




Sieving, K. E., Y. Liu, and O. V. J. Maurelli. 2024. Intermittent and chronic noise impacts on hatching success and incubation behavior of Eastern Bluebirds (*Sialia sialis*). *Avian Conservation and Ecology* 19(1):15. <https://doi.org/10.5751/ACE-02623-190115>  
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Research Paper

## Intermittent and chronic noise impacts on hatching success and incubation behavior of Eastern Bluebirds (*Sialia sialis*)

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**ABSTRACT.** Noise pollution can degrade the behavioral, physiological, and psychological health of humans and other creatures. We used breeding pairs of Eastern Bluebirds (*Sialia sialis*) to assess behavioral and reproductive responses to both chronic roadway noise and experimental intermittent playbacks of construction noise. Active nests in boxes placed near and far from large roads were randomly assigned as treatments or controls for experimental playbacks during incubation. Using temperature signatures from iButtons placed within nest cups we quantified certain female incubation behaviors (# and length of bouts, # of small temperature fluctuations, and total warming minutes per day) and hatching success was recorded for 40 nests in spring of 2019. Nests in quiet areas that received no additional playback treatments of construction noise had markedly higher nest success than any exposed to noise. Nests exposed to chronic traffic noise only, and quiet nests that received 3–4 days of construction noise had the lowest hatching success. Females in traffic-quiet nests increased restlessness (small temperature fluctuations) and experienced decreasing hatching success as the number of days of construction noise playback increased. Thus, birds choosing either quiet or noisy boxes had contrasting responses to bouts of construction noise. Other female incubation behaviors we could detect were unaffected by noise but changed in expected ways with seasonal progression. In sum, both types of noise can decrease hatch rate, but with intermittent noise this is likely due to female restlessness, or too many small drops in temperature to maintain optimal embryo development.

### Effets de bruits intermittent ou chronique sur le succès d'éclosion et le comportement d'incubation de Merlebleus de l'Est (*Sialia sialis*)

**RÉSUMÉ.** La pollution sonore peut avoir un effet négatif sur la santé comportementale, physiologique et psychologique d'humains et d'autres créatures. Nous avons examiné les réactions comportementales et reproductives de couples nicheurs de Merlebleu de l'Est (*Sialia sialis*) face au bruit routier chronique et à la diffusion intermittente expérimentale de bruits de construction. Des nids actifs dans des nichoirs installés près ou loin de grandes routes ont été assignés au hasard comme traitements ou contrôles pour la diffusion d'enregistrements pendant l'incubation. Au moyen de signatures de température d'iButtons placés dans les coupelles de nids, nous avons quantifié certains comportements d'incubation des femelles (# et durée des épisodes, # de petites fluctuations de température et durée totale d'incubation par jour) et noté le succès d'éclosion de 40 nids au printemps 2019. Les nids situés dans les lieux calmes n'ayant reçu aucune diffusion de bruits de construction ont eu un succès de nidification nettement plus élevé que les nids exposés au bruit. Les nids exposés au bruit routier chronique seulement et les nids calmes mais ayant subi 3–4 jours de diffusion de bruits de construction ont eu le succès d'éclosion le plus faible. Les femelles de nids situés en lieux calmes ont augmenté leur agitation (petites fluctuations de température) et ont connu une diminution du succès d'éclosion au fur et à mesure que le nombre de jours avec diffusion de bruits de construction augmentait. Ainsi, les oiseaux choisissant des nids en lieux calmes ou bruyants ont eu des réactions différentes aux bruits de construction. D'autres comportements d'incubation des femelles que nous avons pu détecter n'ont pas été affectés par le bruit mais ont changé de manière attendue avec la progression saisonnière. En résumé, les deux types de bruits peuvent contribuer à diminuer le taux d'éclosion; dans le cas d'un bruit intermittent, l'agitation des femelles est probablement en cause ou le trop grand nombre de petites baisses de température pour permettre de maintenir un développement embryonnaire optimal.

**Key Words:** *construction noise; Eastern Bluebird; hatching success; incubation behavior; intermittent versus chronic urban noise; nest box; traffic noise*

## INTRODUCTION

### Noise pollution effects

Noise pollution is defined as the diffusion of noise in natural or human-made environments occurring in ways detrimental to the physiological or psychological health of humans and other creatures. Anthropogenic noise comes from many sources including power operations, transportation (land, air, and water

vehicles), construction and machinery works, and human activities (Schomer et al. 2001, Haviland-Howell et al. 2007). Like other forms of pollution, noise sources can be point (e.g., airports, power plants, construction sites) or non-point (traffic noises, ground, and air), and noise can be chronic (constant; freeways, power lines) or episodic and acute (fireworks, sonic booms, mechanical tools). Because of human infrastructure expansion, anthropogenic noise is increasingly extensive and its intensity in

urban and even natural/rural lands frequently exceeds government standards limiting noise pollution (Buxton et al. 2017, Yuan et al. 2019, Farooqi et al. 2020). Some effects of noise pollution on people include interference with communication, insomnia followed by decreased work efficiency, and even deafness and mental breakdown can occur (Singh and Davar 2004). Known physiological and mental health declines occur when humans live and work in noisy environments (Cohen and Weinstein 1981, Ahmadi Kanrash et al. 2019). Similarly, detections of negative effects of noise on wildlife activity, community integrity, population viability, individual health, and communication, in both urban and natural areas, are rising fast (McClure et al. 2013, Basner et al. 2015, Halfwerk et al. 2016, Shannon et al. 2016, Buxton et al. 2017, Ciach and Fröhlich 2017, Madadi et al. 2017, Injaian et al. 2018, Aulsebrook 2020). Understanding how animals survive and operate in noise polluted environments is important to continue improving wildlife conservation and education about noise effects (Miller 1974, Fardell et al. 2022).

