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Original Article

Anthropogenic noise alters parental behavior and nestling developmental patterns, but not fledging condition

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Anthropogenic noise is a ubiquitous feature of the American landscape, and is a known stressor for many bird species, leading to negative effects in behavior, physiology, reproduction, and ultimately fitness. While a number of studies have examined how anthropogenic noise affects avian fitness, there are few that simultaneously examine how anthropogenic noise impacts the relationship between parental care behavior and nestling fitness. We conducted Brownian noise playbacks for 6 h a day during the nesting cycle on Eastern Bluebird (*Sialia sialis*) nest boxes to investigate if experimentally elevated noise affected parental care behavior, nestling body conditions, and nestling stress indices. We documented nest attendance by adult females using radio frequency identification (RFID), and we assessed nestling stress by measuring baseline corticosterone levels and telomere lengths. Based on the RFID data collected during individual brood cycles, adult bluebirds exposed to noise had significantly higher feeding rates earlier in the brood cycle than adults in the control group, but reduced feeding rates later in the cycle. Nestlings exposed to noise had higher body conditions than the control nestlings at 11 days of age, but conditions equalized between treatments by day 14. We found no differences in nestling baseline corticosterone levels or nestling telomere lengths between the two treatment groups. Our results revealed that noise altered adult behavior, which corresponded with altered nestling body condition. However, the absence of indicators of longer-term effects of noise on offspring suggests adult behavior may have been a short-term response.

Key words: **anthropogenic noise, corticosterone, ecological trap, parental care, radio-frequency identification**

INTRODUCTION

Anthropogenic noise is a common feature of modern landscapes due to increasing human development (Brumm 2014; Mennitt et al. 2014). Under elevated noise levels, birds often face novel selection pressures that can lead to increased stress and reduced reproductive success (Shannon et al. 2016; Yoo and Koper 2017; Kleist et al. 2018). This noise can negatively impact birds at both the community (Slabbekoorn and Halfwerk 2009), population (McClure et al. 2017), and individual level (Kight et al. 2012; Injaian, Taff, and Patricelli 2018). Studies demonstrate that some bird species exposed to high levels of anthropogenic noise decrease in population size and that noise can alter population demographics in others (Reijnen and Foppen 1995; Slabbekoorn and Ripmeester 2008; Benítez-López et al. 2010; Kociolek et al. 2011; Alquezar et al. 2020). At the individual level, anthropogenic noise can negatively

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affect avian acoustic communication (Slabbekoorn and Peet 2003; Kociolek et al. 2011), physiology (Kight and Swaddle 2011; Crino et al. 2013; Injaian, Taff, Pearson, et al. 2018; Kleist et al. 2018; Injaian et al. 2019), telomere length (Meillère et al. 2015; Dorado-Correa et al. 2018), neural development (Potvin et al. 2016), and fitness (Schroeder et al. 2012).

Anthropogenic noise can directly affect adults and nestlings in a variety of ways, which can ultimately impact fitness and population composition (Reijnen and Foppen 2006; Ware et al. 2015; McClure et al. 2017). For example, elevated noise was associated with fewer eggs and a reduced likelihood of fledging in Great Tits (*Parus major*) (Halfwerk et al. 2016). Eastern Bluebird (*Sialia sialis*) brood size and productivity (i.e., number of fledglings produced) was lower near sources of anthropogenic noise, such as roads, compared to bluebird nests in low noise habitats (Kight et al. 2012). However, other studies found that anthropogenic noise did not affect reproductive success (e.g., Great Tits; Halfwerk et al. 2016). Nevertheless, noise impacts on fitness may be present even when the number of young being produced is not altered. Multiple studies have demonstrated that elevated noise levels can lead to increased nestling stress, which likely affects long-term fitness. For example, one study on Tree Swallows (*Tachycineta bicolor*) found that elevated noise playbacks led to higher oxidative stress and lower mass in nestlings compared to control trials, even though fledging success between the treatment groups did not differ (Injaian, Taff, and Patricelli 2018). Noise can lead to food scarcity, due to insects moving away from noisy habitats (Ware et al. 2015), being less detectable by the adults due to the noise (Montgomerie and Weatherhead 1997), or from natural variation in insect abundance in urban environments (Kutschbach-Brohl et al. 2010), which could negatively affect a parent's ability to effectively feed their nestlings. Noise can lead to higher corticosterone levels, which leads to reduced resource allocation for other physiological processes such as reproduction or maintenance (Crino et al. 2013; Mulholland et al. 2018; Ng et al. 2019). Long-term elevated corticosterone levels can also lead to shorter life spans (Kleist et al. 2018). In addition, house sparrows and great tits raised in noisy conditions have shorter telomeres (Meillère et al. 2015; Salmón et al. 2016; Salmón et al. 2017), another indicator of shorter lifespans (Angelier et al. 2013).

