Female Aggression Level Mediates the Impact of Anthropogenic Noise Pollution in Eastern Bluebirds

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A Thesis presented to the Graduate Faculty of The College of William & Mary in Candidacy for the Degree of

Master of Science

Department of Biology

College of William & Mary

August 2020

APPROVAL PAGE

This Thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

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COMPLIANCE PAGE

Research approved by

Institutional Animal Care and Use Committee (IACUC)

Protocol number(s): IACUC-2018-12-07-13294-dacris

Date(s) of approval: January 30, 2019

ABSTRACT

We asked whether anthropogenic noise and animal personality interact to influence the settlement patterns and parental behaviors of individual eastern bluebirds (*Sialia sialis*) in a suburban landscape. Our hypothesis was that individuals with bold-type personalities would be less sensitive to noise pollution because they are more risk-tolerant. We collected repeated measures of neophobia, aggression, and nestling feeding rate in adult bluebirds while manipulating the sound environment at nest boxes. First, we added a recording of traffic noise during the nestling stage. We found that when exposed to experimental noise, more aggressive females had higher feeding rates than less aggressive females. Individual bluebirds were moderately repeatable in aggression and neophobia, but the two behaviors did not correlate to form bold-type and shy-type personalities. In a second experiment, we manipulated the noise environment during territory establishment, nest-building, and egg-laying. We found that less-aggressive females tended to settle in noise-treated nests, and these females delayed egg-laying by an average of four days, although this was not statistically different from controls. These results suggest that female aggression level is important for mediating the effects of anthropogenic noise pollution on this population bluebirds. Less-aggressive females may be at a disadvantage because they were more likely to occupy noisy areas yet did not increase nestling feeding rate under noisy conditions. Identifying the role of personality in mediating human impacts on animal populations will allow us to implement more finely tuned conservation and management programs.

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ACKNOWLEDGEMENTS

I would like to thank my advisor, Dan, for his honest feedback and helpful guidance with a healthy dose of cynical humor. I'm grateful that he called me out when needed, and he has certainly helped me become a better scientist and a better person. I am also grateful to my committee members, John and Matthias, for providing useful advice during all stages of my thesis project. I am particularly grateful to Matthias for encouraging my interest in statistics, and for always being positive and excited about my research. Very special thanks to Sarah Weber, Anna Kashmanian, and Jackie Golden for their help collecting data in the field, as well as thanks to the many other undergraduates who dedicated their time to the project: Elizabeth McLaughlin, Ryan Lauzardo, Anna Gleason, Caroline Taylor, Charlotte Deering, Daria Moody, Eileen Dinn, Maeve Mungovan, Rachel Akers, and Sadie Stott. I'm also grateful for the friends and colleagues who assisted me with fieldwork: Yi Hao, Caroline Schlutius, Bob Galvin, Sam Mason, and Hari Duddela. Additionally, I'd like to acknowledge and thank Tom Meier for designing and constructing my experimental speaker housings, and Bryan Watts for adding me to his State and Federal bird banding permits. Daniel Vasiliu generously gave his time and assistance to help me understand generalized linear mixed effect models for my analyses, and I'm also grateful to Sam Mason for his assistance with data analysis and visualization. Thank you to my lab group, the iibbs lab, for teaching me about bird memes, and special thanks to my lab mates Tim Boycott and Casey McLaughlin for all their support and encouragement, both professionally and personally, during our graduate experience.

I'd like to give a huge thank you to the Historic Rivers Chapter Master Naturalists members who shared their bluebird monitoring data and allowed me to harass the bluebirds at their nest box trails. Special thanks to Jan Lockwood and the trail leaders for showing me their field sites, for coordinating their monitoring to accommodate my research, and for always being very encouraging, excited about my fieldwork, and willing to help in any way possible. It was a genuine pleasure to work with this group of dedicated citizen scientists and I was inspired by their love of bluebirds.

I am grateful to the funding sources that made my research possible, especially the Garden Club of Virginia, Williamsburg Bird Club, Coastal Virginia Wildlife Observatory, and William & Mary Arts and Sciences. I also received financial support through the National Science Foundation Graduate Research Fellowship Program.

Finally, thank you to my boyfriend, Harikrishna Duddela, for his wonderful love and support over the past two years.

This thesis is dedicated to my mom, Gail Kenny, for teaching me to appreciate nature, for encouraging me to study wildlife biology, and for sharing her love of birds. I'm so grateful to have such a loving mother and enthusiastic birding partner.

INTRODUCTION

Wildlife species are increasingly confronted with the challenges of living in human-altered and human-dominated landscapes. Features such as lawns and paved cul-de-sacs are evolutionarily novel and exert different selective pressures on wildlife than the meadows and forest in which they evolved (Sih et al., 2011; Swaddle et al., 2015). Documenting differences in the fitness and behavior of animals living in urban vs. rural areas has been an important step towards understanding the ecological impacts of urban development (reviewed in Lowry et al., 2013), but more work is still needed to clarify the roles of specific urban stressors in shaping animal behavior and evolution. One such stressor is anthropogenic noise pollution. Human-generated sounds like noise from traffic, construction, and resource extraction are chronic stressors that can affect animals relying heavily on acoustic signals, such as songbirds. It has been well documented that songbirds can change the timing (Arroyo-Solís et al., 2013), structure, amplitude (Brumm, 2004), or frequency (Kight & Swaddle, 2015; Shannon et al., 2016) of their songs in response to anthropogenic noise which masks vocal communication. Noise pollution can also have important impacts on non-vocal behaviors such as receptiveness towards a mate (Huet des Aunay et al., 2017), choice of a breeding site (Kleist et al., 2017), or care of young (Schroeder et al., 2012). These non-vocal behaviors in particular can be important in explaining fitness differences between populations in noisy and quiet sites (Injaian, Taff, et al., 2018; Kight & Swaddle, 2011; Kleist et al., 2018).

It is vital to investigate behavioral variation at multiple scales – from populations over generations, to individuals over days or even hours – in order to gain insight as to how and why behavioral differences occur. Evaluating the *average* behavioral response to noise in a population is useful for identifying broad trends, but it should be complimented by a finer-scale focus that illuminates the variation in these responses between individual birds, and even within a single bird over time. Examining behaviors at the level of the individual organism can provide insight into the mechanisms by which population-level changes are occurring (Wong &

Candolin, 2015). In particular, knowing whether the average expression of a behavior changes in a population because individuals in the population alter their behavior, or because the composition of individuals in the population changes, informs us about the likelihood of genetic changes and evolution.

Across short time scales, if individuals are flexible in their behavior, then when confronted with a stressor such as noise, they may be able to simply alter their behavior to cope with the stressor and continue to survive in the population (Derryberry et al., 2017). In this case, noise is less likely to cause genetic changes in the population because there is no change in the population composition. The mean expression of a behavioral trait could also change on a short time scale if individuals are not flexible in their behavior, but individuals with certain trait values leave or enter the population (Bejder et al., 2006). Over generational time scales, one way the average behavior could change is through developmental plasticity if mothers or offspring are able to respond to the environmental stressor when traits are forming during offspring development (Badyaev & Oh, 2008; Pfennig, 1990). Finally, across many generations and in cases where behavioral traits are heritable, the population mean can change through evolution by natural selection for the behavioral trait that endows the greatest fitness in a noisy environment (Atwell et al., 2012). By understanding the scale at which behavioral change is happening in bird populations, we can better understand the likelihood of evolution, and the implications of this change for populations and individuals. This type of knowledge is relevant for conservation because effective management actions can be tailored to address the specific processes at work in a particular population. To achieve this comprehensive understanding, noise response must be studied at the level of the individual organism.

Behavioral flexibility is one mechanism for behavioral change in response to noise (Kight & Swaddle, 2015), and behaviors are generally considered to be the most flexible type of trait. However, there is a growing body of literature documenting that individual animals show consistent differences in their level of trait expression for behaviors such as aggression and exploration (Dingemanse et al., 2002; Huntingford, 1982), and can even be rigid to an extent that appears maladaptive (Henriksson, 1997). For example, one bird might be highly aggressive towards both a competitor and a potential nest predator, while another individual might be consistently non-aggressive in both contexts. These distinct behavioral differences between individuals of the same species are termed “personality types” or “behavioral syndromes” when multiple different behavioral traits covary within an individual (Dall et al., 2004; Sih et al., 2004). Personality types are often classified into two broad groups of risk-tolerant “bold-types” and risk-averse “shy-types”. A bold-type individual is typically aggressive, likely to investigate an unfamiliar object, and quick to explore an unfamiliar area. A shy-type individual is typically non-aggressive, unlikely to approach an unfamiliar object, and slower to explore. Behavioral traits associated with personality can be heritable (Dingemanse et al., 2002; Drent et al., 2003; Riyahi et al., 2017), and correspond with differences in survival and reproduction of individuals (Wolf & Weissing, 2010). For example, bold-types may benefit from highly active foraging in an environment with low predation risk, but when predation risk is high, active foraging may render those individuals more conspicuous to predators and consequently increase their mortality (Hall et al., 2015; Wolf & Weissing, 2010). The sound environment may be another factor, in addition to predation risk, which influences the relative fitness benefits of being bold and shy. If so, noise environments might sort the population and lead to over- or under-representation of particular personality types in loud or quiet areas. Many studies have documented differences in personality traits between urban and rural populations of birds (Bókony et al., 2012; Carrete & Tella, 2017; J. Evans et al., 2010; Riyahi et al., 2017), but our understanding of how a specific urban stressor, anthropogenic noise, contributes to these patterns remains limited.

There is reason to believe that bold-type and shy-type birds may have different abilities to cope with anthropogenic noise because the two types employ different strategies for dealing with risk, and noise can alter the riskiness of an environment. Noise can alter predation risk by deterring nest predators (Francis et al., 2009), by masking the sounds of predators that remain

(Barber et al., 2010), or by masking the sound of conspecific alarm calls (Kern & Radford, 2016; Templeton et al., 2016). Some songbirds respond to noise with anti-predator behaviors such as increasing flock density (Owens et al., 2012) and increasing vigilance at the expense of foraging efficiency (J. C. Evans et al., 2018; Quinn et al., 2006). Despite these overall patterns, we know that not all members of a population respond to increased noise in the same way or to the same extent (reviewed in Harding et al., 2019), and some types of individuals may pay a higher cost of inhabiting noisy areas. Great tits (*Parus major*) experimentally exposed to noise differed by sex and personality in their nest box visitation rate and latency to enter the nest box after disturbance (Naguib et al. 2013). Fast-exploring (bold) tits were quicker to return to the nest overall, but fast-exploring females and slow-exploring (shy) males reduced their visitation rate under noisy conditions. At the individual level, this suggests that bold females and shy males may perceive a higher cost of noise than other birds in the population because they showed the greatest change in their feeding behavior. At a population level, noise exposure could reduce productivity and nestling fitness by reducing the amount of food delivered by the parents to nestlings. This mechanism might be particularly important in populations with more shy-type birds since shy-type parents were slower to resume feeding overall. This is one example of how characterizing behaviors at the individual level can provide important information for tailoring management strategies to specific populations.

In addition to comparing behaviors between noisy and quiet conditions, we can also investigate the spatial arrangement of individuals to further understand how bold and shy birds cope with noise pollution. Spatial sorting of individuals based on behavioral traits has been documented in many species in relation to environmental factors such as urbanization (Carrete & Tella, 2017; Charmantier et al., 2017; J. Evans et al., 2010), microhabitat (Schirmer et al., 2019; Spiegel et al., 2015), and perceived predation risk (Griffen et al., 2012; Pearish et al., 2013). Such environment-trait correlations could be the result of behavioral flexibility, habitat-trait matching, or competitive exclusion. If individuals are entirely flexible in response to anthropogenic noise, spatial patterns of behavior should correlate with the sound environment but be independent of individual identity and personality type. In habitat-trait matching, individuals should choose the habitat that maximizes the fitness of their particular phenotype (Carrete & Tella, 2010; Fretwell, 1969). For example, more aggressive western bluebirds (*Sialia mexicana*) have higher fitness at population edges where they successfully compete against mountain bluebirds (*Sialia currudoides*) (Duckworth, 2006b). If a main effect of noise pollution is to increase perceived predation risk, then we would expect more risk-tolerant individuals to occur in noisy areas. Alternatively, noise could decrease actual predation risk (Francis et al., 2009) in which case risk-averse individuals might preferentially choose noisy areas.

Finally, noise pollution could alter habitat quality and cause bold-type and shy-type individuals to sort into quiet and loud areas based on competitive ability. Studies on ovenbirds (*Seiurus aurocapilla*) and tree swallows (*Tachycineta bicolor*) have shown that noisy areas were settled later than quiet areas, and lower-quality individuals tended to occupy the noisy territories (Habib et al., 2006; Injaian, Poon, et al., 2018). Since bold-type individuals are more aggressive, they likely have higher resource-holding potential (Parker, 1974), and spatial sorting by competitive ability should result in bold-type birds disproportionately occupying the preferred, quiet areas. It is important to consider how the sound environment may influence the spatial arrangement of personality types because intraspecific variation in behavior can influence ecological processes like species interactions (Des Roches et al., 2018; Raffard et al., 2019), seed dispersal (Brehm et al., 2019), and conservation efforts (Mimura et al., 2017).

