



Poke, gape, or escape? Diurnal anthropogenic noise disrupts Eastern Bluebird (*Sialia sialis*) incubation and nest attendance behavior

¿Picar, asomarse o escapar? El ruido antropogénico diurno perturba la incubación y el comportamiento de atención al nido de *Sialia sialis*

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ABSTRACT. Anthropogenic noise pollution disrupts wildlife behavior, physiology, and demography yet species characterized as urban adapters, such as the Eastern Bluebird (*Sialia sialis*), willingly breed in urban areas. Hypothesizing that noise levels could disrupt incubation behavior, we examined the effect of (a) chronic traffic and (b) episodic construction noises on nest attendance (males, females) and in-nest incubation behaviors (females) in Eastern Bluebird pairs. We used photos taken at nest boxes placed along an anthropogenic noise gradient on the University of Florida campus to identify key behaviors. Nest boxes were in quiet (< 70dB) or traffic noise-exposed areas (> 70dB) and some boxes in each category received additional intermittent playback of construction noises. We used Chi² tests, Mahalanobis distances, and confusion matrices to ascertain whether treatments distinctly altered a suite of nest attendance behaviors exhibited by pairs. Playback significantly increased the frequency of peeking and poking from the nest hole by females; males spent more time atop nest boxes in traffic noise-exposed sites; and males spent almost no time on quiet boxes exposed to playback. Findings are consistent with current understanding that anthropogenic noise, especially intermittent loud bursts, disrupts incubation stage behaviors in birds, reducing incubation constancy and, in turn, hatching success.

RESUMEN. La contaminación acústica antropogénica altera el comportamiento, la fisiología y la demografía de la fauna silvestre, pero las especies caracterizadas por su adaptación urbana, como *Sialia sialis*, se reproducen voluntariamente en zonas urbanas. Hipotetizando que los niveles de ruido podrían alterar el comportamiento de incubación, examinamos el efecto del (a) tráfico crónico y (b) los ruidos episódicos de la construcción sobre la atención al nido (machos, hembras) y los comportamientos de incubación en el nido (hembras) en parejas de *Sialia sialis*. Utilizamos fotos tomadas en cajas nido colocadas a lo largo de un gradiente de ruido antropogénico en el campus de la Universidad de Florida para identificar los comportamientos clave. Las cajas nido se encontraban en zonas tranquilas (< 70 dB) o expuestas al ruido del tráfico (> 70 dB) y algunas cajas de cada categoría recibieron una reproducción intermitente adicional de ruidos de construcción. Utilizamos pruebas Chi², distancias de Mahalanobis y matrices de confusión para determinar si los tratamientos alteraban de forma clara un conjunto de comportamientos de asistencia al nido exhibidos por las parejas. El playback aumentó significativamente la frecuencia con la que las hembras se asomaban y hurgaban en el agujero del nido; los machos pasaban más tiempo en lo alto de las cajas nido en los sitios expuestos al ruido del tráfico; y los machos casi no pasaban tiempo en las cajas tranquilas expuestas al playback. Los resultados concuerdan con la comprensión actual de que el ruido antropogénico, especialmente los estallidos intermitentes y fuertes, perturba los comportamientos de las aves en la etapa de incubación, lo que reduce la constancia de la incubación y, a su vez, el éxito de la eclosión.

Key Words: *anthropogenic noise; Eastern Bluebird (Sialia sialis); incubation behavior; nest attendance; playback experiments*

INTRODUCTION

Noise pollution is a growing issue for urban-dwelling humans and wildlife; as human infrastructure continues to expand, anthropogenic noise increases in intensity (Buxton et al. 2017). Impacts of anthropogenic noise on humans and animals are increasingly well understood and can have severe impacts on well-being, health, and population viability (Kunc and Schmidt 2019, Kryter 2023). Sources of anthropogenic noise include traffic, machinery, construction, and other forms of human activity, and noise pollution can have negative impacts on the function, demography, and physiology of many different wildlife species (Jerem and Mathews 2021). For example, increased noise can reduce an individual's ability to reproduce, detect predators, locate food, and communicate (Engel et al. 2024).

Behavioral phenotypes are highly flexible in animals and changes in behavior are often the first sign of negative systemic (e.g., demographic and physiological) change in populations affected

by environmental shifts (Gruber et al. 2019). Thus, investigations of anthropogenic noise impacts should include behavior analysis as a cue to selection pressures on urban wildlife populations (Jokimäki et al. 2011), aiding in designing effective conservation interventions (Fardell et al. 2022). This is particularly true for species that are urban adapters. Such species are increasing in urbanized areas and thus may be putting themselves at risk for negative impacts of anthropogenic noise and other urban factors. Urban adapters may be falling into behavioral traps where typical habitat selection cues attract species into areas that have novel, and unrecognized, threats to well-being (Zuñiga-Palacios 2021). One such species may be the Eastern Bluebird (*Sialia sialis*; Cornell et al. 2011, Plummer et al. 2021).

Noise reduces bluebird nesting success, but how?

Eastern Bluebirds are secondary cavity nesters; they do not create their own nests but rely on readily available cavities previously excavated by other birds or mammals (Gowaty and Plissner 1998).

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This behavior makes Eastern Bluebirds willing inhabitants of artificial nest boxes in rural and urban areas. Yet, in north central Florida and Virginia, where bluebirds readily inhabit nest boxes, nests in areas near urban noises exhibit significantly decreased hatching success and smaller brood sizes (Kight et al. 2012, Sieving et al. 2024). This suggests that habitat selection behaviors should be under some selection pressure for noise avoidance, but currently there is little evidence indicating bluebirds avoid noise in nest site selection (Plummer et al. 2021).

Although a variety of intrinsic (e.g., age, experience) and extrinsic (weather, food) factors are known causes of nest failure that should be accounted for, noise pollution is increasingly linked to hatching failure (Schroeder et al. 2012, Pandit et al. 2021, Sieving et al. 2024). Noise at extreme levels (110 dB) can be detrimental to avian embryonic development (Kesar 2014), though little evidence indicates that typical urban noise interferes directly with wild bird embryos. Female birds are the principal incubators from laying to hatching (Cockburn 2006) and current focus on the issue is revealing that altered female behavior is typically associated with reduced hatching in response to noise (Williams et al. 2021). Less attention is given to the role of male birds who do not incubate, but are often active around the nest during incubation, feeding females and protecting the nest through vigilance and warning calls (Pinkowski 1976). Such close nest attendance by male birds in monogamous species can positively affect nesting success (Schmidt and Whelan 2005). Male Eastern Bluebirds are vigorous nest attendants, and they do feed incubating females (Wells and Robinette 2020). Given the need to coordinate parental activities (incubation, feeding, nest guarding), male attendance behavior is likely to affect female behaviors and, in turn, indirectly affect reproductive success (Amininasab et al. 2017) via female behavior. If anthropogenic noise alters both female and male incubation stage behaviors, then loss of incubation constancy by females may be, both, directly and indirectly related to noise pollution.