One species with a well-documented pattern of parental care behavior (Belser 1981) and a history of being exposed to noise is the Eastern Bluebird. Due to invasive species like the House Sparrow (*Passer domesticus*) and the European Starling (*Sturnus vulgaris*) outcompeting bluebirds for natural cavities in the 1940's, Eastern Bluebirds were listed as endangered, but with the implementation of artificial nest boxes, bluebird populations made a full recovery (Gowaty and Plissner 2020). However, nest boxes are often placed near sources of anthropogenic noise (i.e., roads) which could create an ecological trap for these birds since they are exposed to a stressor known to be detrimental in other species (Barber et al. 2010; Benítez-López et al. 2010; Wong and Candolin 2015). In two previous studies in eastern bluebirds, anthropogenic noise led to both lower brood sizes and productivity as well as higher frequency, louder songs (Kight et al. 2012; Kight and Swaddle 2015), although these studies used ambient noise as their metric of anthropogenic noise. Another study on Western Bluebirds (*Sialia mexicana*) used experimental traffic noise in nest boxes and found no effect on clutch size, brood size, number of fledglings, or nestling success (Mulholland et al. 2018), indicating that noise may not affect overall breeding success.

To quantify both behavioral and fitness effects of anthropogenic noise simultaneously in Eastern Bluebirds, we presented a standardized noise treatment at 9 nest boxes within four spatially distinct study populations, and monitored box visitation, nestling progression, and nestling fitness. The same variables were monitored in 11 control boxes also within our study sites that did not receive elevated noise playbacks. We hypothesized that noise would negatively impact bluebird behavior and fitness, or more specifically that adult bluebirds exposed to elevated noise levels will visit less, and that nestlings will exhibit lower body condition, higher corticosterone levels, and shorter telomere lengths than control birds. Further we predict that control nestlings would be more likely than noise-exposed nestlings to return to breed at their natal sites.

METHODS

Study sites and box setup

Study bluebird boxes were located at the Goodwillie Environmental School (42.998086 N, 85.461985 W, n = 30), Boulder Creek golf course (43.067277 N, 85.567631 W, n = 47), Egypt Valley golf course (43.0108721 N, 85.493340 W, n = 82), and Flat Iron Lake Preserve (43.1235915 N, 85.384015 W, n = 20) in Kent County, Michigan. We banded bluebirds in all locations except the Flat Iron Lake Preserve for three or more years, with 100+ young being banded each year. Box activity was tracked each week by designated volunteer community scientists and the information was relayed to our research team. All sites also included smaller, but active, Tree Swallow and House Wren (*Troglodytes aedon*) populations. All boxes located on golf courses were exposed to regular, brief mowing events, but were otherwise largely nonimpacted by anthropogenic noise. Boxes utilized within the study were >100 m from medium to high use roads. We monitored and conducted noise manipulation on Eastern bluebird broods between 15 May 2018 and 23 July 2018. This level of human activity has not negatively impacted bluebird nest success in previous field seasons (Burtka and Grindstaff 2015).