In this study, we investigated the role of personality type and experimental anthropogenic noise in determining parental behaviors and settlement patterns in a suburban population of songbirds. Eastern Bluebirds (*Sialia sialis*) are secondary cavity-nesters which frequently use artificial nesting boxes in human-dominated landscapes (Jackson et al., 2013; Stanback & Seifert, 2005). Loud background noise is correlated with reduced average reproductive output in this species, but the mechanisms causing this trend are unclear

(Kight et al., 2012). We hypothesized that this pattern is driven by shy-type bluebirds which are risk-averse and therefore more disturbed by noise than other individuals in the population. To test this hypothesis, we measured personality traits (aggression and neophobia) of individual bluebirds and designed two field-based experiments to investigate possible mechanisms for how noise and personality may influence behaviors related to breeding performance. The first mechanism is that the bluebirds respond to noise pollution by altering their behaviors in suboptimal ways, in particular by reducing their rate of nestling provisioning. If our hypothesis is supported, then bluebirds with high neophobia and low aggression (shy-type) should exhibit the greatest reduction in provisioning rate when exposed to experimentally elevated noise during the nestling stage. The second mechanism is that bluebirds do not modulate their behaviors directly in response to noise, but certain types of birds spatially sort into noisy or quiet sites. If our hypothesis is supported, then bold-type and shy-type birds should sort into different noise environments when we experimentally manipulate noise during settlement. Shy-type birds should sort into quiet environments if they perceive noisy environments to be more risky. Alternatively, shy-type birds may sort into noisy environments if quiet territories are preferred and aggressively defended by the bold-type birds, thus pushing the shy-type birds into the suboptimal noisy environments. These two mechanisms are not mutually exclusive, and we also consider the possibility that shy-type bluebirds could be doubly impacted by noise if they are forced to occupy noisy areas in which they perform particularly poorly.

METHODS

Sites

We chose to study the effects of anthropogenic noise in a suburban environment because it is characterized by a gradient of sound intensity and frequencies and many songbird species utilize this habitat. In order to compare birds across relatively standardized breeding conditions, we only sampled bluebirds that nested in artificial nest boxes. This study made use of existing bluebird nest box trails that were located in public parks near Williamsburg, VA, and were monitored annually by the Historic Rivers Chapter of Virginia Master Naturalists (www.virginiamasternaturalist.org). Nest boxes were constructed of wood with predator guards and mounted on metal posts so that most entrance holes were at a height of 1.5m above the ground (see Appendix 1 for nest box dimensions and additional details). We selected research sites based on the following criteria: a sufficient number of active nest boxes, proximity to the William & Mary campus (for sake of efficiency when traveling to field sites), and either close to, or relatively isolated from, busy roads (providing a wide range of ambient noise environments). We selected focal nest boxes within each site based on constraints imposed by park administrators and on a record of bluebird nesting activity during the previous five years. Nest box locations were recorded using a handheld GPS unit (Garmin International Inc., Olathe, KS) and are provided in Appendix 2 along with a list of the six sites. In 2019 we sampled nests from all six sites, while in 2020 we sampled nests from only three of the sites due to limitations on personnel and equipment.

Study Species

Eastern bluebirds (*Sialia sialis*) are socially monogamous, secondary cavity nesters (i.e., do not excavate their own cavities) that breed in natural cavities as well as artificial nest boxes (Gowaty & Plissner, 2020). During the breeding season, which in Virginia lasts from approximately mid-February through mid-August, males establish and defend a territory with one or more available cavities, and females also defend the territory after pairing with a particular male (Gowaty & Plissner, 2020). This species is partially migratory, and our breeding population likely consists of both migratory and resident birds (J.P.S., unpublished data). Pairs form on the breeding grounds or before arrival, and bluebirds have relatively high mate and site fidelity between years (Coss et al., 2019; Pinkowski, 1974). Females presumable prefer high quality territories and high quality males, but the specific traits used by each sex during mate selection in this species are still unclear (Liu et al., 2007, 2009). Bluebird pairs in our study population typically raise at least two clutches over the course of the breeding season, and some raise three or four (H.V.K., personal observation). Previous behavioral studies of bluebird species have found that individuals show consistency in relative levels of aggression (Burtka & Grindstaff , 2013 - eastern bluebird; Duckworth, 2006b - western bluebird; Gibson & Moehrenschlager, 2008 - mountain bluebird) and neophobia (Pandit, 2017 - eastern bluebird), and there is variation in these behaviors between individuals.

In order to account for factors other than personality that could influence bluebird behavior, we captured birds and collected information on age, sex, and body condition. We recorded age (second year [SY] or after second year [ASY] by amount of white on 1st primary covert, or by "molt limit" which is the retention of feathers from the previous year in adult individuals; Pyle & Howell, 1997), sex, weight in grams (Pesola, Schindellegi Switzerland), wing length (unflattened), tail length, and tarsus length. In 2019, we collected the two central tail feathers for later analysis of corticosterone hormone levels, color metrics, and fluctuating asymmetry. To allow for individual recognition using binoculars during behavioral observations, we marked each adult bird with a unique combination of 4 bands (2 on each leg), including a numbered USGS metal leg band, and three plastic colored bands (random combinations of red, yellow, white, and brown).

We began capturing bluebirds on 18 March, 2019 using two different capture methods. We mist-netted most males and some females during nest building and incubation. For this method, we set up two mist nets (one 6m and one 9m) in a V-formation around the focal nest box and attached a polystyrene foam decoy painted to resemble a male bluebird to the outside of the nest box. We used an audio lure of a bluebird song played from a small speaker placed below the nest box (recording source: https://www.audubon.org/field-guide/bird/eastern-bluebird) to attract the territorial pair. Playback continued until the male was caught, or for a maximum of 20 minutes on a single day. In addition to mist netting, we used trap doors inside the nest box entrance (as described in Stutchbury & Robertson, 1986) to capture females during incubation, and to capture a few males during the first two days of the nestling stage. We checked nest boxes with trap doors at least every 15 minutes. Federal (permit 21567 issued to Bryan Watts, sub-permittee Heather Kenny), State (permit 61790 issued to Bryan Watts, sub-permittee Heather Kenny), and site-specific permissions were obtained before capture and handling began. The William & Mary Institutional Animal Care and Use Committee approved all animal handling (IACUC protocol 2018-12-07-13294-dacris).

We kept detailed track of nesting progress in each nest box because behavioral observations had to be performed on specific days relative to the nesting cycle. In 2019, trained volunteers from the Historic Rivers Chapter of the Virginia Master Naturalists checked the nest boxes on a weekly basis for the duration of the breeding season, beginning in mid-March. Researchers performed additional checks as needed to determine exact dates for the start of incubation and day of hatching (day 0). From nestling day 4 through fledging, researchers visited nests every two days for behavioral observations of the adults, experimental speaker set-up, speaker battery changes, and nestling status checks. In 2020, the volunteers suspended their activities on 20 March due to the coronavirus pandemic, after two weeks of monitoring. Thus, researchers were the only people regularly checking the nest boxes in 2020, visiting nests every two days in order to set up experimental speakers, change batteries, and monitor nesting progress. We maintained this monitoring schedule until the start of egg-laying at each nest. After laying began, we visited nests every 2-6 days to check for predation and to perform banding and behavioral observations. In order to determine overall nest box occupancy rates at each site, we checked all nest boxes at every site on two days during the breeding season (12 April and 2 May 2020) and recorded whether there had been any nesting activity of any species in each nest box.

Experimental noise treatment

<u>Experiment 1: Noise manipulation during the nestling stage</u>

In this experiment we tested whether bluebirds altered their nestling feeding rate or expression of personality traits in response to experimental noise pollution. Based on our hypothesis that noise pollution increases risk level and shy-type bluebirds are more responsive to changes in noise because they are risk-averse, we made the following specific predictions for this experiment: *1.1) if noise increases risk then bluebirds should behave more cautiously under elevated noise conditions by increasing neophobia, decreasing aggression, and decreasing feeding rate; 1.2) if bold-type and shy-type personalities exist in the population then individual identity should be an important predictor of behavior, behaviors (particularly neophobia and aggression) should be repeatable within individuals across the four trials, and neophobia and aggression should be negatively correlated (higher neophobia correlates with lower aggression); 1.3) if shy-type birds are more disturbed by noise than other individuals, then bluebirds with high neophobia and low aggression should show the greatest decrease in feeding rate under the experimental noise treatment*.

We altered the sound environment at the nest boxes by playing looped traffic sounds at noise-treatment nest boxes during daylight hours every day from nestling day 8 until fledging (playback duration approximately 10 days; see below for details of experimental set-up), and we measured the ambient sound levels at unmanipulated control nest boxes to verify that they were quieter than noise-treatment nests during speaker playback. We measured behaviors of the adult bluebirds (details below) on nestling days 4, 6 (before sound treatment), 10, and 12 (during sound treatment) and tested whether the behaviors of noise-treatment birds were different from the behaviors of control birds. We conducted the nestling stage noise manipulations for bluebirds breeding between 9 May and 31 July 2019, and did not differentiate between first, second, or third nestling attempts. In 2020 we measured adult behaviors during the nestling stage using the same protocol, but under unmanipulated conditions (no control or noise-treatment speakers). These measurements were included in the “control” group for analysis.

Only nests that succeeded past nestling day 8 were included in the experimental group, so treatments were assigned in an on-going process throughout the breeding season. Control or noise treatment was determined by a coin flip, but control and treatment boxes were paired within sites and across time so treatment assignment was stratified. Typically, if nestlings in two focal boxes at a single site hatched within a few days of each other, then the treatment of the earlier hatching box was determined by coin flip, and the later hatching box was assigned the other treatment (median number of days between initiation of control and treatment boxes was 4.5, range 0-22 days).

Experiment 2: Noise manipulation during settlement

In this experiment we tested whether bluebird behavior was correlated with the sound environment during settlement, nest-building, and egg-laying. Based on our hypothesis that noise pollution increases risk level and shy-type bluebirds are more responsive to changes in noise because they are risk-averse, we made the following specific predictions for this experiment: *2.1) shy-type bluebirds with high neophobia and low aggression should be more likely to settle in the quiet control nest boxes than the loud noise-treatment nest boxes; 2.2) if nest box settlement patterns are determined primarily by personality type and the sound environment during settlement, there should be no difference in the quality of birds in the control and noise-treatment groups in terms of settlement and egg-laying dates, age, or body condition.*

We set up the experimental speakers and began the traffic noise playback on or slightly after 24 February 2020 (latest start date in the noise treatment group was 2 March, latest start date in the control group was 25 March), and we did not detect any nesting activity at the nest boxes before the experiment initiation dates. We played looped traffic sounds at noise-treatment nest boxes every day during daylight hours, and continued the treatment at each nest box until the female at the nest laid her first egg (median playback duration 47 days, range 11 to 68 days). We ended the experimental manipulation at the start of egg-laying because bluebirds should be less likely to abandon the nest after laying eggs, so this should be a reliable signal that the pair has committed to breed in that nest box. We did not continue the sound treatment through the end of egg-laying because we did not want to influence clutch size or the timing of incubation initiation. If no eggs were laid in experimental boxes by 2 May we stopped the treatment and marked that nest box as unoccupied. We then conducted behavioral observations at occupied nests under ambient sound conditions on nestling days 4, 6, 10, and 12 and compared whether there was a difference in the behavior of birds that settled in the noise-treatment or control nest boxes. By only manipulating the sound environment during settlement we were able to separate the effect of noise pollution on settlement decisions from the direct effect of noise on behaviors during the nestling stage.

We monitored nest-building activity in the nest boxes during the treatment period by visiting the nest boxes every two days and photographing the nest box contents. We recorded the date that we first observed any nesting material inside the nest box (tagging or prospecting date), the date we first observed a partial nest (full layer of nesting material covering the bottom of the nest box, but no nest cup), the date we first observed a complete nest (nest cup with lining of small fibers), and the date when the first egg was laid (egg-laying date).

We only sampled three sites in 2020 (Newport News Park, New Quarter Park, York River State Park), and we chose experimental nest boxes based on nesting records from the previous 5 years, provided by the Historic Rivers Chapter of Master Naturalists. We selected nest boxes with relatively high occupancy rates across years, and paired the boxes based on whether the bluebirds tended to initiate egg-laying consistently earlier or later than the site-level average (see Appendix 3 for further details). This approach allowed us to maximize the probability of bluebirds nesting in our experimental nest boxes (as opposed to other unmanipulated nest boxes nearby) and provided for control and noise-treatment groupings that were relatively similar with regards to history of occupancy and timing of nesting. We collected behavioral observations from 14 April through 10 June 2020 and only included first nesting attempts of the season.

Sound measures and experimental playback:

By design, both experiments included nest boxes with a range of ambient sound levels, which varied between sites and as well as between nest boxes within a single site. This variation was mainly due to differences in proximity to roads, road size and traffic patterns, and proximity to park features such as playgrounds, parking lots, and visitor centers (H.V.K. unpublished data). We quantified variation in the sound environment between nest boxes by collecting sound measurements of ambient noise and speaker-generated traffic noise. The volume of the speaker-generated noise was not completely constant due to variation within the recording itself, occasional loud sounds from the ambient environment, and small variations between the speakers or the speaker volume settings. We measured sound levels in decibels using a hand-held sound meter (407730 Sound Level Meter, Extech Instruments, Boston MA; A-weighting and Fast mode) which was held at arm's length in front of the nest box entrance hole (about 15 cm away from the front wall of the box) by an observer who was standing beside the nest box.

Experimental speakers and playback settings:

We experimentally increased the volume of anthropogenic sounds at noise treatment nest boxes by playing looped traffic sounds at these nest boxes from 6:00 19:00 daily during the treatment period using a small wireless speaker (VTIN Technology Company Ltd., Hong Kong, HK). We left the nighttime hours unmanipulated because we wanted to simulate suburban traffic patterns where the highest amount of activity and sound volume is during the day. We controlled the timing of traffic playback using a 24-hour playlist with 13 hours of traffic noise and 11 hours of silence which played on repeat from an mp3 player (Eleston/Ruizu, Shenzhen, China) attached to the speaker. We adjusted the volume on the speaker to play at approximately 70dB as measured 15cm in front of the nest box (2.85m in front of the speaker) using a hand-held sound meter (see description of ambient sound measures above). The mp3 player was set to maximum volume, and then the volume on the speaker was adjusted and checked using the sound meter.