Consequences of anthropogenic noise on ecosystems can include altered forest soundscape patterns (Munro et al. 2018), changes in the structure and function of wildlife communities (Chen and Koprowski 2015, Brischoux et al. 2017, Blom et al. 2019), interference with animal communication (Rossi-Santos 2015, Grade and Sieving 2016), as well as reductions in reproductive success (Lagardère 1982, Siemers and Schaub 2011, Luo et al. 2015, Senzaki et al. 2016, Ru et al. 2018, Blom et al. 2019, Elmer et al. 2021). Proximate effects of noise pollution include hormonal signatures of stress in adults and juveniles (Kleist et al. 2018), reduced clutch size and juvenile growth rates, and shortened telomeres in offspring (Salmon et al. 2016, Dorado-Correa et al. 2018, Injaian et al. 2018, Zollinger et al. 2019). The latter suggests chronic noise exposure may shorten attainable lifespan (Monaghan and Hausmann 2006). Grade and Sieving (2016) identified that 500 m on either side of interstate highways in natural areas show significant negative effects of noise on communication effectiveness. Along with urbanized areas and additional episodic noise from oil and gas development, military training (aircraft sonic booms, explosions, gunfire: Wakstein 2019, Kuehne and Olden 2020) and recreational activities outside of urban areas (concerts, off-road vehicles, fireworks: Taylor 2006, Bernat-Ponce et al. 2021) North American land areas affected by unhealthful noise levels are extensive (Hammer et al. 2014). Given mounting evidence of noise-caused reproductive declines in wildlife, and failure by some species to avoid these areas (e.g., Plummer et al. 2021), this raises the possibility that large areas exposed to diverse human noise may create population sinks (Schlaepfer et al. 2002, Rodewald et al. 2011, Francis and Barber 2013, Robertson et al. 2013, Swaddle et al. 2015).

Most studies addressing wildlife responses to noise at community, population, and individual levels concern chronic or continuously produced noises (e.g., Bayne et al. 2008, McClure et al. 2017) but increasingly the focus is on episodic and intermittent noises (de Jong et al. 2020, Hahn and Yosef 2021, Rosa and Koper 2022). Presumably, mobile species such as birds can choose to settle on quieter ends of noise gradients and community structure does indeed vary with distance to noise sources (McClure et al. 2017). Whereas some species like bluebirds (*Sialia* spp) appear indiscriminate regarding nest site choice along chronic noise

gradients (Ferraro et al. 2020, Plummer et al. 2021), other species prefer quieter sites (Injaian et al. 2018). In species choosing to nest in chronically noisy areas, different traits (e.g., personality) may be more common in noisy habitats because of assortative habitat selection, adaptation, and/or transgenerational effects (Caizergues et al. 2022, Caspi et al. 2022). Episodic noise impacts on wildlife responses are less well understood than chronic highway noise (Francis and Barber 2013, Kok et al. 2023) but are also abundant in human landscapes, and less predictable in time and space. For humans, intermittent noises are highly disruptive of sleep, concentration, emotional well-being, and physiological stress responses, typically more so than constant noise of similar loudness (Kawada 2011). In general, chronic, and episodic noise disturbances appear to have different effects on animals, including some observable behaviors (Shannon et al. 2016, Berkhout et al. 2023). For example, chronic noise increases vigilance (Meillère et al. 2015) but may be accepted during a nesting cycle, whereas intermittent loud noises may cause serious disruptions to nesting (i.e., nest abandonment: Ortega 2012; reduced incubation time: Williams et al. 2021).

### **Is female incubation behavior linked to nest failure?**

A common mechanism underlying reproductive failure in birds is disruption of incubation behaviors, but this has generally been overlooked when explaining noise-related failures (e.g., Schroeder et al. 2012). In most songbirds, females are the primary incubating parent, alternating between sitting on the eggs all night and most of the day with frequent brief foraging forays during daylight hours (Matysioková and Remeš 2014). Males can significantly reduce the burden of maintaining high incubation temperatures by trading off incubation bouts with females or by feeding the female and reducing the foraging opportunity costs of incubation (Reid et al. 2002). Indeed, females incubating alone can achieve 60–80% constancy (% of time eggs are being warmed) whereas when males of a species also feed the female frequently or solely (e.g., Kemp 1969) or share incubation duties, constancy can be higher (Skutch 1962). Maintaining optimal egg temperatures for sufficient time is key to successful hatching in birds (French 2009). Embryos of most passerine species stop developing at or below physiological zero (approx. = 26 °C: Webb 1987, Haftorn 1988, Cooper et al. 2005) and develop best between 35 °C and 39 °C. Extended time periods at or below physiological zero or outside of the optimal zone can halt or slow development, cause egg mortality, and reduce hatching success (Wang and Beissinger 2009). Even in species where females incubate alone, effective behavioral responses can buffer eggs from moderate and predictable environmental fluctuations, such as nightly cooling and inclement weather, with fine adjustments in time spent sitting quietly on eggs (Williams and DeLeon 2020). However, the physiological limits of females, which must balance food intake with sitting on eggs (Jones 1987) can be exceeded. For example, in the earliest and coldest days of temperate breeding seasons, optimal egg temperatures are regularly unattainable by lone female incubators (Ardia et al. 2009) and unseasonable cold snaps can significantly exceed females' foraging-incubation trade-offs, and mass nest failures ensue (Moreno et al. 2015, Gładalski et al. 2020). Thus, incubation behaviors within the nest are key to hatching and reproductive success. Parents must continually adjust to changing environmental conditions (Conway and

Martin 2000, Coe et al. 2015) to maintain egg development given constraints of the incubator (age, condition, whether mate helps or not; Skutch 1962, Jones 1987). If noise disrupts typical behavioral states of incubators, then additional challenges are likely to arise.