Adult capture and monitoring box visitation

Once a volunteer community scientist reported that a box had a complete nest, we monitored the nest box every 1–2 days until the eggs hatched to obtain the hatch date. Between 0 and 3 days post-hatch, we caught the adult female of the focal nest box using a Van Ert Universal Sparrow box trap (Van Ert Enterprises). We banded each female bluebird with a USFWS aluminum band and a pink passive integrated transponder (PIT) tag designed to quantify box visitation using a custom-built radio frequency identification (RFID) system (Bridge et al. 2019). We also collected a blood sample (between 50 and 100 µL) within 3 min of capture from the left brachial vein with a 22-gauge needle and heparinized capillary tube for hormone and telomere length assays (Romero and Reed 2005). Blood samples were kept on ice and separated into plasma and red blood cells within 5 h of capture. Adult blood samples were collected before the experiment began and therefore do not reflect baseline corticosterone level changes in response to noise, but we wanted to ensure that adult baseline corticosterone levels did not affect nestling baseline corticosterone levels, as seen in other bird species (Hayward and Wingfield 2004; Saino et al. 2005).

We attached the RFID readers to the nest box 0–3 days post-hatch by placing the reader in a plastic container and attaching it directly to the box with L-brackets and duct tape or underneath the box on a wooden shelf. Antennas were attached to the box entrance with duct tape or with a 3D printed antenna holder, depending on the nest box (e.g., slot or round opening) that was used (Figure 1). To ensure that the antenna did not impede box entrance after RFID installation, we visually confirmed from a distance > 30 m from the nest box that all adults returned to the nest box within 20 min. Nests were assigned to either the control group, which only received the RFID reader setup, or the noise treatment group, which received the RFID reader setup and noise playbacks during the brood cycle.

We measured parental care behavior from hatch through 16 days post-hatch using RFID to determine whether the noise treatments affected visitation rate to the nest box. The RFID system recorded all box visits by a female bluebird banded with a PIT tag (n = 17). Since the reader was positioned at the box entrance, and adults regularly perched on the box entrance, we reduced repeated detections separated by ≤ 1 s into a single detection. We quantified visitation rate as the number of individual visits per hour for the entire monitoring period. Since the RFID reader could not determine directionality, we divided the total number of visits by two to account for the notion that each visit includes a bird entering and exiting the nest box. Due to the high-power consumption (~400 mAh per hour), batteries were drained around every 2 days. Although efforts were made to facilitate continual operation, occasional gaps in RFID reader activity occurred—although there was no significant bias between treatment groups. Nest visitation rates were calculated only for periods when the RFID readers were active (0500–2100) to remove periods when the female bluebird brooded the nestlings.

Figure 1
RFID reader and external speaker setup. The RFID readers were retrofitted onto existing nest boxes by placing the readers in plastic containers and placing the containers on a wooden shelf. RFID antennas were held in place using entrance guards.

Bluebirds typically produce two broods per season (Peakall 1970) and two broods were included from three adult pairs. One female bluebird received the control treatment during the first brood and noise treatment during the second brood, while the other two female bluebirds received the opposite pattern. This reversal of treatment groups was to maximize data from all RFID banded females. Only a single nest was included in the study for the remaining 14 females. Since many of the single brood females were caught later in the breeding season, we were unable to determine if the remaining 14 females were on their first brood or second brood. We balanced the noise treatments across nest box trail sites, with the same number of control and noise treatments within each site.

Noise treatments

We presented Brownian noise at experimental noise boxes to expose adult and nestling bluebirds to elevated noise levels similar in frequency to anthropogenic noise. We chose Brownian noise because the lower frequencies of Brownian noise have higher energy, similar to anthropogenic noise having more energy within the 1–2 kHz frequency range (Patange et al. 2013). We started the noise treatment immediately after capture of the female bluebird, which was within 0–3 days post-hatch. Noise was played continuously for 6 h daily from 0530 to 1130 h because this was the peak parental visitation period within a day (McCarty 2002; personal observation), the time period coincided with high levels of anthropogenic noise due to rush hour traffic (Robbins 1981), and we were limited by our power supply. Daily noise playback continued until the day the nestlings fledged.

We used a 1 min WAV file of synthetically produced (Audacity 2.3.3) Brownian noise played on repeat and broadcasted from a speaker disguised as a rock placed on the ground three meters in front of the box opening (Frequency Response: 28Hz–20 kHz; Acoustic Audio RS6). The speaker was driven by a motorcycle audio amplifier (HS-9004 Cheng Sheng, China) and powered by a lead acid battery (18Ah 12V) connected to a 50 W solar panel (RNG 50-P, Renogy, Ontario, Canada) and an MPPT charge controller (GV-5, Genasun, Cambridge, MA; Schepers and Proppe 2017; Proppe et al. 2020). The speaker, battery, and solar panel had no apparent effect on willingness to enter the box during post-setup observation periods. Playback amplitude was standardized at 65 ± 2 dB at the box entrance. Noise level was assessed for 1 min at the beginning of the noise playback experiment for each nest box (A weighting CEL-633 type 1 sound level meter, Casella CEL, NY).