The objective of this study is to examine the effect of anthropogenic noise on both male and female Eastern Bluebird nest attendance and incubation behavior as observed via cameras placed outside nest. A previous analysis reported in Sieving et al. (2024) documented that noise, especially intermittent playbacks of construction noise, caused females to be more agitated during incubation bouts, as evidenced by an increased frequency of short drops in nest cup temperature in noise-exposed nests measured via temperature loggers. We hypothesize that in nest boxes exposed to noise, particularly during playback treatments, camera images will confirm the assumption that these drops in temperature were due to female agitation. We expected that under noise exposure (high traffic noise, and added playback of construction noise), incubating females would be less settled on their eggs and therefore more frequently visible through the nest hole (Martin and Guepel 1993). Because males were also observable near or on the nest boxes in photo data and given that male passerines will perch close to nests during times of perceived threat (Schmidt and Whelan 2005), we predicted that males perching on the box would be more frequent in noise treatments.

METHODS

Data collection

We used previously unanalyzed photographic data collected by Liu (2020; MS thesis) on a population of bluebirds in north-central Florida. Bluebirds' selection of nest sites for this study was reported in Plummer et al. (2021) and nest temperature and hatching success data associated with noise-exposure were reported in Sieving et al. (2024). One hundred Gilbertson-style nest boxes mounted on metal poles were placed at the recommended 100 m apart across an anthropogenic noise gradient on the University of Florida campus (29.6503° N, 82.3414° W). We set a metal pole holding a time-lapse camera (Wingscapes Birdcam Pro) in front of each nest box (within 3 m) set to take one photo every 10 seconds, and a Wildlife Acoustics SM3 recording unit was mounted below the camera to record audio. Nest box poles were smeared with heavy axle grease as pairs began nest building to prevent climbing predators. Of the 100 boxes placed, 37 were occupied by nesting birds, with a total of 66 nesting attempts. Fifty-seven of these attempts were made by Eastern Bluebirds. Ambient noise levels (mainly traffic) at each nest box were estimated using the mobile phone software Decibel X, to make four three-minute recordings taken on different days and times to obtain a robust average ambient noise level. Because half the boxes were chronically exposed to either more or less than 70 dBA, we grouped nests into quiet or high noise categories around this threshold; > 65 dB was considered very loud and 50 dB was very quiet (reviewed in Grade and Sieving 2016). Playback treatments were randomly assigned to half of the occupied boxes in each noise category to minimize impacts of individual-specific factors (age, clutch size, experience). Individual differences may have driven birds' selection of high and low traffic noise nests, but we could not address this in our analysis. In playback treatments, construction noise playback was broadcast from a speaker (OontZ Angle3, 3rd gen) connected to an mp3 player (RUIZU X02) mounted to the metal pole in front of the box. Playback was activated for one day, then inactivated for two days; this cycle of playback on and off was repeated at an incubating nest until hatching. On active days, playback began between 8 AM and 10 AM and ended between 6 PM and 8 PM. The recording contained bursts of noise (jackhammers, engine noise, etc.) lasting 5–15 minutes every 30 minutes and included a two-hour quiet period in the middle of the day to mimic lunch breaks at construction sites (see Liu 2020, Sieving et al. 2024).

Sixteen pairs of Eastern Bluebirds (32 individuals) had sufficient high quality photo data to identify parent behavior around the nest using manual review of photos in Microsoft Photo. Each pair's data came from a single nest attempt. Nine behaviors were initially summarized. Behaviors included PEEK, POKE, GAPE, ONBOX, ATHOLE, PCH_NEAR, IN, OUT, and FLIGHT (Table 1, Fig. 1). Each line of data summarized an hour of photographs (60 min x 6 photos per minute) taken at a nest box for either the male or the female of each pair. Pairs varied in the number of hours of useable data from 1 (2 nests) to 16 (1 nest), and the mean was 8.3 hours per pair. The data set was limited by availability of cameras to cover all nests during incubation, and some hours of data were lost owing to sun glare and physical displacement of cameras, etc. Photos from a total of 125 hours

Table 1. Ethogram of bluebird incubation stage behaviors we observed with codes and their descriptions. The first three were only observed in females.

Behavior code	Description
PEEK	Female face visible through nest hole
POKE	Female head pushed out of the nest through nest hole
GAPE	Female holding bill open in PEEK or POKE position
ONBOX	Bird perched on top of nest box
ATHOLE	Bird hanging on side of nest box with head by nest hole
PCH_NEAR	Bird perched within view of the camera but not on the nest box
IN	Bird entering box (body half in) through nest hole
OUT	Bird exiting box (body half out) through nest hole
FLIGHT	Bird in flight near nest box

of photo data were summarized and because males and females were active simultaneously, a total of 250 lines of data were created. All data were extracted from images taken between 9 AM and noon between 20 March and 9 July 2019. Samples occurred at nests beginning at least 3 days after clutch completion until 3 days before hatching, but we could not control more than that. Male and female data were analyzed separately owing to the difference in applicable behavioral categories.

Data reduction

Observed behaviors were classified into sex-specific ethograms (Table 1) and data-deficient behavior categories were dropped or combined. We dropped PCH_NEAR and FLIGHT for both sexes because they were not reliably detectable given unstandardized perch availability near to nest boxes. PEEK, POKE, and GAPE were incubation behaviors unique to females, as sole incubators. ATHOLE, IN, and OUT behaviors were nearly all observed for males, and were dropped from female analysis. Final behaviors analyzed for each sex are pictured in Figure 1. To establish noise categories for analysis, we examined the samples we could use to see what noise treatments would work. Following the flow chart in Figure 2, noise categories N and NP were lumped together for analysis in both sexes because of low sample size for NP (nests exposed to > 70 dBA traffic noise that also received playback; only 6 hours of data). Unlike the assessment of nest success at the end of incubation, our response measures were labile behaviors that change with immediate exposure to stimuli. Therefore, given the 3-day cycle of playback (in)activation we split the playback treatment (QP) into two categories to indicate if birds were receiving playback in the hour that photos were taken (QPA) or not (QPI). Finally, an initial discriminant function analysis run for the males revealed that their behaviors were indistinguishable between QPI and QPA noise categories, so we opted to combine QPI and QPA into one category (QP - quiet nests with playback assigned) for the final male analysis, but not females. Ultimately, we were left with four female behaviors (PEEK, POKE, GAPE, ONBOX) under four noise categories (N, Q, QPI, QPA) and four male behaviors (ATHOLE, IN, OUT, ONBOX) under three noise categories (N, Q, QP; Fig. 1, Fig. 2).

