\beta_{Species\_TRES}$ = 1.05, P < 0.001) but did not differ between adult age classes for either younger (GLM, β_{Age_SY} = 0.156, P = 0.41) or older nestlings (GLM, β_{Age_SY} = 0.075, P = 0.92).

In nesting attempts where at least 1 young fledged, the probability of young that hatched fledging from the nest did not differ significantly between noisy and control boxes (GLM, β_{Noise} = 0.16, P = 0.79) or between species (GLM, $\beta_{Species\_TRES}$ = 0.54, P = 0.40) or age class (GLM, β_{Age_SY} = 0.54 P = 0.86). However, the probability of an egg developing and surviving to fledge differed by treatment (GLM, β_{Noise} = −0.96, P = 0.02) but not by species (GLM, $\beta_{Species\_TRES}$ = 0.61, P = 0.16) or age class (GLM, β_{Age_SY} = 0.05, P = 0.89). The probability of a bluebird egg in a successful nest developing and surviving to fledge was 0.85 in a control box and 0.71 in a noisy box. For Tree Swallows, the probability of an egg developing and surviving to fledge in a control box was 0.92 and 0.83 in a noisy box. This represents a 14% decline in the probability of an egg surviving to fledge for bluebirds and a 9% decline for Tree Swallows in noisy boxes compared to control boxes. When silent

TABLE 2. Daily nest survival models for Eastern Bluebirds and Tree Swallows nesting in control (quiet) and treatment (exposed to shale gas compressor noise) nest boxes. Models were run in program MARK and include species, treatment, and female age. w_i = AIC$_c$ weight.

Model	B	ΔAIC$_c$	w_i	Model likelihood
Intercept	5.1	0	0.42	1.0
Species (TRES)	0.52	1.4	0.21	0.50
Treatment (noisy)	−0.18	1.8	0.17	0.40
Age (SY)	−0.17	1.9	0.16	0.38
Global (species, treatment, age)	0.41	5.0	0.03	0.08
	−0.26			
	−0.52			

controls were included as a separate group, the probability of an egg surviving to fledge was lower in noisy boxes (GLM, β_{Noise} = −1.3, P = 0.009) and was marginally lower in silent controls (GLM, β_{Silent} = −1.35, P = 0.06).

Nest success (the probability of fledging at least 1 young from the nest) did not differ between noisy and control boxes or between species or age classes. The null model (intercept only) had the lowest AIC$_c$ value (Table 2). The daily survival rate estimate for the best model was 0.994 ± 0.002 giving an expected survival rate for the 37-day nesting period of 0.80. The models containing treatment, species, and age in separate models were all within 2 AIC$_c$ values of the best model. The global model, containing all 3 variables in the same model, had an AIC$_c$ = 5.0.

DISCUSSION

Our study included an experimental approach conducted on 2 human-tolerant secondary cavity-nesting species combined with an assessment of behavior. This enabled us to determine when in the nesting cycle noise had its greatest effect and to identify the possible mechanism of action. We found that noise was primarily affecting Eastern Bluebirds and Tree Swallows during incubation. Individuals nesting in boxes exposed to noise from compressor stations had lower incubation rates and lower hatching and fledging success than those nesting in control boxes. Nest success (probability of fledging at least one young) was not affected by noise in either species, suggesting that noise did not increase rates of either depredation or abandonment but instead negatively impacted fitness through reduced hatching and fledging success. These results allow us to link several effects together to understand how shale gas compressor noise affects breeding birds.

In both species, hatching success rates in noisy boxes were reduced by 9–15% compared to quiet boxes. Published hatching failure rates for Eastern Bluebirds range from 6.8% to 8.9% annually (Cooper et al. 2006). In our study, hatching failure rates for Eastern Bluebirds and

Tree Swallows in quiet boxes were below average at 5% and 3%, respectively. However, failure rates were much higher in noisy boxes at 20% in Eastern Bluebirds and 12% in Tree Swallows. These results are in agreement with Kleist et al. (2018) who found lower hatching rates for Western Bluebirds (*Sialia mexicana*) exposed to shale gas compressor noise. The authors linked reduced hatching success to maternal corticosterone levels but also speculated that a change in incubation behavior might have played a role in the reduced hatching success (Kleist et al. 2018).