Nesting physiology and body condition

To assess individual nestling body condition, we marked individual nestlings on day 5 post-hatch by painting the nestling digits with different colored nail polish. Nail polish remains visible on the nestling digits until >11 days post-hatch. At 11 days post-hatch, we banded nestlings with a USFWS aluminum band. On 14 days post-hatch, we banded the nestlings with a green PIT tag to differentiate them from the adult bluebirds with PIT tags, which received pink PIT tags. We measured nestling body conditions during development by obtaining wing length (mm) and body mass (g) on days 5, 11, and 14 post-hatch. We ran a linear regression of wing length against body mass and used the residuals to obtain body condition measurements (Gabriel and Black 2010). To evaluate baseline corticosterone in nestling bluebirds, we collected up to 75 µL of blood at 14 days post-hatch from the brachial vein. Only samples that were acquired under 3 min after being caught were used in the analyses to obtain baseline corticosterone levels before handling-induced corticosterone began circulating in the blood (Owen 2011; Johnstone et al. 2012).

Processing of blood samples

Blood samples were immediately stored on ice in the field and processed within 5 h of collection. In the laboratory, we separated plasma from red blood cells by centrifuging the sample for 7 min at 5000 rpm. We used an enzyme-linked immunosorbent assay (ELISA; Enzo Life Sciences, ADI-900-097) that has been optimized for Eastern Bluebird hormones to determine the baseline corticosterone levels (ng/mL). To determine if noise treatments had any potential long-term effect, we measured telomere lengths on 46 nestlings from 19 different nest boxes. We used a DNeasy Blood and Tissue Kit (Qiagen) to extract DNA from frozen red blood cells and we conducted a quantitative polymerase chain reaction (qPCR) with glyceraldehyde-3-phosphae dehydrogenase (GAPDH) as the single control gene to amplify the number of telomeric (TTAGGG) sequences using specific oligonucleotide primers (5′-3′ forward: TGACCACTGTCCATGCCATCAC, reverse: TCCAGACGGCAGGTCAGGTC) described in previous studies (Criscuolo et al. 2009; Meillère et al. 2015; Quirici et al. 2016; Dorado-Correa et al. 2018; Scholten et al. 2020). We ran the 20 ng DNA samples from each individual in triplicate, and we averaged Ct values and quantified based on a plate-specific standard curve and a pooled sample to serve as a reference sample to account for interplate variability. We used a Southern blot analysis to determine the differences in telomere terminal restriction fragment lengths of individuals among the treatment groups.

Return rate

During the following spring (2019), we identified returning second year (SY) individuals that were exposed to either the control or noise treatment group by visually identifying individuals with green PIT tags with binoculars and recording their visits to nest boxes with the RFID readers. Relocation was done through regular surveys and using band information provided by volunteer community scientists.

Statistical analyses

We used the feedR package in R to calculate the RFID visitation rates as visits/hr; LaZerte et al. 2017). The "feedR" package was originally designed for total visits to a bird feeder; to adapt it to our study, we divided the total number of visits by two to obtain the assumed number of entries and exits to the nest box. We created linear mixed models with the "lme4" package in R version 3.5.2 to determine if treatment group affected 1) adult visitation rates, 2) nestling body conditions, 3) nestling baseline corticosterone levels, and 4) nestling telomere lengths (Kuznetsova et al. 2017). In addition, we used a linear model to examine if there was a difference in adult female bluebird baseline corticosterone levels between the control and noise treatment. We assessed the distribution of residuals for all dependent variables for normality and tested for overdispersion by examining q-q plots. We used the natural log transformation of these values to achieve normality where needed. In addition to treatment, visitation models included nestling age (i.e., days post-hatch), treatment time (our RFID time window divided into the noise broadcast time (0530–1130) and silent time (1130–2100), and brood size as fixed terms. Band number (ID) was also included as a random effect. To account for potential variance due to brood number, and the presence of double broods for the three adult bluebird females, we included the Julian hatch date as a fixed effect. This term (which was quantifiable) accounts for variance across the season, which correlates with brood number (which would have to be assumed in many cases). Julian date and brood size were also included as fixed terms in models for adult and nestling baseline corticosterone level, nestling body condition, and nestling telomere length because these variables can affect each of these parameters (Ilmonen et al. 2003; Bowers et al. 2014; Quirici et al. 2016). Body condition models also included a fixed term for day since hatch (specifically day 5, 11, and 14). Nestling corticosterone models also included sex, since male and female nestlings were included. Band number (ID) and box number (brood) were included as random terms for the nestling body condition model. Since each bird had only one data point in corticosteroid and telomere models, box number was the only random term.