Data analysis

To examine how individual behaviors of each sex varied by each noise category in univariate tests, we conducted non-parametric Kruskal-Wallis equality-of-populations tests followed by Dunn's

pairwise comparisons because parametric generalized linear models would not converge properly with this data set. The Kruskal-Wallis test ranks all observations (here, counts per hour), sums the ranks within each treatment group, and computes an H statistic (assuming a χ^2 distribution) to compare the average rank in each group against the expected mean if all samples were from the same population. Technically, our data included pseudo replication in that individuals were sampled more than once but, given the nature of our data set, these repeated measures could not be accounted for. To correct this issue in the Kruskal-Wallis test, the recommended approach is to take each bird's median count per behavior for each treatment, then run significance tests on the reduced data set. In this case that would be 16 lines of data (each for males and females; 32 total). However, in the playback treatments for females, some individuals experienced both QPI and QPA treatments in different hours of sampled data, whereas birds in N and Q treatments experienced no others. Therefore, individual behavior medians for each treatment group cannot be summarized in a straightforward manner for each bird. Therefore, to satisfy model assumptions as best we could, we dropped the two birds from each data set that had only a single hour of data, leaving the remaining 14 birds of each sex with at least 4 hours of sampled data (except 1 with 2 hours), thereby better balancing the influence of all the birds in the data set. Final sample sizes included 14 birds and 246 total hours of data (8 pairs in Q boxes, 75 hours of photo data summarized for each sex; 3 pairs in QP, 29 hours for each sex; 3 pairs occupied N nests, 19 hours for each sex). All three females in QP treatments experienced both QPI (19 hours) and QPA days (10 hours total).

We also performed canonical discriminant function analysis for males and females separately across noise treatment categories. This analysis creates linear combinations of the counts (per hour) of the different behaviors, called discriminant functions, that maximize the separation between groups at the group means. This allowed us to test whether the combined behavior patterns for each sex varied distinctively by noise treatment using squared Mahalanobis distances between group means (e.g., McCleery 2009). Pairwise contrasts of distances used the first discriminant function and Wilks' lambda test; a multivariate generalization of the t-test for testing differences between two means (Kramer et al. 2009). We present other results of the canonical discriminant analysis in scatterplots of individual birds' canonical scores, and for easier interpretation of the latter, we provide loading plots showing each behavior's contribution to the canonical functions. The analysis also generates confusion matrices that indicate how accurately birds in each treatment can be identified correctly based on the combination of behaviors displayed. All data analysis was completed using Stata 19.0 (StataCorp 2025).

RESULTS

Univariate tests for each behavior by noise category

Two of four individual female behaviors (PEEK, $\chi^2(3) = 32.88$, $P = 0.0001$ and POKE, $\chi^2(3) = 15.08$, $P = 0.0017$) and two of four male behaviors (IN, $\chi^2(3) = 6.44$, $P = 0.04$ and ONBOX, $\chi^2(3) = 14.62$, $P = 0.0007$) varied significantly in K-W tests. Other tests of (female GAPE, ONBOX and male OUT) were ns but P-values were all less the 0.2 therefore we proceeded to pairwise comparisons for all but male ATHOLE behavior (p value was 0.5). In results of the Dunn's pairwise comparisons, note that ">"

Fig. 1. Nest attendance and incubation behaviors of Eastern Bluebirds (*Sialia sialis*) that are visible in photos taken during the study. The top row shows the definitive male nest attendance behaviors, and the female incubation and nest attendance behaviors are shown across the bottom. Refer to Table 1 for the ethogram of these behaviors.

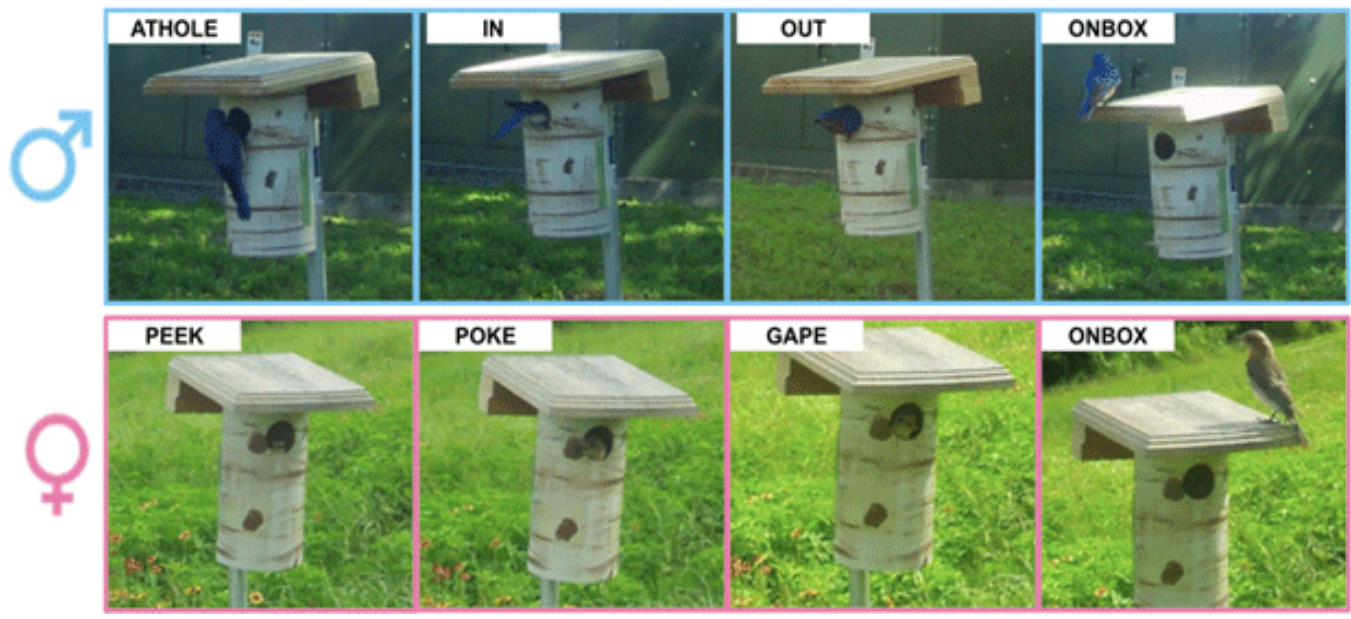
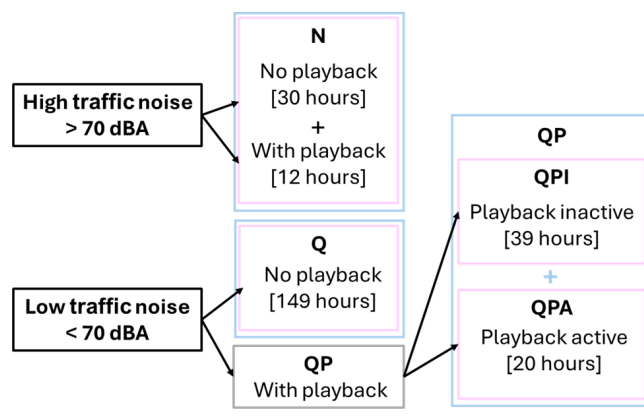