We mounted the speakers 3m in front of the noise-treatment nest boxes at a height of approximately 1m. The sound treatment was highly localized around the nest box, and sound levels were equivalent to ambient levels at 20-30m away from the speaker. Speakers were protected from weather and vandalism inside a lockable metal housing box with small holes added to allow more sound to escape (see Appendix 3 for additional details of playback equipment). We installed empty housing boxes at the control nest boxes to account for the visual disturbance of the equipment. We changed out the speaker battery packs every other day (approx. 48 hours), and we also visited the control nest boxes on the same schedule and stood near the speaker housing for 10 minutes to equalize the amount of human disturbance between the treatment groups.

Behavioral assays

<u>Timeline and general protocol</u>

We measured three behaviors of adult bluebirds in order to 1) assess the existence of personality types in our study population, 2) quantify variation in these traits between individuals, and 3) evaluate the influence of noise pollution and personality type on parental care, settlement patterns, nest-building and egg-laying . The two personality traits were aggression and neophobia which each measure different aspects of risk-tolerance (Greenberg & Mettke-Hofmann, 2001; Wolf et al., 2007). We wanted to evaluate risk-tolerance because we hypothesized that bluebirds assess noisy environments as being higher risk than quiet environments. Our measure of parental care was nestling feeding rate because previous research in this system found that bluebirds nesting in noisy areas fledged fewer chicks than bluebirds in quiet areas, but there was no difference in the number of eggs laid nor the number of eggs that successfully hatched (Kight et al., 2012). Thus, we hypothesized that noise has a particularly important impact during the nestling stage.

For both of our experiments, we collected repeated measures of each behavior for each bird in order to calculate within-individual consistency in behavior as a quantitative metric for the strength of personality (Dingemanse & Dochtermann, 2013). We standardized the timing of our repeated measures relative to the nesting cycle in order to minimize the influence of changing hormone levels and reproductive stages (for example incubation vs. feeding nestlings for females) on our personality measurements. We limited our observations to the nestling stage because this allowed us to measure feeding rate as an easily observed metric of parental care that is performed by both males and females. We performed behavioral assays on days 4, 6, 10, and 12 of the nestling stage (+/- one day), such that a total of four replicates of each of the three behaviors were collected.

Whenever possible, a single observer (HK, AK, or SW) conducted all 3 assays back-to-back (always in the same order – feeding rate, neophobia, aggression) on the same day in order to minimize the effects of observer and day on the within-trial correlation between the three behaviors. If it was not possible to perform the assay on the scheduled day due to bad weather or logistical constraints, we rescheduled for the following day. Observers stood or sat a minimum of 25 m away from the box during the assays and conducted observations between 06:26 and 18:05. We did not perform assays in heavy rain, but if it began to lightly rain during observations we continued observations as long as birds didn't appear to alter their behaviors. Birds were given at least one full day and night of acclimation time between banding and the start of behavioral assays. If a nest failed before we completed all four trials, we excluded that nest from our analysis. In the settlement experiment, two nests failed during the egg stage but the birds re-nested in the same nest box so we still collected behavioral observations from the successful clutch.

<u>Feeding rate</u>*:*

We recorded the frequency at which adult bluebirds visited the nest box as a proxy for nestling feeding rate. Feeding rate serves as a measure of parental investment, and may be correlated with nestling growth rate and quality (Dunn et al., 2010; Rytkönen et al., 1995; Scheuerlein & Gwinner, 2006). Trials started once one of the adults went inside the nest box and lasted for 30 minutes. This was done to ensure the birds were actively feeding, and this feeding event was included in the total number observed. If the pair did not feed after a full hour of observation, then the assay was rescheduled for the next day. There was one instance where a bluebird pair did not feed during the second observation attempt, although they were observed perching near to and on top of the nest box. In this case we recorded a feeding rate of zero. Birds were often observed with obvious food items in their bills, but we counted every time the bird entered the nest box as a feeding event, even if food was not obviously being carried by the parent. In order to compare feeding rate between nests as effort per nestling, we standardized by dividing the number of feeds by the number of nestlings present in the nest on the day of observation.

Neophobia*:*

We measured neophobia, or hesitation to approach a novel object, immediately after a feeding rate assay was completed. Neophobia is a common assay used to assess animal personality in terms of boldness (Bókony et al., 2012; Mainwaring et al., 2011; Wilson et al., 1993), where individuals that approach the object quickly are classified as more bold and less neophobic. One of 10 objects (5 in each year; see appendix 3 for photos of objects) was randomly selected for each observation and we never repeated objects within an individual bird. An observer attached the object to the top right corner of the roof of the nest box using a piece of wire. The observation began as soon as the observer had attached the object, at which point they started recording observations verbally into a mobile phone. The observer walked back to the same spot where they were positioned during the feeding rate observation and narrated the movements of the birds as they occurred. Specifically, we noted when the male or female landed on or went inside the nest box. The observation lasted until both birds had landed on the nest box (2020) or gone fully inside the box (2019 only), or for a maximum of 15 minutes (900 seconds). We later transcribed the audio recordings to determine the latency in seconds for each bird to land on the nest box. Birds that never landed were given a latency of 901 seconds.

Aggression*:*

To cause an aggressive response that was not reproductively motivated, we used a specimen of another species that competes for nest boxes. A freeze-dried tree swallow specimen salvaged as part of another study was attached to the front right corner of the nest box roof using wire and a large binder clip. We used three different tree swallow specimens for the aggression trials (specimens A and B in 2019 and specimens B and C in 2020) so that multiple observations could be conducted simultaneously at different nest boxes. Tree swallow ID was randomly determined by a coin toss before the first aggression assay for a focal pair. Once we selected a tree swallow it was kept consistent within individual bluebirds and the same specimen was used for all successive assays. We conducted aggression assays immediately after a neophobia assay was completed. Assays lasted 10 min and began as soon as the observer attached the swallow to the nest box. The observation began as soon as the observer had attached the object, at which point they started recording observations verbally into a mobile phone. Observers narrated any hovers or dives within 3 meters of the tree swallow, and any times the bluebirds struck the tree swallow. If an aggressive bluebird knocked the swallow to the ground then the observer continued the observation but walked over and set up the specimen again. If the swallow was knocked down more than three times then it was left on the ground until the end of the 10-min observation period. We transcribed the recordings and aggression was recorded as the total number of aggressive actions (sum of hovers, dives, and strikes).

Statistical analyses

Experiment 1: noise manipulation during the nestling stage

Prediction 1.1: bluebirds behave more cautiously under noisy conditions

In order to test whether the sound treatment was correlated with more cautions behaviors (increased neophobia, decreased aggression, decreased feeding rate), we modeled the three response behaviors and included the variable “speaker” to indicate whether the traffic noise playback was present or not during each behavioral observation. We used information criterion to determine whether adding the “speaker” variable improved the likelihood of the models. We modeled aggression and feeding rate using generalized linear mixed-effect models, and we modeled neophobia using survival analysis. All analyses were conducted in the statistical software R (R Core Team, 2019). We analyzed behavioral observations from both 2019 and 2020, and for bluebirds that were sampled in both years we only used the 2019 observations. All observations from 2020 were classified as controls for the nestling stage experiment analyses, regardless of their treatment assignment during the 2020 settlement experiment. This is reasonable because we conducted all behavioral observations with an unmanipulated sound environment. While the sound environment during settlement could influence which individuals decided to occupy the nest box, it is unlikely to influence an individual’s change in behavior across nestling days 4-12.

Mixed-effect models for feeding rate and aggression

For both feeding rate and aggression, we used bird ID (band number) as a random intercept to account for repeated measures of individuals. Feeding counts were Poisson distributed and were modeled using the “glmer” function in the “lme4” package (Bates et al., 2014) with a log link and number of nestlings as an offset. The offset term allowed us to assess the effect of the predictor variables on feeding rate (feeds per nestling), while taking advantage of the known Poisson parameterization of the raw count data for our modeling. Our aggression metric was also count based, but was over dispersed and a zero-inflated negative binomial model provided a better fit than the Poisson model. We modeled aggression using the “glmmTMB” package (Bolker, 2019; Brooks et al., 2017), with a negative binomial distribution, a quadratic error structure, and log link. We modeled males and females separately to avoid the problem of males and females influencing each other's behavior during a trial. We checked that models were properly specified using the "DHARMa" package which calculates scaled residuals and provides plots which are suitable for assessing the fit of generalized linear models (Hartig, 2020). We performed model selection using Akaike Information Criterion (AICc, AIC adjusted for small sample size; Burnham & Anderson, 2002). We wrote univariate models for all predictor variables, and used predictors that were better than the null model in subsequent multivariate models.

We checked for an effect of body size on behavior by included body condition index (BCI) as a predictor variable. We combined weight, tarsus length, wing length, and tail length into a body condition index separately for each sex. We performed a principal component analysis with tarsus, wing, and tail lengths to create a composite metric for body size. We selected the principal component on which all three body measures positively loaded (either PC1 or PC2) and performed a linear regression between this size PC and weight. We used residuals from the regression as an indicator of body condition, where positive values indicate above average weight for a given size, and negative values indicate a below average weight for a given size (Weimerskirch & Cherel, 1998).

Survival analysis for neophobia

Our neophobia metric was right-censored because we ended trials after 15 minutes even if the birds had not landed on the nest box by that time. This type of censored, time-to-event data can be properly handled using survival analysis where birds are "alive" until they land on the nest box. We hypothesized that noise treatment should make birds behave more cautiously so the traffic noise playback should cause birds to be more reluctant to land on the nest box and therefore have a higher "survival" rate over the course of the 15-minute trial. Likewise, a bird's "hazard" is its instantaneous probability of landing on the nest box, so bolder (less neophobic) birds should have higher hazards. We used mixed-effect Cox-proportional hazard models to test for an effect of speaker playback and other predictor variables on the latency to land on the nest box (Austin, 2017). The Cox proportional hazards model calculates hazard ratios for each observation by estimating how a baseline hazards ratio is modified by the different explanatory variables. This is a non-parametric approach because the baseline hazard is not calculated directly, and thus the parametric form of the hazard does not need to be defined. The baseline hazard is free to vary over time, but the Cox model assumes a constant hazards ratio. In other words, it assumes that the relationship between the baseline hazard and the explanatory variables is constant over time. Mixed-effect survival models were developed to handle clustered survival data, and in our case, observations are clustered by the individual bird. In a mixed-effect hazards model, a separate baseline hazards ratio is calculated for each level of a clustering term, also called a "frailty" term. We wrote separate mixed-effect Cox models for males and females using the "coxme" package (Therneau, 2020) and included bird ID as the frailty term. We also tested neophobia object as a crossed random effect because the same bird was exposed to four different objects which may differ from each other in how threatening they appear to the bluebirds. We used penalized likelihood AIC for model selection to determine top models.

Prediction 1.2: bluebirds exhibit consistent bold-type and shy-type personalities

To test whether individual bird ID was an important determinant of behavior, we compared mixed effect models with bird ID as a random intercept with null models that did not include the mixed effect. We used AIC to determine whether the mixed effect term improved the model likelihood. To test whether neophobia and aggression were correlated within individuals, we tested neophobia score as a predictor variable in the aggression model. We predicted a negative relationship between neophobia and aggression where bold individual have low neophobia and high aggression, and shy individuals have high neophobia and low aggression.

To test whether individual birds were consistent in aggression and feeding rate across the repeated trials, we calculated intra-class correlation coefficients (ICC, also called repeatability) from the male and female aggression models. As explained in (Dingemanse &

Dochtermann, 2013), the use of mixed-effect models allows researchers to calculate the between-individual variation (variance of the random intercept), within-individual variation (variance around each intercept), and individual repeatability. When variance among groups is high and variance within groups is low, within-group repeatability is high. When among group variance is low, and within group variance is high, it means within-group repeatability is low. In other words, observations within a group are no more similar to each other than they are to observations in other groups. For the repeatability value in this case, we are interested in the amount of the residual variation (total phenotypic variation minus variation explained by model fixed effects) that is attributable to between-individual differences. We used the "icc" command in the "performance" package (for the zero-inflated model; Ludecke et al., 2020), and the "rptPoisson" command in the "rptR" package (for the Poisson model; Stoffel et al., 2017) to calculate adjusted ICC, where the variance of the fixed effects is not included in the denominator term (Nakagawa et al., 2017).

Prediction 1.3: shy-type bluebirds will decrease feeding frequency the most in noisy conditions

To test whether personality type mediates feeding rate under noisy conditions, we included interaction terms of aggression score with speaker noise, and neophobia with speaker noise, in the feeding rate models. We used AICc model selection to determine if adding these interaction terms improved the likelihood of the model.

<u>Experiment 2: noise manipulation during settlement</u>

Prediction 2.1: shy-type bluebirds should be more likely to settle in the quiet control nest boxes

We tested for spatial sorting relative to noise based on personality type by calculating the average level of neophobia, aggression, and feeding rate for each bird across the four repeated trials. We then compared these average scores between birds that settled in the control and the noise-treated nest boxes using Kolmogorov-Smirnov tests or Wilcoxon rank sum tests depending on whether control and noise treatment groups had equivalent variance. Our sample size was not large enough to perform linear modeling for this experiment, so we assessed repeatability by comparing behavioral levels between the control and noise-treatment groups during each of the four trials separately. We used Spearman rank correlation tests to check for significant correlations between continuous variables. Three nests failed in the egg or nestling stage and the adults did not re-nest in the same box, and one male disappeared during the nestling stage, so we did not collect behavioral data for these birds. 11 birds that were sampled in 2019 returned and were included in the 2020 experiment

Prediction 2.2: no difference in the quality of birds that settle in control or noise-treatment nests

We compared the quality of the birds that nested in the control and noise-treatment nest boxes using settlement and egg-laying dates, age, and body condition. For our analysis of settlement timing and egg-laying, we included all birds that nested in experimental nest boxes during 2020. Not all partial nests were completed, so the sample size for prospected and partial nests is larger than the sample size for egg dates. We had a relatively small sample size for this experiment and could not be confident that the data were normally distributed, so we used unpaired Wilcoxon rank sum tests to compare the egg-date between control and noise groups. We compared the body condition index between groups using Wilcoxon tests, and visually checked the age distribution between control and noise-treatment nest boxes.