Statement on animal subjects

The University of Oklahoma IACUC (protocol number: R16-0-10B), Calvin University IACUC (protocol number: BR2018-02), the Michigan Department of Fish and Wildlife (permit number: SC 1609), and the Federal Bird Banding Lab (permit number: 23215 and 23918) approved these research protocols.

RESULTS

Parental care behavior and adult physiology

A total of 25 nest boxes were used for this study. Eleven nest boxes were used for the control while nine were used for the noise treatment. For some broods, females could not be captured for RFID purposes, but noise/control playback was initiated anyway to increase nestling condition sample sizes. With RFID readers, we collected nest box visitation data for 17 female bluebirds, 14 females with only one brood and 3 females with two broods. Visitation rate significantly varied for the interaction between treatment groups and nestling age (Table 1). Specifically, when we examined within brood cycle visitation rates, we found that adults in the noise treatment group had higher visitation rates earlier in the brood cycle, but significantly lower visitation rates later in the brood cycle (Figure 2). Visitation rates did not significantly differ between the noise broadcast time and the silent time across treatment groups (Table 1). Finally, adult baseline corticosterone levels at the beginning of each treatment did not differ between the treatment groups (Table 2).

Nestling condition and physiology

The interaction between treatment and log of the measuring day (Table 3) indicates that nestlings in the noise treatment group had higher body conditions at 11 days post-hatch than

Table 1

Linear mixed model with random effects, parameters, Beta estimates, standard errors, degrees of freedom (df), *t*-values, and *P*-values that best predict how noise treatment, nestling age, treatment time, Julian hatch date, and brood size affected the natural log of female visitation rates. Bolded values represent significant *P*-values (α = 0.05)

Response variable	Random effect	Parameter	Beta estimate	Std. Error	df	*t* value	*P* value
Log(Visits/hr)	Band Number	**Intercept**	**−5.766**	**0.676**	**140.700**	**−8.536**	**<0.001**
		Noise	**0.600**	**1.842**	**2166**	**8.140**	**<0.001**
		Nestling Age	**0.071**	**0.003**	**3898**	**21.698**	**<0.001**
		Treatment Time	**0.063**	**0.029**	**3892**	**2.162**	**0.031**
		Julian Hatch Date	**0.018**	**0.002**	**34.150**	**6.783**	**<0.001**
		Brood Size	**1.051**	**0.010**	**19.820**	**10.732**	**<0.001**
		Noise × Nestling Age	**−0.043**	**0.005**	**3914**	**−7.872**	**<0.001**
		Noise × Treatment Time	−0.027	0.047	3895	−0.569	0.570

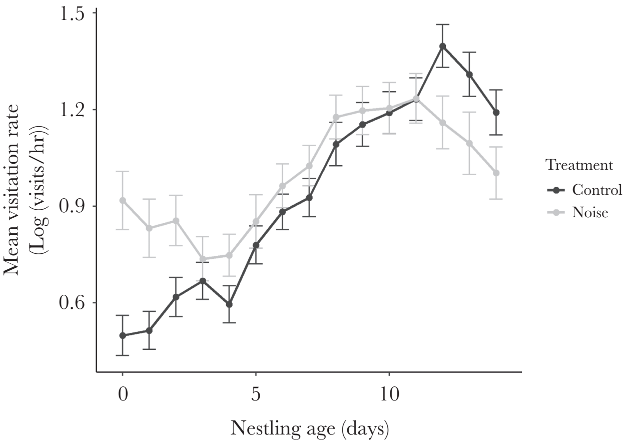

Figure 2

Adult female visitation rates within brood cycles. Adult visitation rates under the noise treatment were initially higher earlier within the brood cycle, but significantly decreased after 11 days post-hatch. Error bars represent standard error.