Fig. 2. Overview of the noise categories and their descriptions broken down by sex and in brackets is [the # of hours of data analyzed]. Bolded capital letters indicate the final 5 categories of noise used in analysis. N and Q categories were the same for male and female analyses (indicated by the parallel pink and blue boxes). QPI and QPA were lumped together into QP for male analysis (e.g., both inside a surrounding blue box). For females, QP was split into QPI and QPA, indicated by the two pink boxes within QP. The noise categories are defined as the following: N = high levels of traffic noise + playback, Q = low levels of traffic noise, QPI = low levels of traffic noise + inactive playback, QPA = low levels of traffic noise + active playback, QP = QPI + QPA.



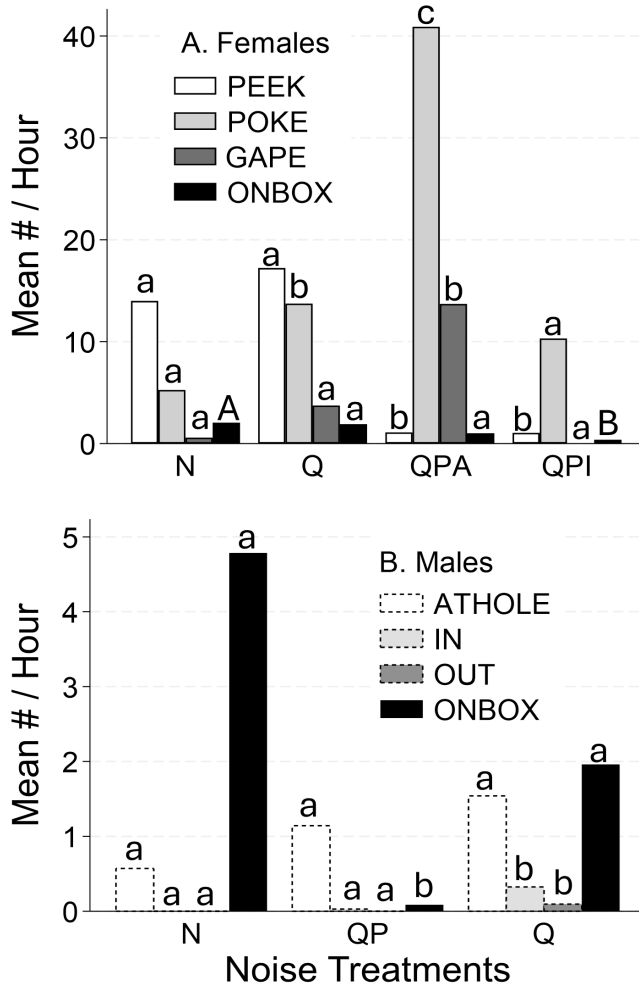
indicates significance at $p \leq 0.05$, “>>” indicates $p \leq 0.005$, and “=” means ns result. For females: POKE [QPA >> Q > (N = QPI)]; PEEK [(Q = N) >> (QPI = QPA)]; GAPE [QPA > (Q = N = QPI)]; ONBOX [N > QPI, N = Q = QPA]. For males: ONBOX [(N = Q) >> QP]; IN [Q > (QP = N)]; ATHOLE [all ns]; OUT [Q > P]. In Figure 3A and B, significant pairwise contrasts are coded using different letters above the bars for each behavior.

Canonical discriminant function analysis

For females, the frequency of PEEK, POKE, GAPE, ONBOX were submitted to canonical discriminant function analysis, and two significant discriminant functions (of three) were extracted: the first explained 76% of the variance ($F_{12, 307} = 4.88$, $P < 0.001$) and the second 24% of the variance ($F_{6, 234} = 2.45$, $P = 0.03$). For female bluebirds, the Mahalanobis group mean for QPA nests was significantly different from the other three groups (Table 2). Comparing Figures 4A with 4C, we can see that PEEK behavior characterized Q and some N nests (lower right quadrants), whereas POKE and GAPE (and lack of PEEK) behaviors identified QPA birds (upper central left quadrant). A confusion matrix for females indicated that treatments QPI (84% accuracy) and QPA (70%) are highly distinguishable from the others (Table 2A, bolded numbers on the diagonal) based on female behaviors.

For males, IN, OUT, ATHOLE, and ONBOX were submitted to canonical discriminant function analysis and two significant discriminant functions (of two) were extracted: the first explained 69% of the variance ($F_{8, 238} = 2.92$, $P = 0.004$) and the second explaining 31% of the variance ($F_{3, 120} = 2.5$, $P = 0.06$). For males, discriminant analysis found that all Mahalanobis group means were significantly different, though the magnitude of these

Fig. 3. Mean raw frequencies / hour of behaviors of interest across noise categories for females (A) and males (B). The noise categories are defined as: N = high levels of traffic noise + playback, Q = low levels of traffic noise, QPI = low levels of traffic noise + inactive playback, QPA = low levels of traffic noise + active playback, QP = QPI + QPA. Dunn's contrast results for each behavior are coded with letters: ns contrasts have the same letter and significantly different noise categories have different letters.



intergroup distances was less than for females (Table 2B). ONBOX behavior clearly distinguished males in N treatments from QP birds and most of the birds in quiet nest boxes (Figs. 4B and 4D, upper right quadrants). Comparison of loadings with location of score clouds in Figure 4 shows males exposed to N (high traffic noise) were most often ONBOX and those exposed to playback were only ATHOLE, and males at quiet nest boxes did some of all four behaviors. Confusion matrices indicated that playback treatments (QP) could be readily distinguished from N and Q with 94% accuracy (bolded diagonal in Table 2B).