RESULTS

<u>Experiment 1: noise manipulation during nestling stage</u>

Prediction 1.1: bluebirds behave more cautiously under noisy conditions

Our traffic noise playback significantly increased the sound volume at noise treatment nest boxes compared with control nest boxes for the subset of nest boxes where we measured sound levels in 2019 (control mean dBA=49.9, sd=6.90, N=10; noise treatment mean dBA=69.95 sd=1.46, N=11; two-sample Kolmogorov-Smirnov test D=1, p<0.001). However, the speaker variable was not included as a main effect in the top models for aggression, (Table 2), neophobia (Table 3), or feeding rate (Appendix 4 Table A8). Some of the models including speaker as a main effect have similar AICc scores as the top performing model, but we followed the convention of

Table 1: Sample sizes for nestling stage experiment

Sex	Year	Treatment	Birds
Female	2019	Control	14
		Noise	13
	2020	Control	8
Male	2019	Control	15
		Noise	14
	2020	Control	9

Table 2: AICc tables for female and male aggression models. K is the number of parameters. All continuous covariates were scaled and centered before being added to the model, and interaction terms are indicated using a colon. The variable "tree swallow ID" is a categorical variable with 3 levels for the different tree swallow specimens. The variable "speaker" is a categorical variable for speaker playback on or off. "Treatment" is a categorical variable for control or noise treatment group. "Date" is calendar date. "BCI" is body condition index. "Neophobia" is approach latency in seconds. Total number of aggressive actions is the response variable, and all models are zero-inflated negative binomial with quadratic error structure and a log link, with bird ID as a random intercept.

AICc table for top models of female aggression

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	Cum.Wt
tree swallow ID	6	612.06	0.00	1.00	0.19	0.19
tree swallow ID + speaker	7	612.69	0.64	0.73	0.14	0.33
tree swallow ID + neophobia	7	613.12	1.06	0.59	0.11	0.45
tree swallow ID + time of day	7	613.24	1.18	0.55	0.11	0.56
tree swallow ID + treatment	7	613.76	1.71	0.43	0.08	0.64
tree swallow ID + date	7	613.93	1.87	0.39	0.08	0.71
tree swallow ID + nestling age	7	614.22	2.17	0.34	0.07	0.78
tree swallow ID + BCI	7	614.24	2.18	0.34	0.07	0.85
tree swallow ID + number of nestlings	7	614.25	2.19	0.33	0.06	0.91
tree swallow ID + speaker + neophobia + speaker:neophobia	9	615.50	3.44	0.18	0.03	0.94
tree swallow ID + speaker + date + speaker:date	9	615.91	3.85	0.15	0.03	0.97
intercept	4	616.01	3.96	0.14	0.03	1.00

AICc table for top models of male aggression

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	Cum.Wt
year	5	681.87	0.00	1.00	0.15	0.15
date	5	682.01	0.14	0.93	0.14	0.30
date + speaker + date:speaker	7	682.05	0.18	0.92	0.14	0.44
intercept	4	682.95	1.07	0.58	0.09	0.53

Table 3: AIC tables for female and male neophobia models. Model selection was done using penalized AIC, and values here are reported as number of AIC units better than the null model, where higher values indicate better models. All covariates were scaled and centered before being added to the model. "Age" is the age of the adult bluebird and is categorical of SY (second year) or ASY (after second year). Neophobia was modeled using mixed effect Cox proportional hazards models with bird ID as the grouping factor.

AIC table for top female neophobia models

Model	Integrated AIC	Penalized AIC
time of day + number of nestlings + age	12.95	22.34
time of day + number of nestlings	11.47	21.77
time of day + age	9.40	21.02
time of day	8.59	20.66
time of day + number of nestlings + age + speaker	10.95	20.57
age	8.82	19.71
number of nestlings	9.48	19.68
time of day + speaker	6.92	19.64
intercept	8.00	19.32

AIC table for top male neophobia models

Model formula	Integrated AIC	Penalized AIC
nestling age	7.67	19.78
treatment	5.83	19.74
intercept (band + object)	5.83	19.74

considering models that are within 2 delta AICc to be equally likely, and therefore we accept the most parsimonious model (fewest number of parameters) as the best performing model from the top ranked group. The models including speaker as a main effect are not the most parsimonious for any of the three behaviors. This means that overall, bluebirds in our population did not behave more cautiously under experimentally elevated noise conditions, and sound levels may not be correlated with bluebird perception of environmental risk level. Female aggression was best explained by tree swallow ID, and females were less aggressive towards tree swallow #3 than towards tree swallows #1 and #2 (Appendix 4, Table A5). None of the predictor variables that we tested explained male aggression any better than the null model (Appendix 4, Table A4). Female neophobia was best explained by time of day, and male neophobia was best explained by the neophobia object used for each trial (Appendix 4, Table A7).

Prediction 1. 2: bluebirds exhibit consistent bold-type and shy-type personalities

Our model selection showed that including bird ID (Band) as a random intercept term improved the model AIC values for all 3 behaviors for both sexes (Appendix 4, Tables A3, A7, A9), indicating that behavioral differences between individuals is important for explaining the total variation in behaviors. However, we did not find evidence for behavioral correlations forming bold-type and shy-type personalities. Neophobia and aggression were not correlated at the trial level (Spearman's rank correlation test: females S=410907, p=0.819; males S=567135, p=0.549), and neophobia approach latency was not included in the top ranked aggression models for males. Neophobia was a predictor in one of the top ranked models for female aggression, but the model including only tree swallow ID was more parsimonious (Table 3). Additionally, aggression was moderately repeatable within individuals for both sexes (Female ICC = 0.343, conditional R-squared = 0.460; male ICC = 0.339, conditional R-squared = 0.374), as was feeding rate (Female ICC on the scale of the data = 0.253, conditional R-squared = 0.376; male ICC on the data scale = 0.286, conditional R-squared = 0.324). These results indicate that while aggression, neophobia, and feeding rates do vary among individual bluebirds, and individuals are moderately consistent in their aggression and feeding behaviors, there is not a strong correlation between aggression and neophobia so we did not find support for the hypothesis that our population exhibits bold-type and shy-type personalities.

Prediction 1.3: shy-type bluebirds will decrease feeding frequency the most in noisy conditions

Our model selection for feeding rate showed that an interaction between aggression level and speaker playback was present in the top ranked model for females, but not for males (Appendix 4, Table A8) . Estimates from the top female model for the slope coefficients indicate that when speaker playback was present, females with higher aggression scores increased their feeding rate relative to ambient conditions (Table 4). Figure 1 shows the model estimated feeding rate across nestling ages for three females with different aggression levels. These predictions show that there was no difference in feeding rate among females under ambient conditions, but that when speaker playback was present, high-aggression females fed more frequently while low-aggression females did not change their feeding behavior relative to the control condition. These results are in the direction

Table 4: Model outputs and parameters for the two best models of female feeding rate. All covariates were scaled and centered. Models are Poisson generalized linear mixed effect models with a log link, number of nestlings as an offset term, and bird ID (Band) as a random intercept term.

Top model for female feeding rate

		Estimage	SE	p-value
Coefficients	Intercept	-0.405	0.076	<0.001
	nestling age	0.21	0.05	<0.001
	neo	-0.13	0.054	0.017
	agg:spk	0.246	0.095	0.01
Random intercept: Band		Variance: 0.0997		
Observations: 140		Levels of Band: 35		

Female feeding rate model with best AICc

		Estimate	SE	p-value
Coefficients	Intercept	-0.406	0.075	<0.001
	nestling age	0.204	0.05	<0.001
	neo	-0.148	0.055	0.007
	bci	0.0342	0.071	0.632
	neo:bci	0.102	0.048	0.034
	agg:spk	0.22	0.096	0.022
Random intercept: Band		Variance: 0.097		
Observations: 140		Levels of Band: 35		

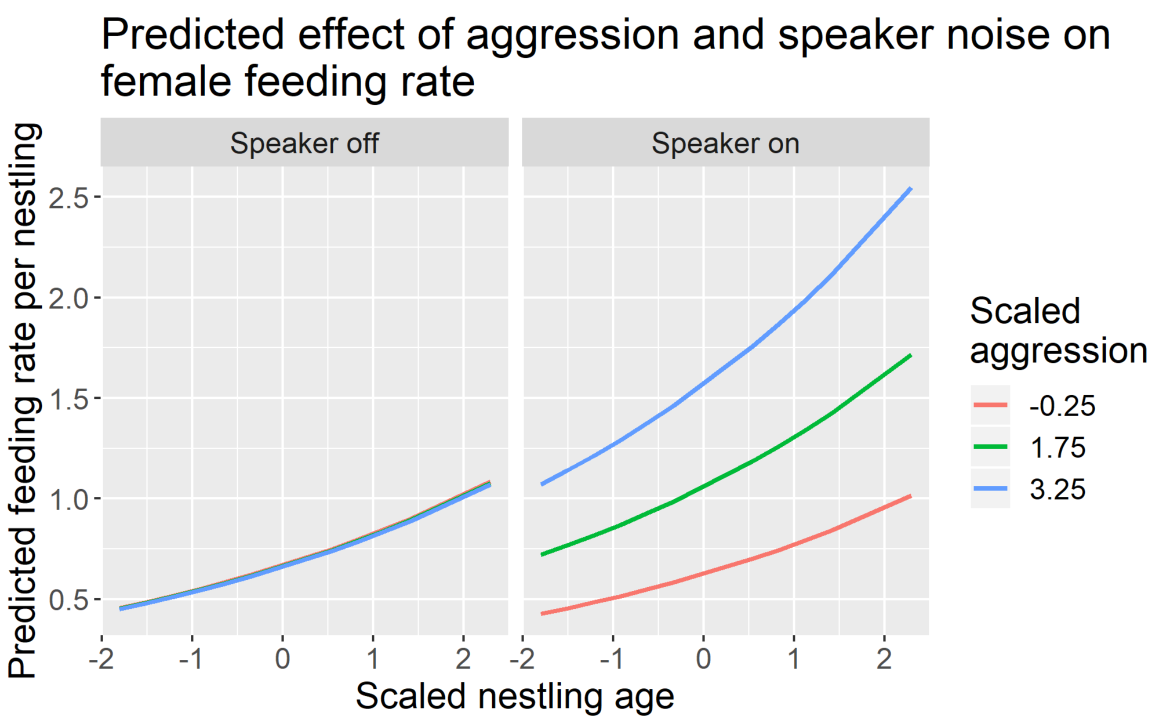

Figure 1: Females with higher aggression increase their feeding rate in the presence of experiment noise. Predictions are from the top performing feeding rate model, which is a generalized linear mixed-effect model with a Poisson distribution, number of nestlings as an offset, and a log link function. The additional model term of neophobia is held constant. (Scaled aggression values are the minimum, median, and maximum observed values for female aggression. In the left panel, feeding rate estimates are identical for the three aggression levels, so the three lines are stacked on top of each other.

we predicted, because low-aggression (more risk-averse) females showed lower feeding rates than high-aggression females (more risk-tolerant) under noisy conditions. However, our hypothesis that low-aggression females are more sensitive to the noise environment was not supported because low-aggression females did not alter their feeding behavior in the presence of our speaker playback. Male feeding rate was best explained by neophobia level, where more neophobic males fed less frequently (Appendix 4, Table A10).

Experiment 2: Noise manipulation during settlement

Prediction 2.1: shy-type bluebirds should be more likely to settle in the quiet control nest boxes

Our speaker playback in 2020 significantly increased the sound volume at noise-treatment nest boxes relative to controls during settlement (control mean dBA=50.5, sd=5.34, N=16 nest boxes; noise treatment mean dBA=69.9, sd=0.79, N=14 nest boxes; two-sample Kolmogorov-Smirnov test D=1, $p<0.001$). The sound levels were similar at control and noise-treatment nest boxes during 2020 behavioral observations, although noise-treatment nest boxes were slightly louder than the control nest boxes (control mean dBA=50.7, sd=5.64, N=7; noise treatment mean dBA=54.9, sd=2.9, N=7; Wilcoxon rank sum test W=12, $p=0.128$). Females that settled in the control nest boxes were more aggressive than the females that settled in noise-treatment nest boxes, although the difference in average aggression score was not statistically significant (Figure 2; two-sample Kolmogorov-Smirnov test D = 0.57143, p-value = 0.2032). Our sample size was too small to quantitatively test for repeatability within individual females, but a qualitative assessment of Figure 3 suggests that most females were consistent in their level of aggression across the four trials. We found no correlation between aggression score and the measured ambient sound level during the trial (Spearman rank correlation of log(aggression) vs.