## Research design

Given that noise disrupts the sleep of incubating females in nest boxes (Grunst et al. 2021) and that incubation behavior of females can influence reproductive success (Nilsson and Smith 1988) and other key responses to noise (e.g., telomere length; Stier et al. 2020, Hope et al. 2023), we propose that noise-related hatching failure may be closely related to disruption of female incubation behavior. Indeed, Williams et al. (2021) used experimental addition of noises at quiet nest boxes and found a connection between the addition of noise and reduced incubation time and hatching success. Greater incubation constancy is known to produce higher incubation temperatures and hatching success (Deeming 2002, Bertin et al. 2018, Wada et al. 2018), but constancy has several dimensions that can vary with disturbances at the nest. An incubation bout is the total time it takes a female to first settle on eggs and incubate, then leave to forage, and then return to settle on the eggs again, and includes both the on and off egg periods. Females can alter the length of each on and off period, the entire incubation bout length, and the number of bouts per day (Ward 1990). When females are distracted from incubation when they should be deeply settled on eggs, they may stand up on the nest rim without leaving the nest, stand and look outside (called head-poking in cavity-nesting birds; Hatakeyama 2017), or they may preen excessively or snap at insects (Maurelli 2022). And if they rise up and down frequently, they will also turn eggs more frequently (Coe et al. 2015). More frequent egg-turning enhances embryo development when temperatures are controlled within the optimal zone (as in incubators; Oliveira et al. 2020), but in natural nests with restless females unable to maintain optimal egg temperatures, frequent egg-turning could contribute to faster cooling.

In this study we tested for the effects of chronic and acute noise on both female incubation behavior and reproductive success in Eastern Bluebirds (*Sialia sialis*). We utilized a gradient of chronic traffic noise (from approximately < 60 to > 75 dBA) and experimentally added intermittent noise disturbances to nest boxes where females were incubating completed clutches of eggs in a combined comparative-experimental design. We assessed whether background traffic noise and added, intermittent construction noise affected (a) hatching success and (b) female incubation behaviors (constancy and others, see below). Over one breeding season, we monitored bluebird nest success in an urban population using nest boxes, and quantified incubation behaviors of female bluebirds using temperature signatures obtained from iButton data loggers placed in nests.

## METHODS

### Study system

The Eastern bluebird (EABL) breeds throughout the Eastern U. S. and prefers nesting in open woodland with sparse ground vegetation (Berger et al. 2001). EABL nests in natural cavities and artificial nesting boxes. After nest building in early spring females typically lay one egg per day (clutch size ranges from three to

seven eggs; four or five is most common) and begin incubating the eggs just before or after the final egg is laid (Cooper et al. 2005). Incubation lasts 11–19 days (14 days is typical; Buxton et al. 2017). In north-central Florida, where this study occurred, females are the principal incubators and mean incubation bout lengths (on bouts) are 15.6 min ( $\pm$  8.7 SD) interspersed with mean off bouts lasting 10.1 min ( $\pm$  9.7 SD; Malone et al. 2017).

The University of Florida campus (in Gainesville, Alachua County, Florida USA; 29.6465° N, 82.3533° W) and its surrounding areas are becoming increasingly urbanized. As an agricultural land grant campus (est. 1862; LaCharite 2016), large areas suitable for EABL nesting still occurred in the year of the study and included a wide range of land uses including livestock and crop fields, open greenspace, high-rise buildings, hardscape, heavily trafficked areas (foot and vehicular), and a range of noise levels. Average annual temperatures range from 26.7 °C (high) to 14.4 °C (low) with annual rainfall at 119.4 cm.

### Nest box placement, monitoring, and hatching success

In January and February 2019, we placed 98 Gilbertson style bluebird boxes in selected areas to attract breeding pairs. This nest box is made of a cylindrical PVC chamber with a drain in a wood bottom and covered by a wood roof that is attached to a stainless-steel pipe (1.27 cm diameter, 1.2 m tall) supported by a 1.5 m length of steel rebar driven halfway into the ground. The Gilbertson nest box was previously tested in this area and performs well for EABL (see Perreau and Sieving 2015 for photos of the box type; Malone et al. 2017). We systematically visited every area of campus with suitable space for EABL nesting with at least a 100 m diameter grassy area at or within 100 m of a suitable nest location. Moreover, all nest boxes were placed in the open without overhanging canopy or vegetation touching the nest pole (Kight and Swaddle 2015; see Plummer et al. 2021 for a map of nest boxes and their occupancy). Such sites were available close to and far from the noisiest traffic arteries surrounding campus (Florida State Routes 441 [E], 24 [S], 121 [W] and 26 [N]). Boxes ended up in a variety of sites, near roads, buildings, on a golf course, in pastures, and open manicured lawns. The spacing between any two nests was at least 100 m to minimize inter-pair aggression.

Student volunteers checked and recorded the status of nest boxes at least once a week from February through early July. If volunteers found any trace of nesting material (dried grass or pine needles), they would increase the frequency of monitoring and identify the nest as potentially active. After the first eggs were laid in a box, a nest was monitored daily until the egg number did not change for 2 days, at which point the nest was randomly assigned as a playback treatment or control nest, and the necessary equipment was set up near the box. Nearby each nest (approx. 3–5 m away from the nest) we placed a second metal post with a time lapse camera (Wingscapes Birdcam Pro) aimed at the nest entrance to sample nest visits from dawn to dusk. At playback treatment nests, a speaker (OontZ Angle 3rd generation) plus an mp3 player (RUIZU X02) wrapped in plastic were also mounted on the pole using duct tape. After a female laid her last egg and before we implemented any playbacks, we placed an iButton (temperature logger; DS1921G-F5) in the bottom of each nest cup set to record nest temperature every 10 minutes. Loggers were secured using a piece of fishing line (glued to the logger and threaded outside the box and tied to the pole).