Table 2. Mahalanobis squared distances and p values for pairwise contrasts in parentheses (below the diagonal) and classification accuracies (**percent** true predictions of each behavior class) bolded on the diagonal for females (A) and males (B).

A. Females				
Noise Categories	N	QPI	QPA	Q
N	47.4	-	-	-
QPI	1.13 (0.04)	84.21	-	-
QPA	6.43 (< 0.001)	3.76 (< 0.001)	70.00	-
Q	0.27 (0.41)	1.16 (0.003)	4.58 (< 0.001)	28.00
B. Males				
Noise Categories	N	QP	Q	
N	42.86	-	-	
QP	1.65 (0.004)	94.29	-	
Q	1.04 (0.02)	0.41 (0.05)	20.27	

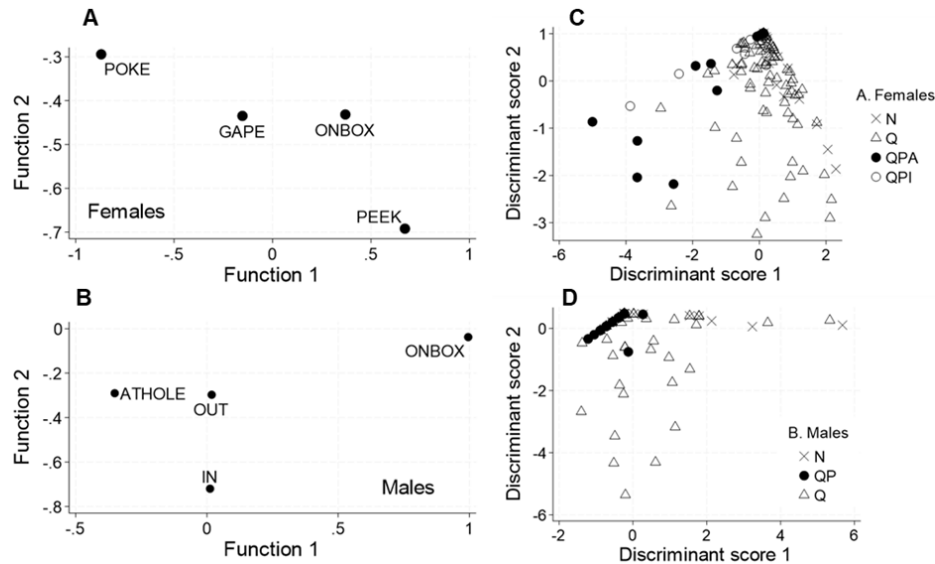
DISCUSSION

We found that anthropogenic noise was associated with significant changes in the visible incubation stage behaviors of both male and female Eastern Bluebirds. Sieving et al. (2024) detected the lowest hatching success and the highest rate of small temperature drops in the nest cups in the quiet nests receiving construction noise, the same treatment where we detected the highest rates of head-poking by females and the lowest rates of male nest box attendance. We conclude that overly frequent head-poking by females in quiet nests with playback likely degrades incubation constancy and, in turn, hatching success. Given the important role of males in helping females maintain the highest levels of incubation constancy (Skutch 1962, Amininasab et al. 2017), our study is among the first to correlate male nest attendance behavior, as influenced by anthropogenic noise, with degraded hatching success.

Noise-altered incubation behavior in females

Proper egg incubation is crucial for successful hatching in birds. The eggs must be kept within an optimal temperature range during development, typically between 35 °C and 39 °C (Berntsen and Bech 2016). Falling below this temperature range can delay embryonic development and lead to egg mortality and decreased hatching success (Olson et al. 2006, Wang and Beissinger 2009). Under normal conditions, females balance time spent on and off the nest to prevent the eggs from cooling down to a harmful level (Haftorn 1988). They do this by foraging off the nest for frequent but short periods during the day, allowing only minimal cooling while out foraging. Then they return to the nest and sit deeply on the eggs (on bouts) between off bouts and during the night (Maurelli 2022). Typical diurnal on-bouts last 15 minutes and off bouts last 10 minutes (Pinkowski 1979). Sieving et al. (2024) reported that although on bout lengths did not vary with noise treatments, small drops of 2 degrees F were detected significantly more often in boxes receiving playback of construction noise. Moreover, these small drops in temperature increased substantially in nests receiving more days of playback (range from 0 to 4 days) during the incubation stage. They concluded that females were disturbed

Fig. 4. Loading plots showing how the different behaviors for (A) females and (B) males are expressed on the two significant functions are shown beside scatterplots of discriminant scores for (C) females and (D) males by noise treatments on the first two significant discriminant functions. Comparison of loadings (left) with location of score clouds (right) shows (for examples) that peeking in females (A) is a normal incubation behavior (associated with quiet nests (in C; triangles) and poking and gaping characterize playback (QPA, QPI; in upper left area of A and C), and males exposed to high traffic noise (N; X's in D) are most often ONBOX.



by playback in some way that causes them to lose contact with eggs and predicted that photo data would show more head-poking or other behaviors requiring standing off the eggs. Here, we confirmed this prediction.