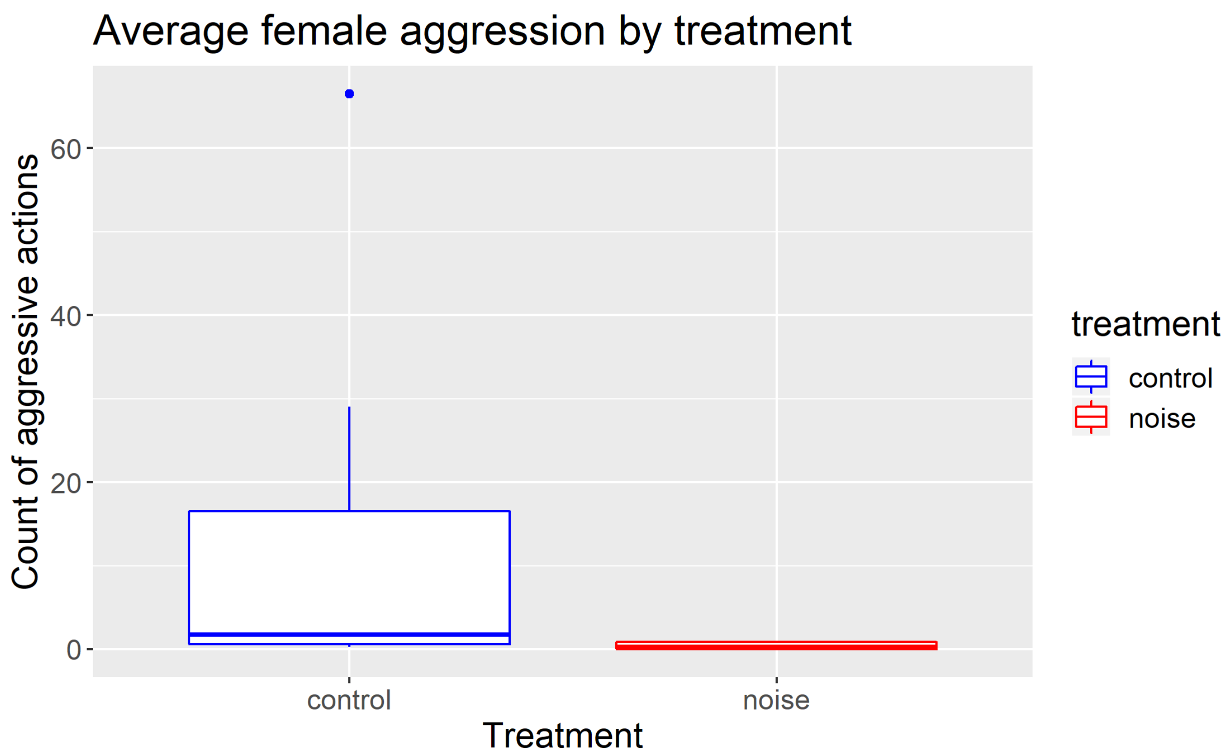

Figure 2: Females that settled in control nest boxes were more aggressive than females that settled in noise treatment nest boxes, but the difference between groups was not statistically significant (two-sample Kolmogorov-Smirnov test D = 0.57143, p-value = 0.2032). The average score for each female was calculated from four repeated measurements on nestling days 4, 6, 10, 12. Sample sizes control = 7, noise =7.

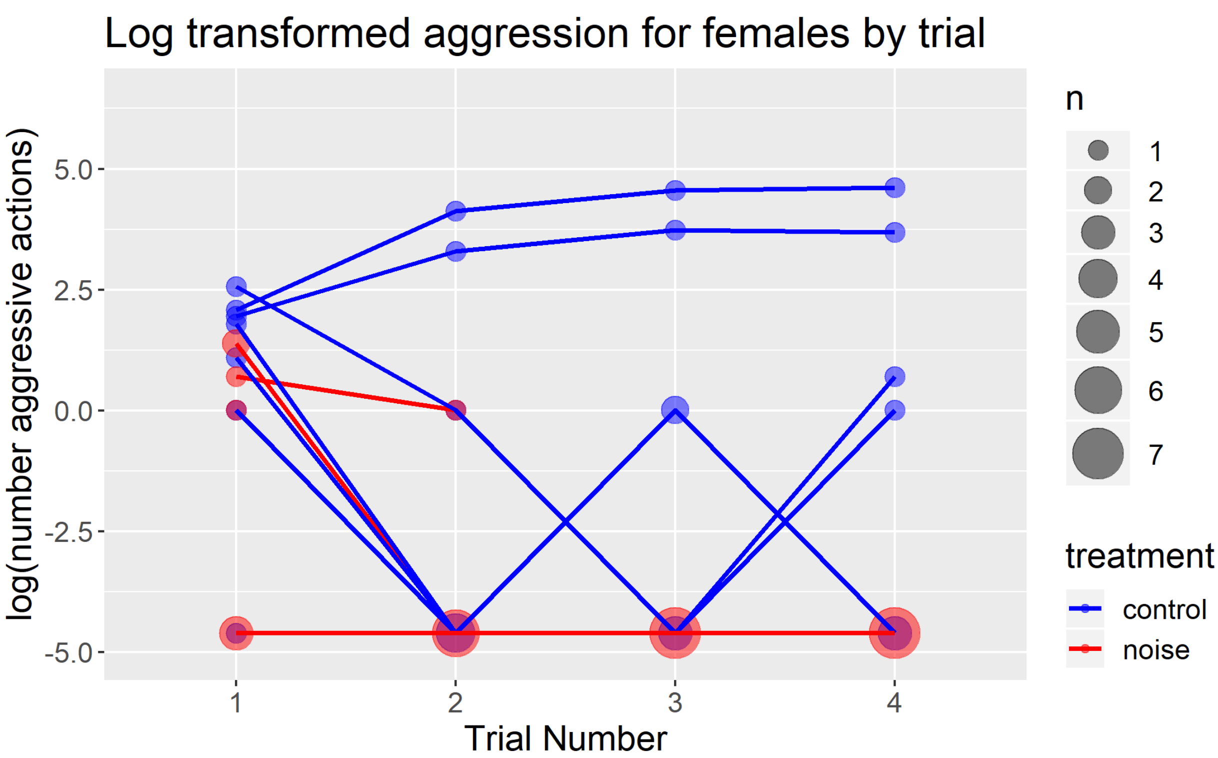

Figure 3: Aggression scores plotted across the four trials for each female. Lines connect measurements of the same female across the four trials. The size of the dots corresponds to the number of overlapping data points. The y-axis is log(count of aggressive actions to better show variation between individual females Most females in the noise-treatment group had consistently low aggression scores across the trials, while female in the control group had higher and more variable aggression scores.

ambient dB, rho=0.1375146, S=34250, p=0.2865). These results support our hypothesis that bluebirds spatially sort relative to noise based on personality traits, but they do not support our hypothesized mechanism of risk-averse (low aggression) birds sorting into the quieter nesting sites.

Prediction 2.2: no difference in the quality of birds that settle in control or noise-treatment nests

Our measures of male and female quality did not indicate substantial differences in the quality of bluebirds that settled in the control and noise treatment nests. When we compared the timing of nest-building and egg-laying between control and noise-treatment nest boxes, we saw a non-significant trend for females in the noise-treatment nest boxes to lay their first egg an average of four days later than the females in the control nest boxes (Figure 4 D). There was little difference in the timing of nest box prospecting and partial nest building by males in the two groups (Figure 4 A and B), but the pattern of delayed phenology became apparent in the

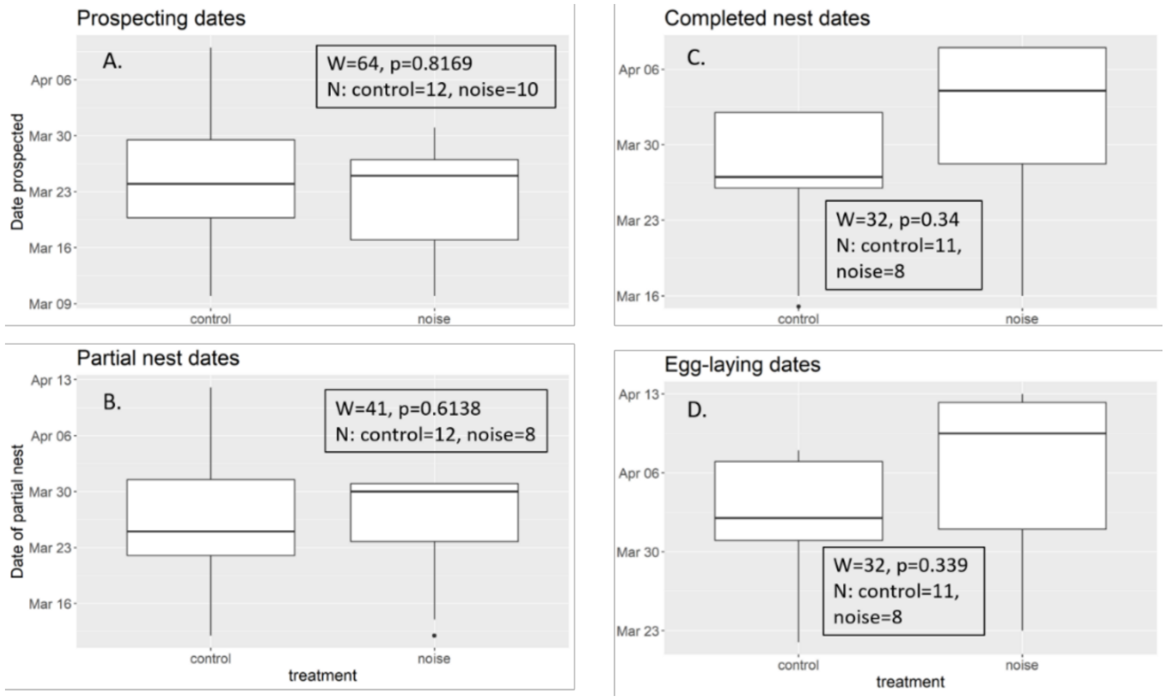

Figure 4: Dates for nesting phenology between control and noise treatment groups. Difference between groups was tested for each nesting stage using Wilcoxon rank sum tests. Prospecting date is the first date that nesting material was observed in the nest box. Partial nest date is the first date a full layer of nesting material was recorded. Completed nest is the first date a fully lined nest cup was recorded. Egg date is the date that the first egg of the clutch was laid.

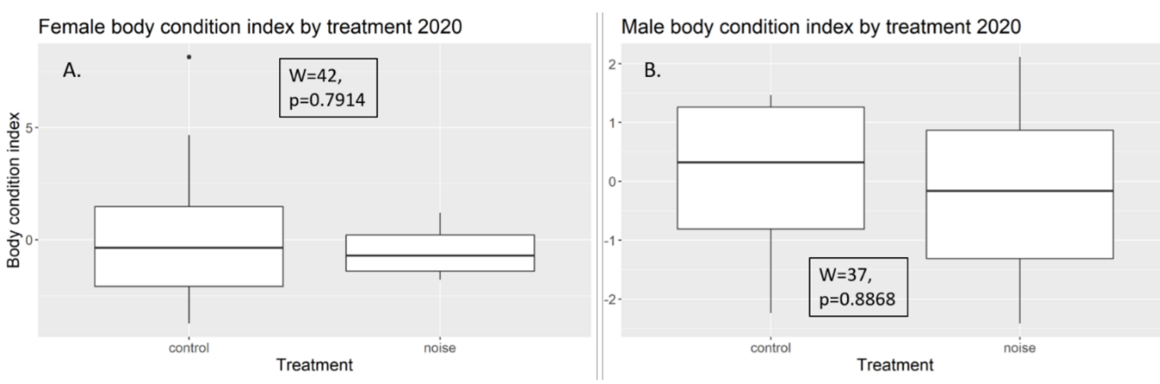

Figure 5: Female (A) and male (B) body condition index for control and noise treatment groups. Difference between groups was tested using a Wilcoxon rank sum test. Females control N=11, noise N=7. Males control N=10, noise=7.

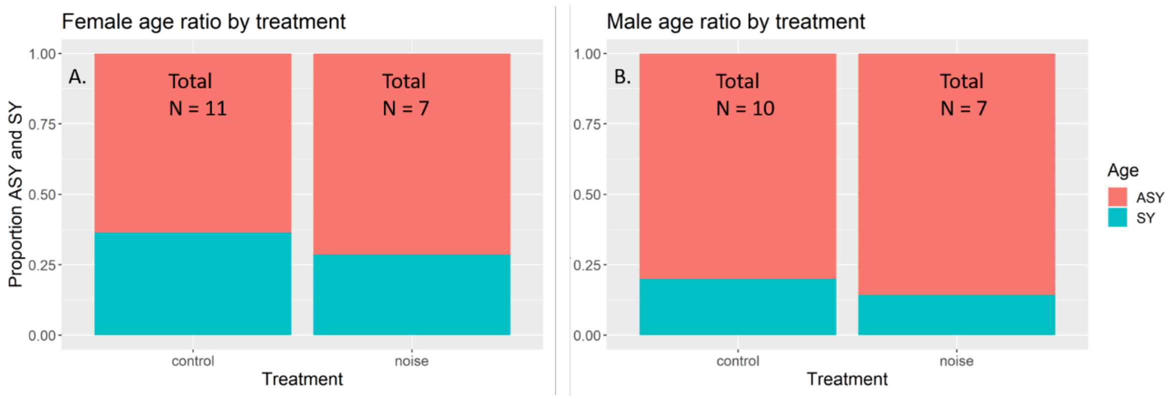

Figure 6: Female (A) and male (B) age distribution at control and noise treatment nest boxes in 2020.

timing of nest completion (Figure 3 C). There was a trend for more aggressive females to lay earlier, but it was not significant (Spearman's rank correlation: rho=-0.2354643, S = 691.86, p-value = 0.3982). There was no difference in female or male body condition between the control and noise treatment nest boxes (Figure 5; Wilcoxon rank sum test.). A visual comparison of the proportion of age classes in each treatment group suggest that there was also no difference in the ratios for either sex (Figure 6)

DISCUSSION

Eastern bluebirds in our study were moderately consistent in their expression of particular behavioral traits, meaning that birds who were more aggressive or neophobic or fed their nestlings more in one context also tended to respond in the same manner in another context. Interestingly, these behavioral consistencies were not altered by our introduction of road noise to nesting environments. The birds did not appear to consistently alter aggression, neophobia, nor feeding rates when presented with local road noise. This indicates that variation in these behaviors alone is unlikely to explain the previously reported reductions in reproductive output observed in noisier areas. Instead, female aggression level appears to mediate important breeding behaviors in noisy conditions. We found evidence that 1) low-aggression females were more likely than high-aggressive females to nest in noisy areas, 2) noise was associated with a delay in nest-building and egg-laying, and 3) low-aggression females exposed to noise when caring for young had lower feeding rates than noise-exposed females with high aggression. Taken together, these patterns suggest that low-aggression females are more negatively impacted by anthropogenic noise pollution than high-aggression females.