Table 2

Linear model with parameters, Beta estimates, standard errors, degrees of freedom (df), *t*-values, and *P*-values that demonstrates the effects of the noise treatment and Julian date on adult baseline corticosterone levels (*n* = 12).

Response variable	Parameter	Beta Estimate	Std. Error	df	*t* value	*P* value
Log(Adult Cort)	Intercept	7.958	10.352	1	0.769	0.471
	Treatment	−6.618	15.208	1	−0.435	0.679
	Julian Date	−0.032	0.049	1	−0.662	0.533
	Brood Size	−0.405	0.959	1	−0.423	0.687
	Treatment × Julian Date	0.007	0.072	1	0.092	0.930
	Treatment × Brood Size	1.444	1.453	6	0.994	0.359

nestlings in the control group (Figure 3), but both groups had similar body condition on days 5 and 14 post-hatch. No differences were found between control and noise treatment baseline corticosterone levels nor telomere lengths were observed for nestlings (Table 3). Finally, no nestling died before fledging in either treatment group.

Returning nestlings

Four nestlings from the control group and four nestlings from the noise treatment group returned as SY adults in the 2019 breeding season. Small sample sizes prevented statistical analysis of return rates, but the even distribution between groups suggest that no trend was evident.

DISCUSSION

Our results indicated that elevated noise levels at the nest box altered parental behavior and nestling growth—but at different stages during the nesting cycle. We found adult female bluebirds exposed to noise playback had a higher visitation rate than adults at control boxes earlier in the brood cycle, which was associated with a more rapid increase in nestling mass. However, after 11 days post-hatch, adult visitation rates in the noise treatment decreased more quickly than at control boxes, and nestling mass equalized between groups. Songbird parental visitation rate naturally increases from day 1 to 11 post-hatch and decreases between day 11 and 14 post-hatch (Conrad and Robertson 1993). This pattern was evident in both treatment groups, but more extreme in the noise-exposed group. The distinct change in nest box visitation rate after 11 days post-hatch in the external noise treatment group could be due to the cumulative impacts of elevated noise and the increasing energetic cost of parental care as the nestlings get older (Injaian, Taff, and Patricelli 2018; Williams 2018). Alternatively, early investment might lead to provisioning later in the cycle to achieve optimal nestling fledging mass.

It is notable that RFID tracking detected a noise-associated change in adult behavior over the breeding cycle that corresponded with fledgling body condition, but that nestlings ultimately fledged in similar condition (Breuner et al. 2008; Crossin et al. 2013; Bowers et al. 2016; Guindre-Parker and Rubenstein 2018). When conditions are subpar or variable, adult birds often adjust their parental behavior accordingly (Schroeder et al. 2012; Varpe 2017). If nestling survival is feasible, adult birds may increase parental care to raise the chance of offspring survival (Hall et al. 2020). Songbirds often increase their own mass as insurance when food sources are less dependable (Macleod et al. 2008), and nestlings will also accelerate growth under stressful conditions (Metcalfe and Monaghan 2001; Farrell et al. 2015).

Thus, it is plausible that the initial increase in parental visitation behavior could represent increased investment in offspring under a soundscape the adults interpreted as subpar. This interpretation is not unwarranted since insects often move away from noisy habitats

Table 3

Linear mixed models with random effects, parameters, Beta estimates, standard errors, degrees of freedom (df), *t*-values, and *P*-values that best predict how nestling body conditions (*n* = 282 nestlings, from 19 different nest boxes), nestling baseline corticosterone (*n* = 47 nestlings from 19 different nest boxes), and nestling telomere lengths (*n* = 46 nestlings from 19 different nest boxes). We included both the nestling measure day (i.e., days 5, 11, and 14 post-hatch in which we measured the nestlings) and the log(measurement day) to demonstrate that nestling body conditions under the noise treatment were initially higher than nestling body conditions under the control treatment until ~11 days post-hatch. The noise treatment nestling body conditions decreased and became more similar to the control nestling body conditions after that day. Bolded values represent significant *P*-values (α = 0.05)