Indeed, we found that playback treatments significantly lowered the frequency of peeking and increased poking. Also gaping, which could occur with head in or out of the hole, was most frequent in QPA treatments (Fig. 3A). The latter two behaviors and likely also peeking could result in loss of contact between a female's belly and the eggs, based on geometry and infrared video footage from cameras placed in Gilbertson style boxes with incubating bluebird females (Maurelli 2022), given that the nest hole is 16 cm above the nest floor, the nest cup rim is typically 5–7 cm high, and a deeply incubating female bluebird's head barely overtops the nest rim. In Maurelli (2022) videos detected a higher rate of restless behaviors at night (egg-turning, standing up, resettling) in noise-exposed nests. It is also clear in these images that females could not head-poke without severing contact with the eggs, since they lost contact just standing up to stretch, with the head well below the hole. Thus, data from our bluebird system aligns with understanding that inconsistent incubation behavior reduces hatching success (Coe et al. 2015), and reflects increased vigilance, distraction, and stress (Sieving et al. 2024). Gaping, in particular (which occurred while head-poking and peeking in this study; Fig. 1) is a clear sign of stress, fear, or aggression (Rogers and Kaplan 2000). We conclude data presented here further confirm that intermittent playback near the nests strongly disturbed, agitated, and distracted female bluebirds from steady incubation contact with eggs. Females exhibit a range of different movements inside the nest that reduce contact with eggs, including egg turning, standing to change position or preen underbelly feathers. They can also crane or turn their heads and snap at

mosquitos without lifting their bodies (Maurelli 2022). All these movements are natural, but they increase in frequency during the night with noise, and our data suggest they do during the day as well. Sieving et al. (2024) speculated that noise-induced female restlessness contributes to reduced hatching success, and results presented here are confirmatory.

Noise-altered nest-attendance behavior in males

Male bluebirds also play a vital role in the incubation and hatching process. They provide females with food during incubation (Gowaty and Plissner 2020) and mate feeding increases hatching success by allowing the female to spend more time on the eggs in bluebirds and other species (Hałupka 1994, Amininasab et al. 2017, Rowher and Purcell 2019). Although we could not detect feeding visits specifically, the male behaviors of IN, OUT, ATHOLE, and ONBOX are all potentially associated with mate feeding by males. These behaviors were collectively most numerous at Q (quiet) nests (Fig. 3B) and statistically distinct from male behaviors at N and QP nests (Table 2B).

Perching on the nest box is also a territorial defense behavior seen in secondary cavity nesting birds (Rendell and Robertson 1994); males spent significantly more time perched on top of the box in high noise compared to quiet areas (Fig. 3B). In part this may be a consequence of heightened vigilance caused by noise (Merrall and Evans 2020), but we also suggest males may seek closer proximity to females to improve intra-pair communication where acoustic cues may be masked by traffic noise. Female song in bluebirds increases pair-bonding and reproductive success (Rose et al. 2019); other, softer acoustic cues exchanged within pairs might be important in incubation coordination as well. Anthropogenic noise interferes with avian communication in many species and hinders the function of acoustic signals related

to territory defense and predator avoidance (Slabbekoorn and Ripmeester 2007, Grade and Sieving 2016, Engel et al. 2024). One behavioral adaptation to noise interference seen in birds is to reduce inter-individual proximity. For example, flocks of Tufted Titmice (*Baeolophus bicolor*) that occur close to roads exhibit tighter inter-individual distances than in quiet habitats and Owens (2013) suggested this reduced proximity can enhance signal transmission and social coordination within groups. In sum, sitting on the box where traffic noise was higher would enhance male opportunity to feed, communicate with, and protect females. Therefore, we suggest that the comparative disappearance of males from the box top in playback treatments may have exacerbated female distress, agitation, and poor incubation constancy leading to the significant increase in temperature drops and low hatching success observed in Sieving et al. (2024). In monogamous passerine birds, males contribute heavily to nestling care, feeding, and protection (Bart and Tornes 1989), and it is increasingly clear they have important roles during incubation and should be included in studies of anthropogenic disruptions of incubation.

Chronic vs intermittent anthropogenic noise

Intermittent anthropogenic noise from playbacks was more disturbing to nesting bluebirds than chronic traffic noise here and in Sieving et al. (2024, see also Rosa and Koper 2023). Individuals exhibited a greater deviation from typical behavior seen in quiet areas under playback of intermittent noise (QP, males; QPA, females) compared to just chronic noise (N; Figs. 3 and 4). Whereas individual animals can acclimate to chronic noise with minimal distraction (Wright et al. 2007), acute bouts of loud noise or bright light are highly disruptive to human rest and concentration (via arousal and distraction; Basner et al. 2015). We suggest the intermittent noise of playback disrupted nest attendance behaviors via similar mechanisms as well as heightened threat perception, especially in females. Head-poking, pecking, and gaping at the nest hole would all function to enhance personal collection of information about potential threats outside the nest (Massaro et al. 2008). For females disturbed by playback, the absence of males, whose protection and communication may be important for females' abilities to settle on eggs, may exacerbate her agitation. Finally, urban noise can reduce foraging efficiency in birds (Merrall and Evans 2020), and this would intensify the compromise of, both, male mate feeding and female foraging versus incubation trade-offs.

Future directions

With nest box technology rapidly improving, it would be beneficial to incorporate smart nest boxes that allow for collection of integrated audio, video, and temperature data (e.g., Zárybnická et al. 2016). In combination with wearable motion sensors (Rafiq et al. 2021) to track pair behaviors outside the nest box and immersive analytics (Klaas and Roopaei 2021) for seamless integration of data streams, behavioral changes to shifting stimuli could be analyzed in real time across anthropogenic gradients. In this way, causal models could disentangle direct, indirect, and interacting causes of nest failure to inform wild bird management in human dominated habitats. Future studies should also take into consideration other sources of breeding stress, such as artificial light at night (ALAN; Ferraro et al. 2020), human/predator intrusions, and severe weather events.

Author Contributions:

MC conducted all data acquisition and screening, crafted the hypotheses, and drafted the manuscript. KS led on statistical analysis and revision efforts.

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Data Availability:

Data are available at <https://zenodo.org/records/15284692>.