Despite the consistency in individual behavioral traits (i.e. personality), we did not find evidence for the existence of bold and shy personality types, or other patterns of covariation between neophobia and aggression (i.e. behavioral syndromes). When personality types exist, such behaviors would be negatively correlated such that individuals with low neophobia have high aggression. However, neophobia and aggression were not correlated at the trial level for either sex. These results are contrary to another study on eastern bluebird personality which reported a positive relationship between aggression and boldness when the two behaviors were measured on an ordinal scale (Pandit, 2017). The difference in our findings may be partially explained by difference in habitat. Other studies of bird personality have found that boldness and aggression were correlated in rural but not urban populations (Carrete & Tella, 2017; Scales et al., 2011). The bluebirds in this study were in a suburban habitat, and the selective pressures acting on aggression and boldness may be different from those in the agricultural setting of previous studies (Burtka & Grindstaff, 2013, 2015; Pandit, 2017). Further research on the behavioral traits of eastern bluebirds across different habitat types (gradient of urbanization, agriculture, and wildlands) would be useful for clarifying the specific ecological contexts which select for bold and shy personality types in eastern bluebirds.

Several of our findings support the idea that noise pollution does not impact all birds equally, and that behavioral traits can mediate the impact of noise pollution on local populations. We did not find an overall shift in the expression of neophobia, aggression, nor feeding rate in the presence of speaker-generated traffic sounds. This means that individual bluebirds vary in either their evaluation of noisy conditions (i.e. whether noisy areas are considered as more or less risky, or higher or lower quality), or their ability to modulate behaviors in response to noise (behavioral flexibility). Our results showed that variation in female bluebird responses to noise was correlated with individual aggression level. Aggressive females had a higher feeding rate than less-aggressive females under the noise treatment conditions, which suggests that less-aggressive females may pay a higher cost of inhabiting noisy areas. This finding is consistent with recent research on tree swallows which found that under experimental noise exposure, chicks of less-aggressive mothers were smaller than chicks of aggressive mothers (Fulk, 2020), but that study did not include a measure of feeding rate. Future studies that measure parental aggression, feeding rate, and nestling mass would help clarify whether chicks of less-aggressive females exposed to noise pollution are smaller because they receive less food. Previous studies on both western and eastern bluebirds found no correlation between aggression and rate of nestling provisioning (Burtka & Grindstaff, 2015; Duckworth, 2006c), but neither of these previous studies examined the additional effect of an environmental stressor. Aggression level might be a reflection of how much a female focuses her attention on the nest vs. other environmental stimuli, or could be related to reactivity and sensitivity to environmental cues (Koolhaas et al., 1999). Less-aggressive females could be more easily distracted by noise pollution(Chan et al., 2010), and the added drain on their attention might lead to poorer parental care. This type of subtle but important effect of noise pollution would be masked when only the population mean is evaluated, instead of the response to noise of individual birds.

An alternative explanation for why high-aggression females had higher feeding rates than low-aggression females is that high-aggression females were able to acquire higher quality territories with more food resources. In tree swallows, it has been experimentally shown that more aggressive females have a higher probability of claiming a nest box when the availability of nest sites is limited (Rosvall, 2008). In our study, territory quality would only be a confounding factor for the birds sampled in 2019, because in 2020 we manipulated the noise environment during settlement but not during behavioral observations. In the settlement experiment we found that aggressive females tended to settle in the quiet control nests, however the control and noise treatments were assigned randomly and should therefore be independent of actual territory quality relative to food resources. If aggressive females select territories solely based on food abundance, then we should not have seen this effect of spatial sorting by aggression level based on noise. Additionally, we might expect that high-aggression females would have higher feeding than low-aggression females under control as well as noise conditions if the difference was being driven primarily by food abundance, but this was not observed. It is possible that there is an optimal feeding rate which all females were able to attain under control conditions, and that foraging efficiency was impeded by noise pollution for all females. In this case, the effect of noise on feeding rate may only be visible for females with low quality territories because food is so abundant in high-quality territories that females are still easily able to find food even with the added stressor of noise pollution. In our statistical model, the influence of territory quality is lumped into the random effect of bird ID because birds are nested within territories. Separating the effects of territory quality and bird level characteristics would require observations of birds across multiple breeding attempts and likely multiple years. This was outside the scope of our study, but is an important area for future research as we continue to explore the ecological importance of individual personality in natural populations.

We should also note that while low-aggression females did not increase their feeding rate when exposed to experimental noise, it is unknown whether this effect impacted nestling mass, the rate of fledging, or probability of fledgling survival. Another study on eastern bluebirds found that male feeding rate was negatively correlated with the number of chicks fledged, while female feeding rate was not related to reproductive success (Burtka & Grindstaff, 2015). Just as we saw the relationship between aggression and feeding rate changed under experimental noise, it is also possible that noise pollution could change the relationship between feeding rate and nestling mass or fledging success. Research conducted in the same population of bluebirds as the current study found that an aggregate measure of nest box visitation rate and time spent in the nest box was positively correlated with brood survivorship and productivity (Kight &

Swaddle, 2007). In stonechats (*Saxicola torquata axillaris*), the relationship between feeding rate and nestling mass varied with supplemental feeding and the presence or absence of a shrike predator (Scheuerlein & Gwinner, 2006). The authors speculated that predator presence reduced the quality of food that parents delivered to their nestlings, and prey size was shown elsewhere to influence growth rate (Schwagmeyer & Mock, 2008). A study on tree swallows found the surprising result that feeding rate was influenced by an interaction between experimental noise exposure and nestling age, where noise-treated parents visited more frequently than control parents when nestlings were older (Injaian, Taff, et al., 2018). That study also found that noise-exposed nestlings were smaller and had higher stress levels than control nestlings, so the effect of noise pollution on the relationship between feeding rate and offspring health remains unclear. Personality type may influence prey selectivity (Exnerova et al., 2010), and further research is needed to determine whether aggression levels are associated with prey item quality in songbirds foraging under optimal and stressful conditions.

When we manipulated the sound environment during bluebird settlement, nest-building, and egg-laying, we saw a trend for females that settled in control nest boxes to have higher levels of aggression than females that settled in noise treatment nest boxes. We believe that this pattern of spatial sorting was most likely caused by competitive exclusion rather than behavioral plasticity or habitat-trait matching. The ambient sound levels were similar between control and noise treatment nest boxes during behavioral observations, and there was no correlation between the background sound levels during the observation and female aggression scores. These facts, along with our findings that noise manipulation did not influence aggression levels during the nestling stage, allows us to rule out the possibility of behavioral plasticity. Habitat-trait matching is also an unlikely explanation for the pattern because less-aggressive females seem to perform more poorly in noise than they would under quiet conditions. We found that less-aggressive females reduced their feeding rate in noise, and we also saw a trend towards delayed egg-laying at the noise-treated nest boxes in our settlement experiment. An earlier first egg-date is correlated with overall higher breeding success in bluebirds and other species (McKellar et al., 2013; Pinkowski, 1974), so a delay in egg-laying is likely to reduce fitness. Finally, it is logical to assume that females which showed high aggression towards a model tree swallow would also show high aggression towards conspecific competitors during territory establishment and defense. Eastern bluebird females are known to attack other females during the nest-building and egg-laying stage, which likely functions to protect the nest-site and discourage extra-pair copulations (Gowaty, 1981; Gowaty & Wagner, 1988).

One alternative explanation for the spatial patterning of female aggression level is that female aggression is influenced by mate or territory quality, rather than being an intrinsic female trait. Female behaviors like mate choice and extra-pair copulations are undoubtedly influenced by male quality, but it is unclear whether mate and territory quality should determine the intensity of female nest defense. Female aggression and singing behavior are receiving more attention in recent research, but the evidence for a relationship between female aggression and territory quality is mixed. Territory quality was positively correlated with female song output during duet singing in a tropical species (Diniz et al., 2019), but female superb fairy-wrens (*Malurus cyaneus*) that responded more aggressively to a model female intruder occupied lower quality territories (Cain & Langmore, 2016). While it is possible that the noise treatment during settlement initially influenced female perception of mate and territory quality, we think it is unlikely that female nest defense aggression was determined only by this first impression.

We have argued that spatial sorting of bluebirds with varying levels of aggression into quiet and noisy areas is caused by competitive exclusion. If this is true, quiet territories are preferred by all bluebirds and we would expect to see that control nest boxes have higher occupancy rates, are settled earlier, and are occupied by birds of higher quality. We found no differences in the occupancy rate between control and noise nest boxes, but our ability to detect a noise effect was likely hampered by a limited sample size, and the fact that we were unable to include all nest boxes at each site in our experimental manipulation. At Newport News Park and

York River State Park, we were only able to include between on quarter and one third of the total nest boxes due to limited equipment and personnel. This means that even if a pair of bluebirds was deterred from nesting in a noise-treated nest box, there was a higher probability of them choosing a non-experimental nest box instead of a control nest box, simply by virtue of their relative abundance. We did note three anecdotal examples of bluebird pairs choosing control nest boxes over noise nest boxes when both options were present within a single territory. It is also possible that our occupancy rate was influenced by the nesting history and site fidelity of pairs from the previous year. Eastern bluebirds have high site fidelity, and a recent study found that 77% of birds that returned between years used the exact same nest box as the previous year (Coss et al., 2019). Nest site occupancy is also influenced by interspecific competition with tree swallows (Jones et al., 2014), but it is currently unknown how physical habitat quality, intensity of competition, and nesting history interact to influence the settlement decisions of individual bluebirds.

We found no difference in the timing of nest box prospecting by males (as measured by the date when nesting material was first added to the nest box), and this was consistent with results in tree swallows where experimental noise did not significantly delay the timing of male settlement (Injaian, Poon, et al., 2018). In our case, this may have been because males acquire and defend the whole territory, while females decide which specific nest site to use within the territory (Pinkowski, 1974). Our noise treatment was localized at the nest box, and females may be more sensitive than males to nest box-specific characteristics. The pattern of delayed egg-laying at noise-treated nest boxes could be correlated with the timing of female settlement, and therefore be an indicator of territory quality. However, egg-date and settlement date were not correlated in female tree swallows (Stutchbury & Robertson, 1987). In addition, it is common for eastern bluebirds to already be paired with their mate when they arrive on the breeding grounds (Pinkowski, 1974) so there may not be a meaningful difference in male and female settlement dates. Body condition and age can also be correlated with quality and egg-date (Pinkowski, 1977), but we also found no difference in either of these variables for males or females. This indicates that the observed delay in egg-laying was not caused by lower quality females sorting into noise-treated nest boxes.

Rather, it seems most likely that noise had a direct effect on the timing of egg-laying by prolonging the nest building process. We saw that the difference in nesting phenology became apparent between the partial nest and completed nest stages, but there was no added delay in the time between nest completion and laying of the first egg. We speculate that noise caused female bluebirds to be more cautious and hesitant when entering the nest box to add nesting material. It is common for both male and female bluebirds to spend several seconds perched at the entrance of the nest box before going inside. Presumably birds are assessing the safety of entering during this pause. If females in noisy conditions take longer pauses each time they bring nesting material, this could add up to delayed nest completion. Alternatively, females in the noise treated nest boxes may have been slower to begin nest building if they perceived the noisy nest cavity to be less preferred. Females may have spent more time evaluating other possible nesting sites before deciding to build a full nest in the noisy nest box.

The differences in nest site selection and parental care behaviors in noise that we documented between high-aggression and low-aggression females likely impact female fitness. A low-aggression female is more likely to experience chronic noise pollution during breeding, and she is more likely to suffer negative consequences of noise through delayed egg-laying and a reduction in nestling feeding rate. Delayed egg-laying may limit the total number of clutches a pair can raise in a single breeding season, and the later in the season that chicks fledge, the lower their chances of recruiting into the population (Verboven & Visser, 1998). Pinkowski (1974) reported that eastern bluebirds breeding in New York attempted second clutches if the first egg of their first clutch was laid by approximately 14 May, and a delay of four days would be enough to move a pair from the early window where they are likely to raise a second clutch, to the intermediate window where they are likely to attempt only a single clutch in the season. This means that the pattern of delayed egg-laying that we observed in response to noise pollution could cause a pair of bluebirds to produce only one half the number of fledglings as another pair in a quiet area. Furthermore, fledging rate of chicks raised in noise may be reduced due to lower feeding rates by females and a subsequent poorer body condition of chicks. The previously observed disparity in reproductive output between bluebirds in noisy and quiet areas was likely driven by low-aggression females in the population. We did not directly measure nestling body condition nor season-long reproductive output in this study, and more research is needed to establish a direct connection between aggression, noise level, and breeding success.

In addition to direct impacts on reproduction, we showed that noise pollution influenced the spatial structure of the bluebird population. Here we provide evidence that behavioral differences between bluebirds in noisy and quiet areas are caused by spatial sorting of female bluebirds based on intrinsic aggression levels. While several other researchers have suggested spatial sorting of individuals as a mechanism for population-level differences in behavior (Arroyo et al., 2017; Holtmann et al., 2017; Sprau & Dingemanse, 2017; Stansell, 2018), the current study is one of the first to provide experimental evidence for this mechanism. This effect alone could lead to important changes in species interactions (Moran et al., 2017; Winandy & Denoël, 2015) , disease dynamics (Found, 2017), gene flow and local adaptation (Edelaar et al., 2008). A study on western bluebirds found that aggressive males acquired territories more often in open habitat and experienced stronger selection for long tails and tarsi which are advantageous for aerial foraging in those habitats (Duckworth, 2006a). In our population of bluebirds, low-aggression females could experience stronger selection for traits associated with noise tolerance, or tolerance of environmental characteristics that are associated with noise such as human activity, novel food sources, or chemical pollution.