We retrieved mean ambient temperatures for each day of observation (for 10 AM and 6 PM) from the Florida Automated Weather Network (FAWN, <https://fawn.ifas.ufl.edu/>), using data from the closest station to campus (Gainesville Regional Airport). Ambient temperatures are typically strongly correlated with female incubation behaviors and hatching success in birds (Coe et al. 2015). Given that optimal incubation temperatures for avian embryos fall between 35.5 °C and 38.5 °C, females will experience a wide range of ambient temperatures well below this range early in the season and closer to this range later in the breeding season, and ambient temperatures can influence incubation behavior (Webb 1987, Simmonds et al. 2017). Therefore, a range of activity levels in incubating females was expected over the course of the study in response to widely varying ambient temperatures. For all nests that successfully reached hatching stage, we recorded the number of eggs at clutch completion as well as the number of chicks that hatched at the end of the incubation stage.

### Ambient noise and application of noise treatments

To classify nests into noisier and quieter classes, volunteers measured the ambient noise levels at all nest boxes using mobile phone software (the app, Decibel X). Four different ambient noise measurements were taken on different days throughout the season. For each measurement taken, the phone was placed on top of the nest box and the app was opened to record for at least 3 minutes to derive the average ambient noise levels (decibels, A scale) per minute. We summarized the mean dBA per nest box taking the mean of 3 minutes per day averaged over 4 days. The grand mean ambient traffic noise was 70 dBA, and we used this value to identify two classes of nest boxes: quieter (< 70 dBA) versus noisier ( $\geq$  70 dBA). Range of noise overall was 55–88 dBA. We note that smartphone sound apps do not allow precise estimation of sound levels (Cheng 2020). However, they do produce values highly correlated with high quality sound meters (Crossley et al. 2021), typically overestimating true sound pressure levels. Therefore, although we note that the actual sound levels reported here are likely to be overestimated, we simply needed them to identify two classes of nests: noisier and quieter (Table 1).

As active nests were identified, we attempted to assign playback to a comparable number of clutches in each category of background noise (noisy and quiet), but this was not entirely under our control. Different numbers of playback days were dictated by the total days of active incubation we could monitor at each nest. This varied depending on how soon we could begin playbacks after a clutch was complete and on how many days total a nest was incubated. The former was influenced by when volunteers spotted an active nest and when equipment could be freed from another nest to begin the playback period. Actual playback treatments varied from 0 (control) up to 4 (1–4) treatment days of construction noise playback (Table 1). Each clutch receiving playback treatment was exposed to at least one full day of playback (up to four days maximum) during the incubation period. If a nest received more than one day of playback, nests received noise on one day, then the speakers were silenced for two days and then noise was broadcast again for a day (etc.). In this way, background noise (noisy or quiet) was a

categorical variable, but days of playback (0–4) was treated as a quantitative variable because the number of nests receiving 0 or 1 or 2 (etc.) playbacks varied opportunistically.

On playback days, construction noise was broadcast from the speaker and mp3 player mounted on the poles set near the nest boxes. Construction noises included jackhammers, drills, hammering, excavators, and other noises associated with building construction. Recordings were constructed to have noisy and quiet sections to mimic the tempo of a construction site with bursts of noise either every few minutes (5–10) or every 30 minutes. All recordings included a quiet period in the middle of the day (2 hours) to represent a lunch break. Sections with noise included a sequence of all five types of construction noises but on different recording copies the sequence of each type of sound was randomized. We made five different recordings with the same timing (noisy and quiet bouts) but with different sequences of the sound types (sound effects obtained from <https://www.zapsplat.com>). Sound levels of all playbacks were normalized to 90% of the maximum pressure levels, and playback volumes at each nest were standardized to ~60 dBA at the nest hole (using a professional sound meter; Extech 407730), and the total length of each playback file was 10 hours. On treatment days, the recordings were started manually between 8 and 10 AM, and ended between 6 and 8 PM such that each nest received 8 hours of exposure.

### Characterizing female incubation behavior

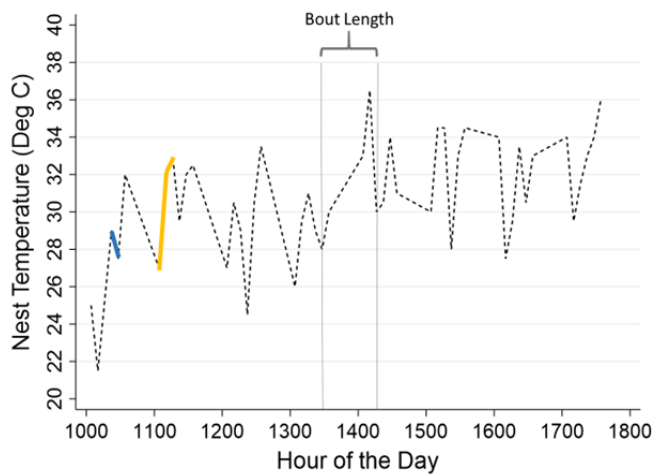
iButtons recorded the temperature inside the nest cup every 10 minutes, and we downloaded all data for each nest recorded during daylight hours, and for each 10-minute period we retrieved the average nest temperature. Using the detailed iButton data, we created nest temperature plots for the hours between 10 AM to 6 PM (all nests shared this time span: Fig. 1). Using the iButton temperature plots created for each active nest for each day of incubation, we counted the number of (1) incubation bouts, the (2) mean bout length over each day, the number of (3) small drops in temperature (< 2 °C; fluctuations), and the (4) total minutes during each day that nests were increasing in temperature (warming minutes) as measures expressing the range of female incubation behaviors. Normal incubation bouts (attentive periods) are characterized by regular cycles of significant box temperature increases and decreases as females first settle on eggs, and then leave the nest to forage. We defined a bout as a warming temperature rise of more than 2 °C, and bout length was equal to the total amount of time between the start of a bout and when the temperature peaked. If a nest temperature rise did not exceed 2 °C before falling again, we identified the pattern as a small fluctuation that we interpreted as restless or agitated incubation behavior (blue line in Fig. 1). Total warming minutes per day was calculated as the total time, summarized over the 8 hours between 10 AM and 6 PM, over which the nest temperature was rising because of female warming efforts during regular bouts. The latter represents incubation constancy (Skutch 1962).