We do not know why birds in noisy boxes spent less time incubating their eggs. Only female bluebirds incubate, and they leave the nest frequently during the day to forage (Cooper et al. 2006, Gowaty and Plissner 2020). It is possible that females spent more time being vigilant and less time foraging in response to the noise as was shown in a study on bird response to road noise (Ware et al. 2015) and therefore needed to spend more time off the nest in order to obtain the same amount of food. It is also possible that changes in the insect community in response to noise (Bunkley et al. 2017) occurred such that birds needed to travel farther or spend more time searching for prey. We did not see a difference in provisioning rates, but they may have compensated for a change in prey or the need to be more vigilant by spending more time off the nest. It is also possible that the birds were just trying to avoid the noise, and incubation is the time when they are most closely associated with the nest box.

Embryo development is dependent on egg temperature, and birds primarily regulate egg temperature through incubation (Webb 1987). Consequently, if an individual incubates less than is optimal, egg viability may decline due to lethal chilling (Webb 1987). We found lower rates of incubation for both bluebirds and Tree Swallows nesting in noise-exposed boxes and suspect that the significantly lower incubation rates resulted in reduced hatching success. For example, in Wood Ducks (*Aix sponsa*), reduced incubation time was associated with lower nest temperatures and subsequently reduced hatching success (Hepp et al. 2006). Other ways that noise can affect hatching rates is through an increase in stress and stress-related hormones (Saino et al. 2005, Kleist et al. 2018) or the noise could directly lead to embryonic death as observed in zebra finches (Potvin and MacDougall-Shackleton 2015).

Provisioning rates (amount of food delivered per nestling per hour) did not differ between nest box types nor did survival rates of nestlings from hatching to fledging. This suggests that in our study the primary effects of noise on bird behavior and fitness occurred during the egg stage. This could be because females are constrained to the nest box at this time. Our speaker system increased noise levels in the area immediately surrounding the nest box, but the noise did not persist at full power throughout the entire territory. During the incubation stage, the female is directly exposed to noise while the female is incubating the eggs. In American Kestrels (*Falco sparverius*), females in disturbed areas had higher stress hormone levels than those in undisturbed areas during incubation, but this effect was not observed in males, likely because they were spending their time outside the disturbed area (Strasser et al. 2013). Birds exposed to actual shale gas compressor noise would not necessarily be able to escape the "sound bubble," as the sound covers a much larger area. This suggests that effects in areas with active gas extraction could be greater than our experimental system. We observed negative effects of noise primarily during the incubation period, which might suggest that birds habituated to the noise by the time they had nestlings. However, our data do not support this hypothesis, as bluebirds that raised 2 or 3 broods on site showed similar patterns of behavior during the second and third nesting attempts.

Despite the detrimental effects noise had on reproduction, the birds were not more likely to settle in quiet boxes over noisy ones, suggesting they did not consider noise when choosing a nest box. Similar settlement patterns to those in our study were shown in Western Bluebirds breeding near compressor stations, although 2 other species (Ash-throated Flycatcher [*Myiarchus cinerascens*] and the Mountain Bluebird [*Sialia currucoides*]) had reduced occupancy in noisy boxes (Kleist et al. 2017). In addition, we did not find a difference in the timing of box settlement between noisy and control boxes. Our results differ from Injaian et al. (2018) who found Tree Swallows settled in territories with quiet boxes earlier than noisy boxes. Injaian et al. (2018) defined settlement by the presence of male activity near the box (Stuchbury and Robertson 1987), whereas we considered a box settled based on the first egg laid. It is possible that our results differ based on how we defined settlement, and there was a slight difference in the timing of settlement that we missed.

Importantly, we cannot attribute settlement choices to high site fidelity since boxes were erected at locations that did not previously have nest boxes. The lack of preference we found could be due to the fact that for secondary cavity nesters, the nest site is often the limiting factor in territory selection, so they could have simply settled in the first available nest box, but at no point during the season were all box pairs occupied, so individuals of both species always had boxes of each treatment type available to choose from. This suggests that noise can act as an equal-preference ecological trap where birds equally prefer a noisy territory to a quiet one even though their fitness may be lower there (Hale and Swearer 2016, Kleist et al. 2018).