Our findings have important implications for conservation and management of eastern bluebirds and other suburban songbirds. In order to maintain high levels of behavioral diversity (which is underpinned by genetic diversity) in bluebird populations, managers should limit the amount of breeding habitat that is impacted by chronic anthropogenic noise pollution. This includes erecting new nest boxes in quiet areas, preventing human development near existing quiet breeding habitat, and mitigating the amount of noise pollution in already impacted habitat by planting vegetation buffers or installing barriers along highways to reduce noise pollution. Furthermore, the fact that we documented aggression-mediated spatial sorting and parental care in eastern bluebirds exposed to noise suggests that these mechanisms may be relevant for other species as well. It is important that we continue to consider the subtle but meaningful ways that individual-level variation in sensitivity to noise pollution may be shaping the evolution and overall success of wildlife populations.

APPENDICIES

APPENDIX 1

Figure A1: Types of nest boxes. Dimensions given as (height x width x depth in inches). Images A and B are of Carl Little box style (13.5 x 4 x 5) with baffle and wire Nole guard, photos by HVK. Image C. North American Bluebird Society box style (10 x 6 x 6.75). Image D. Peterson box style (17.5in x 3.5in x 7in). Image E 2-hole Mansion style (13in x 7.25 x 5.5in). Images C - E from http://www.nestboxbuilder.com/nestbox-plans.html

APPENDIX 2:

Site jurisdiction and nest box GPS coordinates

Focal nest boxes were located in the following parks (jurisdiction in parentheses, plus 4-letter abbreviation): Chickahominy Waterfront Park (James City County CHIC,), Veteran's Park (James City County, VETS), New Quarter Park (York County, NQPK), York River State Park (State of Virginia, YRSP), Newport News Park (City of Newport News, NNPK), and the Colonial Parkway at College Creek (National Park Service, NPSC).

Table A1: Details of nest boxes included in 2019 and 2020 experiments

Box code	Lat	Lon	Years	Box type	Nole guard	Baffle
CHIC-01	37.267056	-76.872854	2019	NABS	yes	yes
CHIC-02	37.266922	-76.874085	2019	2-hole	no	yes
CHIC-10	37.265761	-76.868064	2019	NABS	yes	yes
CHIC-12	37.265163	-76.869686	2019	NABS	yes	yes
CHIC-15	37.265389	-76.871314	2019	2-hole	no	yes
NNPK-02	37.179485	-76.550631	both	NABS	yes	yes
NNPK-03	37.178549	-76.550681	2020	NABS	yes	yes
NNPK-04	37.177997	-76.549952	both	NABS	yes	yes
NNPK-06	37.176934	-76.548895	both	NABS	yes	yes
NNPK-08	37.176939	-76.548237	2019	NABS	yes	yes
NNPK-13	37.17617	-76.545985	both	NABS	yes	yes
NNPK-14A	37.176052	-76.54422	2019	NABS	yes	yes
NNPK-14	37.176487	-76.545025	2020	NABS	yes	yes
NNPK-15	37.176569	-76.544141	2020	NABS	yes	yes
NNPK-16	37.176902	-76.543205	2019	NABS	yes	yes
NNPK-20	37.177554	-76.545289	both	NABS	yes	yes
NNPK-21	37.177202	-76.546799	2020	Carl Little	yes	yes
NNPK-25	37.180112	-76.54945	2019	NABS	yes	yes
NNPK-29	37.180968	-76.537196	2019	NABS	yes	yes
NNPK-35	37.180139	-76.548245	2020	NABS	yes	yes
NPSC-01	37.223276	-76.696142	2019	Carl Little	yes	yes
NQPK-01	37.282686	-76.651033	both	Carl Little	yes	yes
NQPK-02	37.283562	-76.651134	2020	Carl Little	yes	yes
NQPK-04	37.286376	-76.649166	2020	Peterson	no	yes
NQPK-05	37.287856	-76.649267	2019	NABS	yes	yes
NQPK-06	37.28867	-76.648227	2020	Carl Little	yes	yes
NQPK-07	37.289582	-76.647969	both	Carl Little	yes	yes
NQPK-08	37.290109	-76.646638	both	Carl Little	yes	yes
NQPK-09	37.29098	-76.646643	2020	Carl Little	yes	yes
NQPK-12	37.295522	-76.644617	2020	Carl Little	yes	yes
NQPK-15	37.295639	-76.638541	2020	Carl Little	yes	yes
NQPK-16	37.295219	-76.634606	2020	NABS	yes	yes
NQPK-17	37.296358	-76.633492	2020	NABS	yes	yes
VETS-03	37.26694	-76.759555	2019	Carl Little	yes	yes
VETS-05	37.268884	-76.76008	2019	Carl Little	yes	yes
YRSP-01	37.298946	-76.731775	both	NABS	yes	yes
YRSP-02	37.298946	-76.731775	both	NABS	yes	yes
YRSP-03	37.393884	-76.725827	2020	NABS	yes	yes
YRSP-06	37.401937	-76.718334	2019	NABS	yes	yes
YRSP-10	37.403277	-76.718052	2020	NABS	yes	yes
YRSP-13	37.407589	-76.71691	2020	NABS	yes	yes
YRSP-17	37.411551	-76.714045	2020	NABS	yes	yes
YRSP-18	37.411876	-76.714378	both	NABS	yes	yes
YRSP-19	37.412864	-76.714124	2019	NABS	yes	yes
YRSP-24	37.41409	-76.712274	2019	NABS	yes	yes
YRSP-26	37.413681	-76.712019	2020	NABS	yes	yes
YRSP-37	37.401595	-76.717089	2019	NABS	yes	yes
YRSP-38	37.402198	-76.716648	2020	NABS	yes	yes

APPENDIX 3:

Further details about experimental nest box selection and treatment assignment in 2020.

For each site separately, we calculated the median egg-laying date for first clutches for each year. First clutches were assumed to be laid prior to 5 May each year. For each nest box, we calculated the difference in days between the site-level median and the egg-laying date for that specific nest box. This was done to standardize between years in case all birds initiated egg-laying earlier or later in a particular year due to local weather differences. For each nest box we summarized by calculating the median of this difference across the 5 years, the standard deviation of the difference, and the proportion of years the nest box was occupied. This allowed us to determine which nest boxes at each site were occupied more frequently, and if they were consistently occupied earlier or later than the "average" nest box at that particular site. Nest boxes with similar occupancy rates and timing of egg-laying were paired together. Paired boxes differed in timing of nesting by no more than 3 days, and differed in occupancy rate by no more than 0.2. We determined control and

Table A2: Details of 2020 experimental nest boxes and nesting history

Box code	Experimental treatment	2020 pairs	Years of data	Occupancy rate	2020 occupancy	average days before or after site median
NNPK-03	noise	A	5	0.40	1	-6.00
NNPK-15	control	A	5	0.40	0	-9.00
NNPK-02	noise	B	5	0.60	0	2.00
NNPK-04	control	B	5	0.80	1	-1.00
NNPK-06	noise	C	5	0.40	1	3.00
NNPK-35	control	C	5	0.40	0	3.50
NNPK-13	control	D	5	0.60	1	3.33
NNPK-14	noise	D	5	0.40	0	4.00
NNPK-20	noise	E	5	0.40	0	8.00
NNPK-21	control	E	5	0.40	0	5.00
NQPK-02	noise	F	5	0.40	0	-4.50
NQPK-17	control	F	5	0.40	1	-5.50
NQPK-06	control	G	5	1.00	1	-2.40
NQPK-15	noise	G	5	0.80	0	-0.63
NQPK-01	noise	H	5	0.60	1	-2.33
NQPK-12	control	H	5	0.40	1	-0.50
NQPK-04	control	I	5	0.40	1	0.50
NQPK-08	noise	I	5	0.40	1	1.00
NQPK-07	noise	J	5	0.40	1	4.50
NQPK-09	control	J	5	0.40	1	5.00
YRSP-01	noise	K	6	0.83	1	-6.40
YRSP-38	control	K	6	0.17	0	3.00
YRSP-10	control	L	6	0.67	1	-0.88
YRSP-26	noise	L	6	0.17	1	-1.00
YRSP-03	noise	M	6	0.33	0	1.00
YRSP-18	noise	M	6	0.33	0	1.00
YRSP-13	noise	N	6	0.33	1	1.50
YRSP-02	control	N	6	0.33	1	1.25
NQPK-16	control	none	NA	NA	1	NA
YRSP-17	control	none	6	0.33	1	7.00

noise treatments by a coin flip, with one nest box within a pair randomly assigned to control and the other to noise.

<u>Details of speaker set-up:</u>

At each experimental nest box, we installed a 48-inch steel fence post (Grainger, Lake Forest, IL) 3m in front of the nest box, and mounted a metal housing box on top of the post at a height of approximately 1m. This lockable housing served to protect speakers from rain and vandalism, and also ensured that conditions were the same, but for noise, for the control treatment nest boxes. Approximately half of the nest boxes received silent control housing (empty) and half received noise treatment housings (Figure 1). The metal housing box was a modified cash box (Master Lock, Oat Creek, WI) with holes drilled

Figure A2: Experimental speaker housing. A. External view B. Internal view

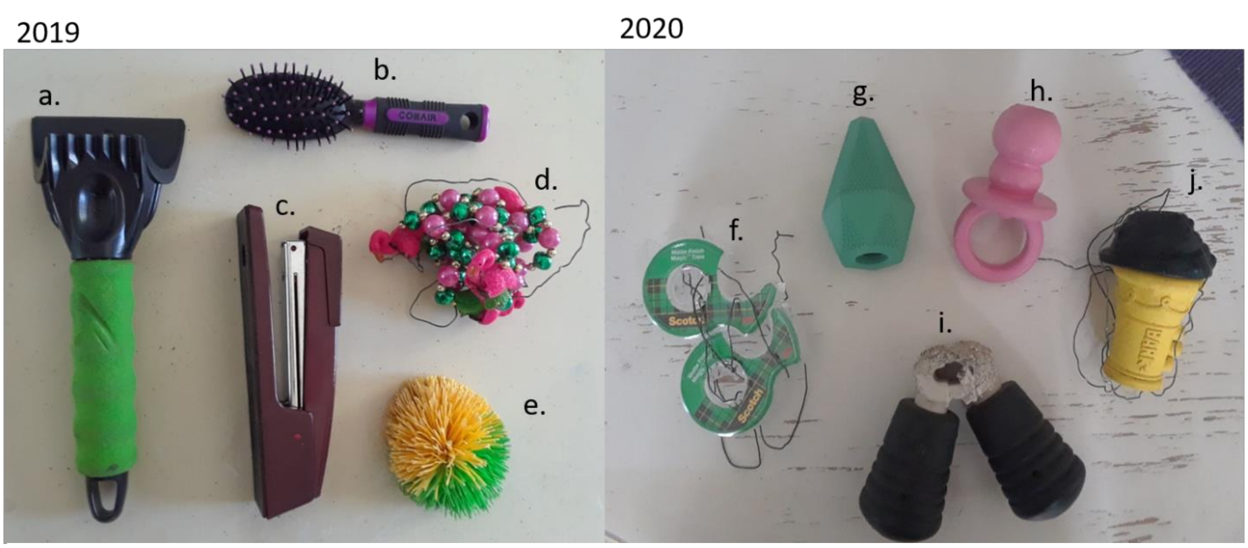

Figure A3: Objects used for neophobia trials. a) ice scraper, b) brush, c) stapler, d) necklace, e) koosh ball, f) tape, g) torpedo toy, h) binky toy, i) grippy toy, j) horn toy.

in the front to allow the speaker noise to escape. We positioned housing boxes so the side with the holes was facing towards the entrance of the nest box. Control and noise-treatment housing boxes were identical on the exterior. Noise-treatment housings contained a small waterproof speaker (VTIN Technology Company Ltd., Hong Kong, HK) connected to an mp3 player (Eleston/Ruizu, Shenzhen, China) and a large USB battery pack (Anker Innovations, Shenzhen, China). Both speaker and mp3 were charged by the battery pack, and the battery pack also powered a USB light (Xaimen Sinywon Innovation Industrial Co. Ltd, Xaimen, China) covered with black tape. The purpose of the light was to provide a constant load for the battery pack to prevent it from automatically turning off.

In 2019 we measured the ambient sound levels at control nest boxes (median number of samples per nest=1, maximum=4) and speaker-generated sound levels at noise-treatment nest boxes (median samples per nest=4, maximum=5) during the nestling stage. In 2020, we systematically measured both ambient and speaker-generated sound levels beginning on 24 February (the date of initiation of the experimental sound treatments), and measurements were taken at each nest box every 2 to 4 days until behavioral observations were completed (median number of measurements per nest box = 20, range 6-29). From these measurements, we determined the average volume at control and noise-treatment nest boxes, as well as the change in volume caused by the noise-treatment. Sound measurements were taken with a hand-held sound meter that displayed the real-time dB level and updated approximately every second. The initial dB was recorded, and then the reading on the screen was photographed every 10 seconds for a full minute, resulting in 7 readings total. We averaged the 7 decibel readings for each nest box from each day to get a single sound intensity measure for that day. We then averaged these daily metrics for each box across the course of the study period.

We created the playlists used for the speaker playback from traffic noise clips and silent tracks. We obtained a 45 second clip of urban traffic noise from http://soundbible.com/641-Urban-Traffic.html and then edited the clip using the program Praat (Boersman & Weenick, 2019). One-hour silence tracks were created using a file obtained from https://bigsoundbank.com/detail-0917-one-minute-of-silence.html.