We confirmed that the large and small temperature changes (bouts and fluctuations) recorded by iButtons represented female on- and off-nest behaviors by using the time lapse photographs taken at nest boxes (Audubon BirdCam Pro). We counted the number of observed exits and entrances made by females as well as the number of head-pokes (when a female stands on the nest and

**Table 1.** Metrics used in statistical analysis, their role in analysis, description, and measure type.

Variable	Role	Description	Metric (range)
Hatching success	Response	Total # of chicks hatched / # of eggs laid for each nest, with an arcsin(sqrt) transformation	Continuous (0–1.57)
Fluctuations	Response	Mean daily # < 2 °C temperature drops per day averaged across observation days	Continuous (0.5–10)
Bouts	Response	Mean daily # incubation bouts per day over all observation days	Continuous (0.75–13.5)
Warming minutes	Response	Mean daily # minutes per day eggs were warmed during bouts over all observation days	Continuous (180–390)
Bout length	Response	Mean daily # minutes per incubation bout over all observation days	Continuous (34.8–705)
Traffic noise	Predictor	Mean of dBA measures taken at the nest box, then grouped as high ( $\geq 70$ dBA) or low ( $< 70$ dBA)	Categorical, 2 levels
Playback days	Predictor	Total number of 8 hour days of playback of construction noise	Count (0–4)
Day of year	Predictor	Day of the year (1 = January 1) when an active nest was detected	Count (68–191)
Nest box ID	Random	A number uniquely identifying nest boxes; nest attempts were identified using different numbers	Numbers (1–98)

**Fig. 1.** Diagram of a typical day (10 AM–6 PM) of incubation-driven temperature changes recorded by iButton sensors. Blue line represents a fluctuation (a < 2 degree decrease from 29 to 27.5 °C), yellow line marks a typical warming bout (steady increase in temperature > 2 °C), and bout length (here = 50 minutes) includes the amount of time during which a female steadily raises the nest temperature (here = 40 minutes) while sitting on the eggs plus the time she spends off the nest (here = 10 minutes) prior to initiating a new warming bout.



pushes only her head out of the nest entrance) captured in photos for the hours between 10 AM and 6 PM for a few of the nests with the highest and lowest number of temperature changes (bouts and fluctuations). We confirmed that on days with high numbers of bouts and/or fluctuations, we also observed the highest number of exits, entrances, and head-pokes in the photo data (authors' unpublished data). Time lapse cannot capture every entry, exit, and head-poke by females, but the numbers were highly correlated with the number of daily up and down changes in nest temperatures.

### Data analysis

All analyses (five in total) were run in STATA (version 17, BE) as generalized linear mixed models with four terms, one random effect (Table 1), maximum likelihood estimation, and identity link function. Predictor variables included metrics representing noise

and daily mean temperatures. We used two separate variables to represent the combination of construction noise playback with ambient noise at the nest. Ambient noise was implemented as a categorical variable identifying either quiet or noisy boxes, depending on whether the mean noise measured at the boxes was less or greater than 70 dBA. Additions of construction noise playbacks were coded as a count variable indicating the number of total days that a single nest received construction noise playback (0–4, 8-hr days) during incubation. All ambient temperature measures obtained from FAWN (hourly and daily mean lows, means and maximums) were strongly correlated with day of the year (counting 1 Jan as the first day). Therefore, in analyses, we used the day of the year when each nest was first identified as a treatment or control nest for playback treatment to represent the seasonal progression in temperature (days of the year marking the beginning of nest observations varied from day 68 to 191). In models, all three of these factors were included as main effects along with one 2-way interaction between ambient noise (categorical) and number of days of construction noise playback for a total of four terms. Because some nest boxes were re-used a maximum of two times (probably by the same pairs) we used the box ID number as a random effect. If a model term produced a p-value < 0.10, we also ran marginal contrasts to determine if any were significant over the predicted range of outcomes. We present significant effects contrasts in graphs.

Response variables included hatching success, and four measures representing female incubation behaviors extracted from iButton data: mean number of bouts, mean bout length, number of fluctuations, and mean total number of warming minutes per day (assessed between the hours of 10 AM to 6 PM in all nests). For hatching success, we divided the total number of chicks that hatched and lived for at least a week by the number of eggs laid to get the proportion of eggs that led to viable nestling. Using an arcsin(sqrt(# hatchlings/# eggs laid)) angular transformation to normalize the data, the proportion of eggs hatched was extended from 0–1.0 to 0–1.57 and was normally distributed (Shapiro-Wilk W test for normality was ns). Unlike hatching success, behavioral measures inferred from iButton data were measured multiple times per day and over 1–11 days during incubation periods. To construct a very conservative analysis that is unlikely to produce a false positive (finding an effect of noise when it does not occur) with our relatively small data set we calculated mean values for fluctuations, bouts, warming minutes, and bout lengths across all days of observation at a nest and obtained grand means of these