LITERATURE CITED

- Amininasab, S. M., M. Birker, S. A. Kingma, H. Hildenbrandt, and J. Komdeur. 2017. The effect of male incubation feeding on female nest attendance and reproductive performance in a socially monogamous bird. *Journal of Ornithology* 158(3):687-696. <https://doi.org/10.1007/s10336-016-1427-2>
- Bart, J., and A. Tornes. 1989. Importance of monogamous male birds in determining reproductive success: evidence for House Wrens and a review of male-removal studies. *Behavioral Ecology and Sociobiology* 24(2):109-116. <https://doi.org/10.1007/BF00299642>
- Basner, M., M. Brink, A. Bristow, Y. De Kluizenaar, L. Finegold, J. Hong, S. A. Janssen, R. Klæboe, T. Leroux, A. Liebl, T. Matsui, D. Schwela, M. Sliwinska-Kowalska, and P. Sörqvist. 2015. IC BEN review of research on the biological effects of noise 2011-2014. *Noise and Health* 17(75):57-82. <https://doi.org/10.4103/1463-1741.153373>
- Berntsen, H. H., and C. Bech. 2016. Incubation temperature influences survival in a small passerine bird. *Journal of Avian Biology* 47(2):141-145. <https://doi.org/10.1111/jav.00688>
- Buxton, R. T., M. F. McKenna, D. Mennitt, K. Fristrup, K. Crooks, L. Angeloni, and G. Wittemyer. 2017. Noise pollution is pervasive in U.S. protected areas. *Science* 356(6337):531-533. <https://doi.org/10.1126/science.aah4783>
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences* 273(1592):1375-1383. <https://doi.org/10.1098/rspb.2005.3458>
- Coe, B. H., M. L. Beck, S. Y. Chin, C. M. Jachowski, and W. A. Hopkins. 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal of Avian Biology* 46(4):385-394. <https://doi.org/10.1111/jav.00581>
- Cornell, K. L., C. R. Kight, R. B. Burdge, A. R. Gunderson, J. K. Hubbard, A. K. Jackson, J. E. LeClerc, M. L. Pitts, J. P. Swaddle, D. A. Cristol. 2011. Reproductive success of Eastern Bluebirds (*Sialia sialis*) on suburban golf courses. *Auk* 128(3):577-586. <https://doi.org/10.1525/auk.2011.10182>
- Engel, M. S., R. J. Young, W. J. Davies, D. Waddington, and M. D. Wood. 2024. A systematic review of anthropogenic noise impact on avian species. *Current Pollution Reports* 10(4):684-709. <https://doi.org/10.1007/s40726-024-00329-3>

- Fardell, L. L., C. R. Pavey, and C. R. Dickman. 2022. Backyard biomes: is anyone there? Improving public awareness of urban wildlife activity. *Diversity* 14(4):263. <https://doi.org/10.3390/d14040263>
- Ferraro, D. M., M. L. T. Le, and C. D. Francis. 2020. Combined effect of anthropogenic noise and artificial night lighting negatively affect Western Bluebird chick development. *Condor* 122(4):duaa037. <https://doi.org/10.1093/condor/duaa037>
- Gowaty, P. A., and J. H. Plissner. 1998. Eastern Bluebird (*Sialia sialis*). In A. Poole and F. Gill, editors. *The birds of North America*, no. 381. Academy of Natural Sciences, Philadelphia, Pennsylvania and American Ornithologists' Union, Washington, D.C., USA.
- Gowaty, P. A., and J. H. Plissner. 2020. Eastern Bluebird (*Sialia sialis*), version 1.0. In A. F. Poole, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.easblu.01>
- Grade, A. M., and K. E. Sieving. 2016. When the birds go unheard: highway noise disrupts information transfer between bird species. *Biology Letters* 12(4):20160113. <https://doi.org/10.1098/rsbl.2016.0113>
- Gruber, T., L. Luncz, J. Mörchen, C. Schuppli, R. L. Kendal, and K. Hockings. 2019. Cultural change in animals: a flexible behavioural adaptation to human disturbance. *Palgrave Communications* 5:64. <https://doi.org/10.1057/s41599-019-0271-4>
- Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. *Ornis Scandinavica* 19(2):97-110. <https://doi.org/10.2307/3676458>
- Hałupka, K. 1994. Incubation feeding in Meadow Pipit *Anthus pratensis* affects female time budget. *Journal of Avian Biology* 25(3):251-253. <https://doi.org/10.2307/3677083>
- Jerem, P., and F. Mathews. 2021. Trends and knowledge gaps in field research investigating effects of anthropogenic noise. *Conservation Biology* 35(1):115-129. <https://doi.org/10.1111/cobi.13510>
- Jokimäki, J., M.-L. Kaisanlahti-Jokimäki, J. Suhonen, P. Clergeau, M. Pautasso, and E. Fernández-Juricic. 2011. Merging wildlife community ecology with animal behavioral ecology for a better urban landscape planning. *Landscape and Urban Planning* 100(4):383-385. <https://doi.org/10.1016/j.landurbplan.2011.02.001>
- Kesar, A. G. 2014. Effect of prenatal chronic noise exposure on the growth and development of body and brain of chick embryo. *International Journal of Applied and Basic Medical Research* 4(1):3-6. <https://doi.org/10.4103/2229-516X.125666>
- Kight, C. R., M. S. Saha, and J. P. Swaddle. 2012. Anthropogenic noise is associated with reductions in the productivity of breeding Eastern Bluebirds (*Sialia sialis*). *Ecological Applications* 22(7):1989-1996. <https://doi.org/10.1890/12-0133.1>
- Klaas, E., and M. Roopaei. 2021. Immersive analytics application in smart agriculture and animal behavior. Pages 0290-0296 in 2021 IEEE 11th Annual Computing and Communication Workshop and Conference (CCWC). Institute of Electrical and Electronics Engineers, New York, New York, USA. <https://doi.org/10.1109/CCWC51732.2021.9375943>
- Kramer, M., P. Weldon, and J. F. Carroll. 2009. Composite scores for concurrent behaviours constructed using canonical discriminant analysis. *Animal Behaviour* 77:763-768. <https://doi.org/10.1016/j.anbehav.2008.12.011>
- Kryter, K. D. 2023. *The handbook of hearing and the effects of noise: physiology, psychology, and public health*. Emerald Group, Bingley, UK. <https://doi.org/10.1163/9789004653443>
- Kunc, H. P., and R. Schmidt. 2019. The effects of anthropogenic noise on animals: a meta-analysis. *Biology Letters* 15(11):0190649. <https://doi.org/10.1098/rsbl.2019.0649>
- Liu, Y. 2020. Effects of anthropogenic noise on reproduction in an urban population of Eastern Bluebirds (*Sialia sialis*). Thesis. University of Florida, Gainesville, Florida, USA.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success (Métodos para localizar nidos y monitorear el éxito de estos). *Journal of Field Ornithology* 64:507-519.
- Massaro, M., A. Starling-Windhof, J. V. Briskie, and T. E. Martin. 2008. Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. *PLoS ONE* 3(6):e2331. <https://doi.org/10.1371/journal.pone.0002331>
- Maurelli, O. V. 2022. Sleepless and restless: effects of traffic noise and mosquito incursions on Eastern Bluebird (*Sialia sialis*) incubation behaviors. Thesis. University of Florida, Gainesville, Florida, USA. https://ufdcimages.uflib.ufl.edu/UF/E0/05/95/05/00001/Maurelli_O.pdf
- McCleery, R. A. 2009. Changes in fox squirrel anti-predator behaviors across the urban-rural gradient. *Landscape Ecology* 24:483-493. <https://doi.org/10.1007/s10980-009-9323-2>
- Merrall, E. S., and K. L. Evans. 2020. Anthropogenic noise reduces avian feeding efficiency and increases vigilance along an urban-rural gradient regardless of species' tolerances to urbanisation. *Journal of Avian Biology* 51(9). <https://doi.org/10.1111/jav.02341>
- Olson, C. R., C. M. Vleck, and D. Vleck. 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiological and Biochemical Zoology* 79(5):927-936. <https://doi.org/10.1086/506003>
- Owens, J. L. 2013. Effects of traffic noise on the social behavior of Tufted Titmice (*Baeolophus bicolor*). Dissertation. University of Tennessee, Knoxville, USA. https://trace.tennessee.edu/utk_graddiss/1767/
- Pandit, M. M., J. Eapen, G. Pineda-Sabillon, M. E. Caulfield, A. Moreno, J. Wilhelm, J. E. Ruyle, E. S. Bridge, and D. S. Proppe. 2021. Anthropogenic noise alters parental behavior and nestling developmental patterns, but not fledging condition. *Behavioral Ecology* 32(4):747-755. <https://doi.org/10.1093/beheco/arab015>
- Pinkowski, B. C. 1976. Behavior and feeding ecology of the Eastern Bluebird (*Sialia sialis*). *Ecological Monographs* 46:291-308.