Response variable	Random effects	Parameter	Beta estimate	Std. Error	df	*t* value	*P* value
Log(Nestling Body Conditions)	Band Number + Nest Box ID	**Intercept**	**−24.283**	**4.821**	**187.082**	**−5.037**	**<0.001**
		Noise	**−12.331**	**5.705**	**185.865**	**−2.161**	**0.032**
		Measure Day	**−3.001**	**0.462**	**183.999**	**−6.489**	**<0.001**
		Log(Measurement Day)	**58.227**	**9.061**	**183.999**	**6.426**	**<0.001**
		Julian Date	−0.006	0.009	55.025	−0.669	0.506
		Brood Size	−0.237	0.311	23.304	−0.763	0.453
		Noise × Measure Day	**−1.329**	**0.634**	**183.999**	**−2.097**	**0.037**
		Noise × Log(Measure Day)	**27.087**	**12.424**	**183.999**	**2.180**	**0.031**
Log(Nestling Cort)	Nest Box ID	Intercept	2.170	1.800	20.385	1.205	0.242
		Noise	1.610	3.363	28.458	0.479	0.636
		Julian Date	−0.010	0.009	23.528	−1.175	0.252
		Brood Size	0.187	0.212	20.475	0.885	0.386
		Sex (Females)	−0.196	0.771	39.249	−0.255	0.800
		Sex (Males)	−0.397	0.235	46.949	−1.685	0.099
		Noise × Julian Date	−0.006	0.015	27.776	−0.390	0.700
		Noise × Brood Size	0.020	0.332	26.041	0.060	0.952
Log(Nestling Telomere Lengths)	Nest Box ID	Intercept	0.203	0.333	46	0.609	0.545
		Noise	−0.292	0.412	46	−0.709	0.482
		Julian Date	−0.001	0.002	46	−0.495	0.623
		Brood Size	0.015	0.020	46	0.751	0.457
		Noise × Julian Date	0.002	0.002	46	0.714	0.479

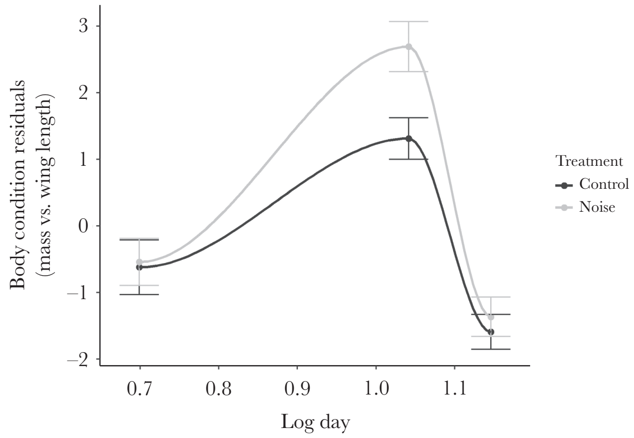

Figure 3

Nestling body conditions across the natural log of the day of the brood cycle. Nestling body morphometric measurements were taken on 5, 11, and 14 days post-hatch. Nestlings in the noise treatment group initially had higher body conditions but this difference was no longer seen at the end of the brood cycle. Error bars represent standard error.

(Ware et al. 2015) and become more difficult to locate (Calhim and Montgomerie 2015). Early investment might drop off later in the breeding cycle to achieve ideal fledgling weight. Alternatively, bluebirds in our study may have recognized the small radius of our noise exposure and responded with more "normal" visitation levels. Testing this alternative hypothesis would require experimentation in areas with noise exposure on a larger spatial scale. A third scenario is that adult bluebirds are simply not able to sustain the higher rates of provisioning for the duration of the breeding cycle. While we cannot conclusively explain the observed behavioral patterns, the equal condition of fledglings in noise and control conditions suggest that parental behavior was altered to counter the potential negative effects of noise on their offspring.