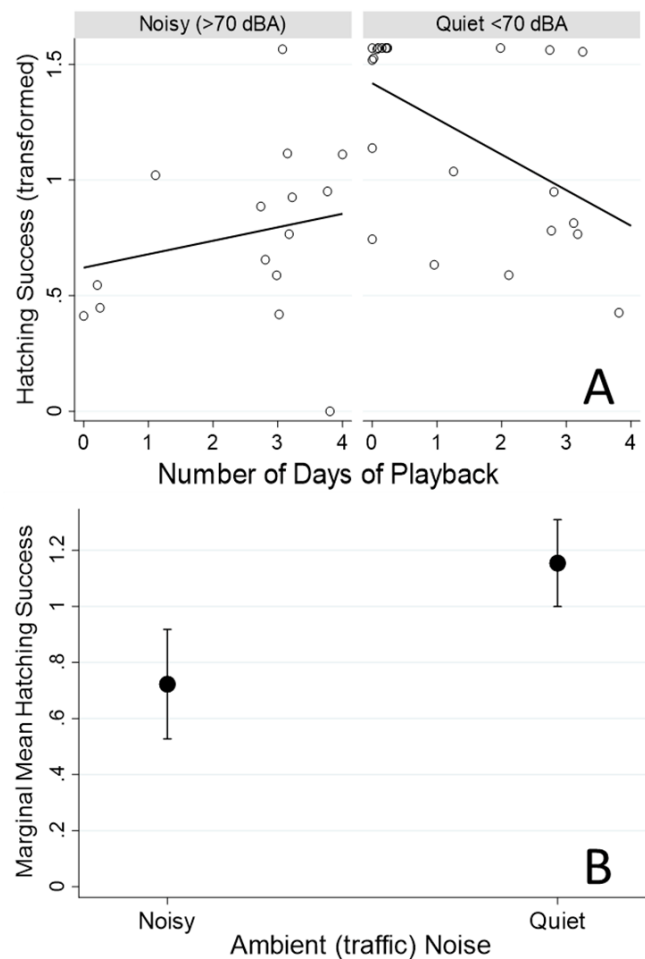
variables (one line of data for each nest). For example, given a nest that received 3 days of construction noise playback, we also had at least 4 days of data when no playback occurred but that came after playback days. If the effects of playback accumulate, we thought it best to average the behaviors on playback and non-playback days to get the most balanced picture of incubation constancy over the course of each female's incubation efforts. Each measure was then tested for normality using the Shapiro-Wilk W test. Mean bout and fluctuation number were both normally distributed according to this test but mean daily warming minutes and bout lengths were skewed in minor ways. To overcome the skew, we applied a Box-Cox transformation, which solved the issues with both. We did not utilize information theoretic approaches and apply model comparisons in analysis because every term included expressed hypothesized causal factors that we designed this study to address. The data set used in these analyses is permanently archived here (<https://original-ufdc.uflib.ufl.edu/IR00012055/00001>). Our research protocol was (1) reviewed and approved by University of Florida's Institutional Animal Care and Use Committee under protocol # 201910544, and (2) further permitted by Bird Banding master permit # 022541 (issued to KES) under USGS Federal Regulation number 16 U.S.C. 703-712 (Migratory Bird Treaty Act).

## RESULTS

Among the 98 nest boxes placed, 37 were occupied by nesting birds and those boxes hosted 66 total nesting attempts, including primarily EABL, but also other species. Considering only Eastern Bluebird nests, the first-egg date was 26 February 2019, and 23 nests were established in a first round of reproduction (all of these fledged by late May). The first re-nest in a box that had already fledged chicks from the first nesting was started 18 April, a date we considered to mark the beginning of the second nesting period more generally. Twenty nests were established in the second round of reproduction, and five nest boxes hosted third clutches initiated in late July. We could not include third clutches in analysis because two failed early and we could not fully apply noise treatments with the remainder. Of the 43 EABL nests in first and second nestings that were completed by June, two were parasitized by a Brown-headed Cowbird (*Molothrus ater*) and another failed for unknown reasons prior to hatching. Figure 2A displays the raw hatching success according to whether the nests were in high or low ambient noise areas and by how many days of construction noise playback they received. N = 40 nests total used in analyses.

Generalized linear models (all results are in Table 2) suggest that hatching success of nests placed in quieter areas (< 70 dBA ambient noise) was significantly greater than for noisy nest boxes (Fig. 2B) and the addition of construction noise playback to quieter nests caused significant reductions in hatching success, but not for already noisy nests (Fig. 3A). Day of the year was not a significant factor in determining hatching success. Regarding the effects of noise on behavioral measures, only fluctuation number appeared to be responsive: mean fluctuation number peaked in nests placed in quiet areas that also received 3 or 4 days of construction noise playback (Fig. 3B). As day of the year increased and temperatures warmed, both fluctuations and mean bout lengths increased significantly and bout number per day decreased significantly (Table 2). Total warming minutes did not vary by sound treatments or by day of the year.

**Fig. 2.** (A) Raw data for hatching success of nests by high and low background noise (clutches combined) and by the # of days of construction noise playback (X axis). Circles with same value are offset for visibility (the cluster of points top, left of right panel = 12 nests). Y axis uses an angular transformation (transformed range = 0–1.57 representing the range of the ratio of eggs hatched per nest [0–1]). (B) Marginal predicted mean hatching success (transformed) by ambient noise category. Marginal contrast result for low versus high ambient noise:  $\chi^2 = 12.10$ ,  $P < 0.001$ . Error bars = 95% CI.