- Pinkowski, B. C. 1979. Time budget and incubation rhythm of the Eastern Bluebird. *American Midland Naturalist* 101:427-433. <https://doi.org/10.2307/2424608>
- Plummer, I., Y. Liu, and K. E. Sieving. 2021. Urban greenspace is for the bluebirds: nest-box selection across a noise gradient on an urbanizing university campus. *Southeastern Naturalist* 20:152-161. <https://doi.org/10.1656/058.020.0115>
- Rafiq, K., B. J. Pitcher, K. Cornelsen, K. W. Hansen, A. J. King, R. G. Appleby, B. Abrahms, and N. R. Jordan. 2021. Animal-borne technologies in wildlife research and conservation. Pages 105-128 in S. A. Wich and A. K. Piel, editors. *Conservation technology*. Oxford Academic, Oxford, UK. <https://doi.org/10.1093/oso/9780198850243.003.0006>
- Rendell, W. B., and R. J. Robertson. 1994. Defense of extra nest-sites by a cavity-nesting bird. *Ardea* 82:273-285.
- Rogers, L. J., and G. T. Kaplan. 2000. *Songs, roars, and rituals: communication in birds, mammals, and other animals*. Harvard University Press, Cambridge, Massachusetts, USA.
- Rohwer, V. G., and J. R. Purcell. 2019. Geographic variation in incubation behavior of a widely distributed passerine bird. *PLoS ONE* 14(8):e0219907. <https://doi.org/10.1371/journal.pone.0219907>
- Rosa, P., and N. Koper. 2023. Comparison of impacts of oil infrastructure on grassland songbirds between landscape-scale noise addition and noise removal experiments. *Frontiers in Ecology and Evolution* 11:1168585. <https://doi.org/10.3389/fevo.2023.1168585>
- Rose, E. M., D. A. Coss, C. D. Haines, S. A. Danquah, C. E. Studds, and K. E. Omland. 2019. Why do females sing? Pair communication and other song functions in Eastern Bluebirds. *Behavioral Ecology* 30(6):1653-1661. <https://doi.org/10.1093/beheco/arz130>
- Schmidt, K. A., and C. J. Whelan. 2005. Quantifying male Wood Thrush nest-attendance and its relationship to nest success. *Condor* 107(1):138-144. <https://doi.org/10.1093/condor/107.1.138>
- Schroeder, J., S. Nakagawa, I. R. Cleasby, and T. Burke. 2012. Passerine birds breeding under chronic noise experience reduced fitness. *PLoS ONE* 7(7):e39200. <https://doi.org/10.1371/journal.pone.0039200>
- 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>
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74(2):115-152.
- Slabbekoorn, H., and E. A. Ripmeester. 2007. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* 17(1):72-83. <https://doi.org/10.1111/j.1365-294X.2007.03487.x>
- StataCorp. 2025. *Stata Statistical Software: Release 19*. StataCorp LLC, College Station, Texas, USA.
- Wang, J. M., and S. R. Beissinger. 2009. Variation in the onset of incubation and its influence on avian hatching success and asynchrony. *Animal Behaviour* 78(3):601-613. <https://doi.org/10.1016/j.anbehav.2009.05.022>
- Wells, S. M., and W. L. Robinette. 2020. Sentinel behavior by male Eastern Bluebirds during incubation: vigilance, nest defense, and female support. *Journal of Field Ornithology* 91(1):56-64.
- Williams, D. P., J. D. Avery, T. B. Gabrielson, and M. C. Brittingham. 2021. Experimental playback of natural gas compressor noise reduces incubation time and hatching success in two secondary cavity-nesting bird species. *Condor* 123(1):duaa066. <https://doi.org/10.1093/ornithapp/duaa066>
- Wright, A. J., N. A. Soto, A. L. Baldwin, M. Bateson, C. M. Beale, C. Clark, T. Deak, E. F. Edwards, A. Fernández, A. Godinho, L. T. Hatch, A. Kakuschke, D. Lusseau, D. Martineau, M. L. Romero, L. S. Weilgart, B. A. Wintle, G. Notarbartolo-di-Sciara, and V. Martin. 2007. Anthropogenic noise as a stressor in animals: a multidisciplinary perspective. *International Journal of Comparative Psychology* 20(2). <https://doi.org/10.46867/IJCP.2007.20.02.02>
- Zárybnická, M., P. Kubizňák, J. Šindelář, and V. Hlaváč. 2016. Smart nest box: a tool and methodology for monitoring of cavity-dwelling animals. *Methods in Ecology and Evolution* 7(4):483-492. <https://doi.org/10.1111/2041-210X.12509>
- Zuñiga-Palacios, J., I. Zuria, I. Castellanos, C. Lara, and G. Sánchez-Rojas. 2021. What do we know (and need to know) about the role of urban habitats as ecological traps? Systematic review and meta-analysis. *Science of the Total Environment* 780:146559. <https://doi.org/10.1016/j.scitotenv.2021.146559>