Adult female bluebirds in our study have similar baseline corticosteroid levels prior to study initiation. Knowing this is necessary since adults with higher baseline corticosterone levels will invest more in parental care and offspring development (Bowers et al. 2016; Guindre-Parker and Rubenstein 2018). However, baseline corticosterone levels also increase with parental care investment and can negatively affect individual state (Breuner et al. 2008; Crossin et al. 2013). Since we did not collect post exposure data in adults, we cannot determine whether noise impacted adult stress level directly. But we can state that the differences in parental visitation behavior between treatments, and any differences in nestling corticosterone levels, were unlikely to be due to adult condition.

Nestlings in the noise treatment did not have significantly higher baseline corticosterone levels when we controlled for brood size or Julian date (Table 3). While previous studies demonstrate that noise can negatively affect nestling physiology (Crino et al. 2013; Kleist et al. 2018; Injaian et al. 2019; Zollinger et al. 2019), the increased provisioning by the noise-exposed adult bluebirds could offset any negative effect from the noise. While noise masking can reduce parental perception and response to begging calls (Lucass et al. 2016), noise can also mask nestling vocalizations that are used as cues by predators. This can reduce the need for nest box guarding by parental birds and leave more time and energy for provisioning nestlings, leading to increases in nestling mass (Crino et al. 2011).

Results from the literature documenting the impacts of external stressors on corticosteroids are somewhat diffuse. One previous study found that zebra finch (*Taeniopygia guttata*) nestlings administered exogenous corticosterone had altered begging acoustic spectra, leading to increased parental provisioning (Perez et al. 2016). However, another study on the same species demonstrated that experimentally elevated levels of baseline corticosterone increased begging rates in nestlings, decreased nestling mass, caused weaker nestling immune responses, and led to less parental provisioning than nestlings that did not receive the experimental corticosterone (Loiseau et al. 2008; Perez et al. 2016). There is evidence that noise altered nestling mass and stress measurements (i.e., baseline corticosterone, heterophil/lymphocyte [H/L] ratios) are altered simultaneously in some species (Injaian, Taff, and Patricelli 2018; Zollinger et al. 2019; Walthers and Barber 2020). Clearly, additional work is needed to understand the mechanisms underlying observed noise-induced changes to parental behavior and nestling condition.

In other bird species, the immediate impacts of noise are also associated with longer term physiological changes. House Sparrow nestlings raised under high levels of anthropogenic noise often have shorter telomeres, potentially indicating a shorter expected lifespan (Meillère et al. 2015; Chatelain et al. 2020). In our study, however, nestling telomere lengths did not differ between control and noise-exposed groups. Again, altered adult behavior and nestling response may have mitigated the longer-term effects of noise. While the data is sparse, the equal return rate of control and noise-exposed nestlings to our field sites the following year suggests support for this hypothesis.

While our observed impacts of noise on bluebird nestlings were short-term, increased noise levels could eventually lead to decreased overall fitness in birds. Bluebirds are conspicuous species that regularly occur alongside human habitation. They may be prone to continue using noisy environments due to the presence of vital resources (i.e., nesting cavities). But higher noise levels are likely to impact prey insect populations since many species communicate through acoustic signals (Morley et al. 2014). Nonetheless, Eastern bluebirds may truly mitigate the negative effects of noise on offspring by altering their parental care behavior. If this is the case, then this species may be an excellent example of a successful noise adapter, and greater examination of its behavioral modifications may be warranted. However, given the negative impacts of productivity shown previously by (Kight et al. 2012), future studies should also focus on whether noise affects long-term survival, fitness, and population recruitment.

In summary, we report that Eastern Bluebird adults increase their nest box visitation rates early during the nestling stage under exposure to anthropogenic noise but reduce visitation rates in comparison to control birds later in the nestling stage. Although we identified corresponding differences in nestling mass, neither corticosteroid levels nor telomere lengths, a longer-term physiological response to stress, differed between control and noise-exposed nestlings. Alterations to the bluebird breeding cycle could still confer long-term challenges for populations breeding in noisy areas, but it is also plausible that plastic adult behavior is able to mitigate the impacts of noise on the next generation. More work is needed to understand the mechanisms underlying altered box visitation rates under noise exposure, but it is clear that even species regularly found alongside noise and human habitation are unable to completely escape the impacts of anthropogenic noise.

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