APPENDIX 4:

Supplemental results

Aggression

Table A3: AICc tables for female and male aggression models, comparing different model forms. K is the number of parameters. Models with less than 2 delta AICc difference are considered equally likely. For both sexes, the zero-inflated negative binomial model with Band as a random effect was the best performing, so this model form was carried forward to test additional covariates. The full model here has predictor variables: treatment + nestlings + nestling age + time of day + date + tree swallow ID + Age + BIC.

AICc table for female aggression models comparing distributions

Model	Random intercept	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
zero-inflated negative binomial	Band	4	616.01	0.00	1.00	0.88	-303.86	0.88
negative binomial with quadratic errors	Band	3	620.92	4.90	0.09	0.08	-307.37	0.96
negative binomial with quadratic errors	Band nested in site	4	623.04	7.02	0.03	0.03	-307.37	0.99
negative binomial with linear errors	Band	3	625.48	9.47	0.01	0.01	-309.65	0.99
full	Band	15	627.28	11.26	0.00	0.00	-296.70	1.00
negative binomial with linear errors	Band nested in site	4	627.60	11.59	0.00	0.00	-309.65	1.00
Poisson	Band	3	630.17	14.16	0.00	0.00	-312.00	1.00
Poisson	Band nested in site	4	632.29	16.28	0.00	0.00	-312.00	1.00
negative binomial with linear errors	(none)	2	635.23	19.21	0.00	0.00	-315.57	1.00

AICc table for male aggression models comparing distributions

Model	Random intercept	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
zero-inflated negative binomial	Band	4	616.01	0.00	1.00	0.88	-303.86	0.88
negative binomial with quadratic errors	Band	3	620.92	4.90	0.09	0.08	-307.37	0.96
negative binomial withquadratic errors	Band nested in site	4	623.04	7.02	0.03	0.03	-307.37	0.99
negative binomial with linear errors	Band	3	625.48	9.47	0.01	0.01	-309.65	0.99
full model	Band	15	627.28	11.26	0.00	0.00	-296.70	1.00
negative binomial with linear errors	Band nested in site	4	627.60	11.59	0.00	0.00	-309.65	1.00
Poisson	Band	3	630.17	14.16	0.00	0.00	-312.00	1.00
Poisson	Band nested in site	4	632.29	16.28	0.00	0.00	-312.00	1.00
negative binomial withlinear errors	(none)	2	635.23	19.21	0.00	0.00	-315.57	1.00

Table A4: AICc tables comparing univariate models for female and male aggression. All models are zero-inflated negative binomial generalized linear mixed effect models with Band as a random intercept and a log link. Models with AICc of at least 2 units less than the intercept only model were carried forward for multivariate model selection.

AICc table of univariate models for female aggression

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
tree swallow ID	6	612.06	0.00	1.00	0.55	-299.71	0.55
intercept only	4	616.01	3.96	0.14	0.08	-303.86	0.62
date	5	616.24	4.18	0.12	0.07	-302.90	0.69
neophobia	5	616.69	4.63	0.10	0.05	-303.12	0.74
number of nestlings	5	616.79	4.74	0.09	0.05	-303.17	0.79
time of day	5	616.95	4.90	0.09	0.05	-303.25	0.84
speaker	5	617.10	5.04	0.08	0.04	-303.33	0.89
trial type (before/after)	5	617.78	5.73	0.06	0.03	-303.67	0.92
BCI	5	617.89	5.84	0.05	0.03	-303.72	0.95
nestling age	5	618.00	5.94	0.05	0.03	-303.78	0.97
treatment (control/noise)	5	618.16	6.10	0.05	0.03	-303.86	1.00

AICc table for univariate male aggression models

Predictor variables	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
date	5	682.01	0.00	1.00	0.24	-335.79	0.24
intercept only	4	682.95	0.94	0.63	0.15	-337.33	0.39
speaker	5	683.92	1.91	0.38	0.09	-336.75	0.48
trial type (before/after)	5	683.95	1.94	0.38	0.09	-336.76	0.57
neophobia	5	684.05	2.04	0.36	0.09	-336.81	0.66
treatment (control/noise)	5	684.11	2.10	0.35	0.08	-336.85	0.74
nestling age	5	684.28	2.27	0.32	0.08	-336.93	0.82
BCI	5	685.05	3.04	0.22	0.05	-337.31	0.87
time of day	5	685.06	3.05	0.22	0.05	-337.32	0.92
number of nestlings	5	685.08	3.07	0.22	0.05	-337.33	0.97
tree swallow ID	6	686.46	4.45	0.11	0.03	-336.93	1.00

Table A5: Model output and parameter estimates for the top model of female aggression. The model form is a zero-inflated negative binomial with quadratic error structure and a log link.

Top aggression model for females		Estimate	SE	p-value
Coefficients	Intercept	1.89	0.382	7.57E-07
	tree swallow #2	0.052	0.466	9.12E-01
	tree swallow #3	-2.609	0.909	0.004
Zero-inflation	Intercept	-0.168	0.223	0.451
Random intercept: Band	Variance: 1.127			
Observations: 140	Levels of Band: 35	Overdispersion parameter: 1.53		

Table A6: Model output and parameter estimates for the top model of female aggression. The model form is a zero-inflated negative binomial with quadratic error structure and a log link.

Top model for male aggression		Estimate	SE	p-value
Coefficients	Intercept	1.985	0.2846	3.09E-12
	year 2020	-1.03	0.549	0.061
Zero-inflation	Intercept	-0.328	0.246	0.184
Random intercept: Band		Variance: 1.181		
Observations: 148	Levels of Band: 37		Overdispersion: 1.2	

Neophobia

Table A7: AIC table for intercept and univariate neophobia models for females and males. Neophobia was modeled using mixed-effect Cox proportional hazards models with Band as the grouping factor. Model comparison was done using penalized AIC, and values reported here are in units better than the null model, so higher values indicate a better performing model

AIC table for univariate and intercept models of female neophobia

Model	**Integrated AIC**	**Penalized AIC**
time of day	8.59	20.66
age	8.82	19.71
number of nestlings	9.48	19.68
intercept (band)	8.00	19.32
intercept (band + object)	5.99	19.30
BCI	6.00	18.50
treatment	6.00	18.48
speaker	6.42	18.40
nestling age	6.00	17.39
intercept (object)	-2.00	-0.01

AIC table for male neophobia models

Model	**Integrated AIC**	**Penalized AIC**
nestling age	7.67	19.78
intercept (band + object)	5.83	19.74
treatment	5.83	19.74
number of nestlings	5.26	19.52
speaker	6.28	19.40
date	3.03	19.03
time of day	3.93	18.85
intercept (band)	7.40	18.06
time of day + speaker	3.31	17.99
age	3.83	17.79
time of day + speaker + time of day:speaker	1.34	16.13
intercept (object)	-1.98	0.03

Table A8: AICc table for female feeding rate models. All covariates were scaled and centered before being added to the model. Variables are: "nestling age" in days; "neophobia" approach latency in seconds during neophobia trial; "BCI" body condition index; "speaker" categorical variable for traffic noise speaker playback off or on; "aggression" is total number of aggressive actions; "weight" is individual body mass in grams; "treatment" is control or noise treatment group; "year" is categorical with levels 2019 and 2020. Interaction terms are indicated with a colon. K is the number of model parameters. Response variable is the count of female feeding visits, and all models are Poisson distributions with log link, number of nestlings as an offset term, and bird ID (Band) as a random intercept

AICc table for top female feeding rate models

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	Cum.Wt
nestling age + neophobia + BCI + neophobia:BCI + aggression:speaker	8	557	0.00	1.00	0.18	0.18
nestling age + neophobia + aggression:speaker	6	557	0.06	0.97	0.17	0.35
nestling age + neophobia + BCI + neophobia:BCI	6	557.2	0.23	0.89	0.16	0.51
nestling age + neophobia + speaker + neophobia:speaker + aggression	7	558.6	1.62	0.45	0.08	0.59
nestling age + neophobia + aggression:speaker + weight	7	559	2.07	0.35	0.06	0.66
nestling age + neophobia + aggression	5	559.3	2.33	0.31	0.06	0.71
nestling age + speaker + neophobia + BCI + neophobia:BCI + aggression	8	559.4	2.46	0.29	0.05	0.76
nestling age + neophobia:BCI + aggression:speaker	6	559.6	2.62	0.27	0.05	0.81
nestling age + BCI + speaker + BCI:speaker + neophobia + aggression:speaker	9	560.3	3.37	0.19	0.03	0.85
nestling age + BCI + speaker + BCI:speaker +neophobia + aggression	8	560.5	3.58	0.17	0.03	0.88
nestling age + speaker + neophobia + aggression	6	560.7	3.72	0.16	0.03	0.90
nestling age	3	560.8	3.79	0.15	0.03	0.93
nestling age + treatment + neophobia + aggression + year	7	561.2	4.18	0.12	0.02	0.95
nestling age + aggression	4	561.4	4.40	0.11	0.02	0.97
nestling age + speaker + neopobia + aggression + BCI	7	562.7	5.74	0.06	0.01	0.98
nestling age + speaker + neophobia + speaker:neophobia + aggression	7	562.9	5.91	0.05	0.01	0.99
nestling age + BCI + aggression	5	563.3	6.37	0.04	0.01	1.00
intercept	2	577.2	20.21	0.00	0.00	1.00

AICc table for top male feeding rate models

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	Cum.Wt
neophobia	3	607.7	0.00	1.00	0.23	0.23
neophobia + aggression	4	609.5	1.79	0.41	0.10	0.33
neophobia + aggression + speaker	5	609.5	1.83	0.40	0.09	0.42
neophobia + BCI	4	609.6	1.86	0.39	0.09	0.52
neophobia + aggression:BCI	4	609.8	2.11	0.35	0.08	0.60
neophobia + aggression:BCI + speaker	5	609.9	2.14	0.34	0.08	0.68
neophobia + aggression:BCI:speaker	5	611.1	3.39	0.18	0.04	0.72
neophobia + aggression + BCI + speaker	6	611.4	3.69	0.16	0.04	0.76
neophobia + aggression + speaker + year + nestling age	7	611.5	3.74	0.15	0.04	0.79
neophobia + aggression + BCI	5	611.5	3.74	0.15	0.04	0.83
neophobia + aggression + speaker + nestling age	6	611.7	3.98	0.14	0.03	0.86
neophobia + aggression:speaker + BCI:speaker	7	612.0	4.33	0.11	0.03	0.89
neophobia + aggression + nestling age + treatment	6	612.2	4.48	0.11	0.02	0.91
neophobia + aggression + BCI:speaker	6	612.3	4.60	0.10	0.02	0.94
neophobia + aggression + BCI + speaker + aggression:BCI	7	612.5	4.81	0.09	0.02	0.96
neophobia + aggression + BCI + aggression:BCI	6	613.1	5.36	0.07	0.02	0.97
intercept	2	613.8	6.04	0.05	0.01	0.98

Table A9: AICc table for intercept models of female and male feeding rate. K is the number of parameters. The top three models performed equally, so we carried forward the Poisson model with Band as a random intercept for further selection of covariates. Our response variable is count data and should be a Poisson process so this model form is parsimonious.

AICc table of intercept models for female feeding rate

Model	Random intercept	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
negative binomial with quadratic errors	Band	3	577.02	0.00	1.00	0.42	-285.42	0.42
Poisson	Band	3	577.80	0.77	0.68	0.28	-285.81	0.70
negative binomial with linear errors	Band	3	577.82	0.79	0.67	0.28	-285.82	0.98
Poisson	(none)	2	584.25	7.23	0.03	0.01	-290.08	1.00
Poisson	Site	3	586.34	9.32	0.01	0.00	-290.08	1.00
Gaussian	Band	3	619.46	42.44	0.00	0.00	-306.64	1.00

AICc table of intercept models for male feeding rate

Model	Random intercept	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
negative binomial with quadratic errors	Band	3	577.02	0.00	1.00	0.42	-285.42	0.42
Poisson	Band	3	577.80	0.77	0.68	0.28	-285.81	0.70
negative binomial with linear errors	Band	3	577.82	0.79	0.67	0.28	-285.82	0.98
Poisson	(none)	2	584.25	7.23	0.03	0.01	-290.08	1.00
Poisson	Site	3	586.34	9.32	0.01	0.00	-290.08	1.00
Gaussian	Band	3	619.46	42.44	0.00	0.00	-306.64	1.00

Table A10: Model output and parameter estimates from the top model for male feeding rate. Model is a generalized linear Poisson distributed model with log link, number of nestlings as an offset, and bird ID as a random intercept.

Top model for male feeding rate		Estimate	SE	p-value
Coefficients	Intercept	-0.291	0.074	<0.001
	neo	-0.152	0.052	0.004
Random intercept: Band		Variance: 0.113		
Number of observations: 148		Levels of Band: 37		

Female neophobia was best explained by time of day, number of nestlings, and female age (Table 3 in main text). Females were less likely to approach the novel object when observations were conducted later in the day, and they were more likely to approach the object when they had a higher number of nestlings. There was a non-significant pattern for SY females to be more likely to approach than ASY females (Table 3 in main text). Male neophobia was best explained by the crossed random intercept effects of Band and neophobia object, but none of the fixed effects we tested improved the model AIC beyond that of the intercept model (Table 8).

Aggression, neophobia, and noise treatment were all important for explaining feeding rate. Female feeding rate was best explained by nestling age, neophobia level, and an interaction between aggression and speaker playback (Table 4 in main text). Females fed more frequently as nestling age increased, and neophobic females fed less frequently than females that approached the novel object more quickly. Aggression did not significantly influence feeding rate under control conditions, but high-aggression females fed more frequently than low-aggression females during the speaker playback.

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