## DISCUSSION

### Both chronic and intermittent noise reduced hatching success

Reduced hatching success was associated with both types of noise, chronic daytime traffic noise from major state roads that mark the perimeter of the University of Florida campus (441, 20, 21, and 26; Plummer et al. 2021) and recorded construction noises broadcast near nests. There was no marked indication that birds preferred quieter nest sites in this study (Plummer et al. 2021), though bluebirds did choose nest sites with more open grass, as

**Table 2.** Summary of generalized linear model results for incubation behaviors. Subscripts used in the model terms column signify reference levels for categorical variables. SE = standard error, Z = Z-score. Statistics for each model summarized in bold. N = 40 nests in all cases.

Response	Term	Coefficient	SE	Z	P value
Hatching	Playback days	0.043	0.071	0.61	0.543
	Traffic noise <sub>low</sub>	0.782	0.207	3.77	< 0.001
	Playback x Traffic noise <sub>low</sub>	-0.199	0.087	-2.30	0.021
	Day of year	-0.001	0.002	-0.45	0.654
<b>Hatching model: Wald chi<sup>2</sup> = 33.46; p &lt; 0.0001</b>					
Fluctuation #	Playback days	-0.137	0.354	-0.39	0.698
	Traffic noise <sub>low</sub>	-0.951	1.036	-0.92	0.359
	Playback x Traffic noise <sub>low</sub>	0.830	0.431	1.93	0.054
	Day of year	0.031	0.009	3.48	<0.001
<b>Fluctuation # model: Wald chi<sup>2</sup> = 24.33; p &lt; 0.001</b>					
Bout #	Playback days	0.034	0.701	0.05	0.961
	Traffic noise <sub>low</sub>	2.200	2.041	1.08	0.281
	Playback x Traffic noise <sub>low</sub>	-0.492	0.851	-0.58	0.563
	Day of year	-0.044	0.018	-2.52	0.012
<b>Bout # model: Wald chi<sup>2</sup> = 2.91; p = 0.573</b>					
Bout length	Playback days	-0.042	0.269	-0.16	0.877
	Traffic noise <sub>low</sub>	-0.805	0.784	-1.03	0.304
	Playback x Traffic noise <sub>low</sub>	0.191	0.327	0.58	0.560
	Day of year	0.016	0.007	2.36	0.018
<b>Bout length model: Wald chi<sup>2</sup> = 2.25; p = 0.690</b>					
Warming minutes	Playback days	-0.013	0.035	-0.38	0.706
	Traffic noise <sub>low</sub>	-0.062	0.102	-0.61	0.545
	Playback x Traffic noise <sub>low</sub>	0.006	0.043	0.14	0.889
	Day of year	-0.001	0.001	-0.19	0.850
<b>Warming minutes model: Wald chi<sup>2</sup> = 6.47; p = 0.167</b>					

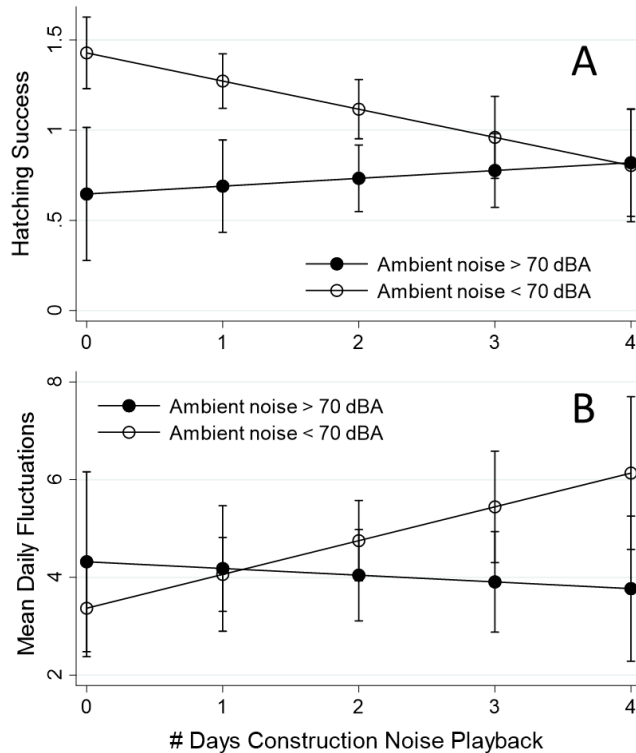
is typical for this species (e.g., Munro and Rounds 1985). More data are needed to see if lack of preference for quiet habitat is a mark of urban adapting species that either already have noise-adapted traits (e.g., parids can adjust social behavior in noisy environs; Owens et al. 2012) or that will eventually develop them (Bowles 1995). Current evidence suggests that negative effects of chronic noise on birds occur beginning around 50 dBA (communication loss; Grade and Sieving 2016) and where reproductive success declines, levels are typically higher (Shannon et al. 2016). Studies that compare incubation versus nestling stage effects of chronic noise find that hatching failure or reduced clutch size drives the reduction in reproductive output, but post-hatching effects on fledgling growth also occur (lab settings: Halfwerk et al. 2011, Potvin and MacDougall-Shackleton 2015; natural settings: Injaian et al. 2018, Kleist et al. 2018).