Shale gas compressor noise in the absence of other development-related disturbance affected reproduction in 2 cavity-nesting species and is likely to affect any species nesting near compressor stations. Cavity nesters allow us

to gain a conservative picture of how sound disturbance affects avian reproductive success. Cavities may provide some buffer between the nest and the noise source, unlike an open-cup nesting species that has no barrier, and nest box use indicates that these species are willing to nest near disturbance. Despite these characteristics, both species reduced incubation time in noisy boxes and suffered reduced hatching and fledging success, and neither species avoided noise when choosing a nesting site. The observed responses to compressor noise suggest that shale gas development particularly in undeveloped natural areas that provide important habitat for breeding birds may be affecting a wide range of species. In addition, birds nesting near actual compressor stations are not able to escape the noise, which covers a much larger area than our speakers were able to recreate. It is also worth noting that the effects we observed were not as apparent as site avoidance or nest failure. Instead, the noise had subtle effects that could slowly impact bird populations in affected areas. This is particularly important as we move into an era with greater reliance upon natural gas reserves and increased gas extraction infrastructure.

The growing body of literature on how noise affects birds and other wildlife suggests that noise levels should be regulated in natural areas. This could be accomplished in a variety of ways. First, construction of new compressor stations could be limited in natural areas that currently lack significant noise disturbance. In cases where this is not possible, consideration of topography and distances that mitigate sound propagation should receive attention. Alternately, compressor stations could include noise suppression measures such as sound-dampening barriers (Francis et al. 2011, Northrup and Wittemyer 2013).

In order to understand which measures would be most effective, further research is needed to understand the fine-scale impacts of noise on birds. Importantly, while some species avoid areas with compressor noise (Kleist et al. 2017), others do not as we clearly found in our experimental study. The lack of a consistent response indicates that we need a greater understanding of settlement patterns for more species or guilds. In addition, experiments that determine thresholds for negative impacts will help the industry and biologists mitigate noise effects. In concurrence with others (Bayne 2008, Francis et al. 2009, 2011), we suggest further research on the following fronts: (1) the efficacy of noise-dampening technology in limiting noise propagation in conjunction with bird response to noise, (2) whether birds learn to avoid noisy areas in successive seasons, and (3) a meta-analysis to understand which effects of compressor noise are generalizable across the avian community and whether there are characteristics of the species that can be used to predict how they will respond. Understanding the full scope of how noise affects birds will be important in regulatory decision-making and

the siting of future gas infrastructure. Research in these areas will help limit impacts to birds and other wildlife and increase human well-being by preserving the soundscape of natural areas (Pijanowski et al. 2011).

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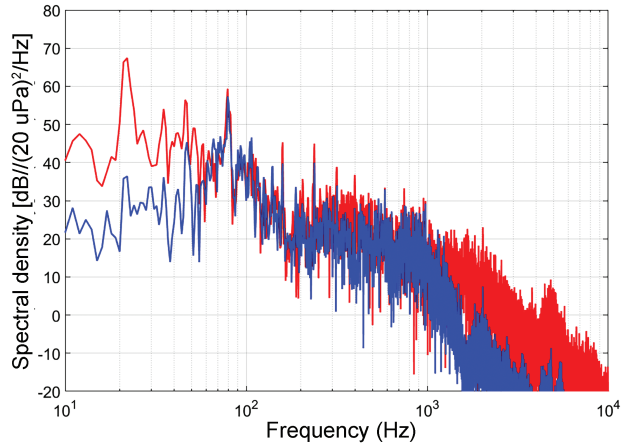
APPENDIX FIGURE 2. Spectral density curves showing a comparison between actual compressor noise in red that was used to develop playback recordings and playback noise in blue. In the playback, power below 60 Hz is under-represented as is power above 1,000 Hz. Playback recordings were used to test the effects of noise on nesting Eastern Bluebirds and Tree Swallows.