### Intermittent noise altered female behavior and hatching success

One robust response we detected was that increases in the number of days of construction noise playback significantly reduced hatching success but only in the quietest of nests (Figs. 2A, 3A). We had less data to assess construction noise additions to noisy nests (> 70 dBA), but patterns suggest little or even an opposite effect of playback in this group (Figs. 2A, 3B). In our experience, the best explanation for playback effects is that intermittent noise causes frequent, periodic arousal of females when resting and/or sleeping. Nocturnal video data (Maurelli 2022) suggest that when females are disturbed, they may stand up or shift and turn eggs more frequently than when undisturbed. Others note that awakened incubating adults are more likely to move, engaging in

preening, egg-turning, or standing on the nest cup off the eggs (Eberhardt 1988, Winkler 2016, Grunst et al. 2021). All such activities are natural, but if artificially increased in frequency, then this could cause more numerous small drops in nest cup temperature (e.g., fluctuations; Fig. 3B) and hatching success (Fig. 3A) that we detected with more construction playback days per quiet nest. We note that additions of construction noise here were only during daylight hours, when traffic volume and noise levels are highest. Yet the behavioral effects we detected in daytime were correlated with hatching success suggesting that birds respond to the highest levels of noise stress experienced during 24-hour incubation cycles, and that reactions to daytime noise might carry over into nighttime incubation behaviors, even considering that traffic drops off in the wee morning hours on most roadways. Daytime winter temperatures in central Florida can be quite mild, but night-time temperatures can be within 5–10 degrees of freezing, especially during first nestings; deviations from steady incubation during the night hours likely also occurred in order to depress hatching success. As others have found, adding intermittent to chronic noise did not decrease reproductive success the most (e.g., Blom et al. 2019). Some have detected a down-regulation of corticosteroid secretions in response to chronic high traffic noise (Rich and Romero 2005, Kleist et al. 2018). Therefore, we can speculate that addition of acute noise stressors might not elicit additional behavioral stress responses (e.g., Katz et al. 1981) connected to hatching failure, but we cannot explain this pattern without additional data (e.g., time synched video, temperature, and noise measures taken continuously day and night inside the nest day).

**Fig. 3.** Marginal predicted mean (A) hatching success (angular transformed) and (B) daily fluctuations by ambient noise category and the number of days that nests received playback of construction noises. In (A) significant marginal contrast result for low versus high ambient noise: joint  $\chi^2 = 17.43$ ,  $P < 0.001$ . In (B) significant marginal contrast result for low versus high ambient noise: joint  $\chi^2 = 160$ ,  $P < 0.001$  (and at 0, 3, and 4 days of playback,  $P = 0.03$ , 0.05 and 0.03, respectively). Error bars = 95% CI.



## CONCLUSIONS

Based on our experiences with low-tech nest box monitoring procedures, we suggest more varied and precise measures will be needed to disentangle the links between noise and decreased reproduction. For example, what specific female behaviors caused the small fluctuations? Video recordings time-synched with temperature readings would have helped understand how temperature fluctuations in the daytime inside the nest were related to hatching success. Nest box technologies are rapidly developing, however, and we suggest future studies consider smart nest boxes with remote sensing tech to obtain and analyze multiple data streams (including sensors for audio, video, temperature, heart rate, etc.; e.g., Caorsi et al. 2019, Kubizňák et al. 2019, Grunst et al. 2020, Williams and DeLeon 2020, Grunst et al. 2021). Remote sensing would eliminate disturbance from nest checks that can be a problem during sensitive incubation periods, and cause abandonment. Smart tech can assess individual level response variation within and between nesting families, another critical factor to address in this type of research (yet often ignored; Harding et al. 2019). Individual-specific measures of personality,

condition, age, and stress response would also allow distinctions between direct and indirect effects of noise and other disturbances on both parents and offspring (Heathcote 2019, Injaian et al. 2019).

We found that (a) increasing exposure (days) to intermittent construction noises at the nest boxes caused restlessness in female incubating bluebirds and this, in turn, may have (b) caused reductions in hatching success and that (c) chronic high traffic noise greatly reduced hatching success. Intermittent noise can disrupt rest, concentration, coordination, and task completion and causes increases activity in vertebrates (Brackbill 1970, Szalma and Hancock 2011, Nassiri et al. 2021). We note again that our analysis was conservative, taking the mean number of fluctuations / per day averaged over all days of incubation observed at a nest. For those nests receiving playback, this includes non-playback and playback days, suggesting that behavioral effects of added days of playback are cumulative, and likely to be affecting restlessness during night-time incubation as well as days without playback. Chronic traffic noise was associated with depressed hatching success in our study, possibly due to direct effects on embryos (Potvin and MacDougall-Shackleton 2015) because we did not register any altered female behaviors in chronic noise. Addition of acute noise (playbacks) to chronically noisy nests had little to no detectable effect on either hatching or female incubation behavior; this aligns with other tests for combined effects of chronic and intermittent stressors in vertebrates (Katz et al. 1981, Rich and Romero 2005).

We detected one clear sign that adult incubation behavior can mediate the impacts of noise on hatching success; female restlessness increased, and hatching success declined, with increasing incidence of intermittent sounds broadcast near quiet nests. Females exposed to high levels of chronic noise did not respond to playback in the same way. Implications for conservation are two-fold. (1) Bluebird boxes should be placed as far from busy roads as possible because they do not necessarily choose available quiet nest boxes (Plummer et al. 2021) despite responding poorly to traffic noise. (2) Once placed, nest boxes should be protected from noisy incursions near the nest.

## Author Contributions:

*YL designed the study, conducted the field work and data curation, and wrote and defended a Master's thesis based on the work. KES designed the study, analyzed the data, and drafted the manuscript for publication. OVJM assisted in analysis and interpretation of incubation behaviors.*

## Acknowledgments:

*We acknowledge the study design insights provided by members of the Sieving Lab, nest box monitoring help provided by numerous undergraduates, especially Hannah Cain, and we thank the helpful staff at Mark Bostick Golf Course for facilitating nest checks with access to golf carts. Field work was supported by a small grant to Y. Liu from the Florida Bluebird Society and the Department of Wildlife Ecology and Conservation at University of Florida, Gainesville, provided a vehicle and other logistical support.*



### Data Availability:

The data set used in these analyses is permanently archived here:  
<https://original-ufdc.uflib.ufl.edu/IR00012055/00001>.

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