CHAPTER 6

CONSTRAINTS ON ACOUSTIC SIGNALING AMONG BIRDS BREEDING IN SECONDARY CAVITIES: THE EFFECTS OF WEATHER, CAVITY MATERIAL, AND NOISE ON SOUND PROPAGATION

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Abstract.—Increasing evidence suggests that anthropogenic noise from urbanization affects animal acoustic communication. We investigated whether the begging calls of nestling Eastern Bluebirds (*Sialia sialis*) varied along a disturbance gradient of ambient noise. Contrary to our prediction and the results of a previous study of nestling Tree Swallows (*Tachycineta bicolor*), we found that nestling Eastern Bluebirds did not increase the amplitude or structural characteristics—including frequency, rate, and duration—of their vocalizations in response to ambient noise. However, we found that prevalent temperature and humidity conditions attenuated begging calls. Specifically, in warmer, more humid weather, vocalizations of nestling Eastern Bluebirds attenuated outside the nest box; this is consistent with research conducted on the propagation of sound in various mediums and temperatures. Finally, our results indicate that increased ambient noise is associated with a decrease in the signal-to-noise ratio of nestling vocalizations. In other words, loud ambient noise likely masks chick begging calls, which suggests that chicks and parents may experience communication difficulties in noisy environments. We suggest that future studies explore the effects of ambient noise on parental behavior and aspects of parent–offspring communication and conflict that are related to raising a brood of nestlings.

Key words: acoustic communication, begging, climate, Eastern Bluebird, noise pollution, vocalization.

Limitaciones de las Señales Acústicas en Aves que se Reproducen en Cavidades Secundarias: Efectos del Clima, el Material de la Cavidad y el Ruido en la Propagación del Sonido

Resumen.—Existe evidencia creciente que sugiere que el ruido de las urbanizaciones humanas afecta la comunicación acústica de los animales. Investigamos si los llamados de los pichones de *Sialia sialis* para reclamar alimento varían a lo largo de un gradiente de disturbio de ruido ambiental. Contrario a nuestras predicciones y a los resultados de un estudio previo con pichones de *Tachycineta bicolor*, encontramos que *S. sialis* no incrementa la amplitud ni otras características estructurales de sus vocalizaciones –incluyendo frecuencia, tasa y duración– en respuesta al ruido ambiental. Sin embargo, encontramos que las condiciones de temperatura y humedad prevalentes atenuaban los llamados. Específicamente, en climas más calientes y húmedos, las vocalizaciones de los pichones de *S. sialis* se atenuaban por fuera de las cajas anidación; esto concuerda con la investigación llevada a cabo sobre propagación del sonido en varios medios y temperaturas. Finalmente, nuestros resultados indican que un incremento en el ruido ambiental está asociado con una disminución en el cociente señal-ruido de las vocalizaciones de los pichones.

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En otras palabras, el ruido ambiental fuerte probablemente enmascara los llamados que emiten los pichones para reclamar alimento, lo que sugiere que los pichones y los padres podrían experimentar dificultades para comunicarse en ambientes ruidosos. Sugerimos que estudios futuros exploren los efectos del ruido ambiental en el comportamiento de cuidado parental y en aspectos de la comunicación de padres a hijos, y en los conflictos que se relacionan con sacar adelante una camada de polluelos.

Acoustic communication signals may be affected by microclimate factors such as temperature, humidity, and air turbulence, as well as structural features such as vegetation, waterfalls, buildings, and even the ground (Marten and Marler 1977, Marten et al. 1977, Wiley and Richards 1978, Slabbekoorn et al. 2007). As a result, acoustic communication patterns in several taxa (Morton 1975, Lugli and Fine 2003, Lugli et al. 2003, Sun and Narins 2005, Witte et al. 2005, Bee and Swanson 2007) have been strongly shaped by the environment. Cumulatively, such environmental features cause acoustic signals to be degraded (Berg and Stork 2004). This is mainly a result of three processes: attenuation, reverberation, and irregular amplitude fluctuations (Slabbekoorn et al. 2007).

Attenuation is the process whereby signal strength decreases (i.e., change in amplitude) as it travels across the environment; in physical terms, it is the reduction in intensity of the sound wave. In general, higher frequencies attenuate faster than lower frequencies (Marten and Marler 1977, Wiley and Richards 1982). Irregular amplitude fluctuations are mainly caused by scattering due to air turbulence (Morton 1975, Richards and Wiley 1980). The degree of amplitude fluctuations varies with the frequency of the wave, prevailing weather conditions, and time of day (Richards and Wiley 1980). Reverberations, or echoes of the original sound reflecting off surfaces (Slabbekoorn et al. 2007), are another cause of signal distortion, especially in habitats with vertical structures such as trees or buildings (Richards and Wiley 1980; Slabbekoorn et al. 2002, 2007; Padgham 2004). Receivers hear reverberated signals after the original signal, which means that the original message may be obscured or masked by the reverberations (Slabbekoorn et al. 2002, 2007).

Because acoustic signals are designed to optimize transmission in specific habitats (Marten and Marler 1977, Marten et al. 1977, Brown and Handford 2000, Derryberry 2009), even minor changes to an animal's acoustic space threaten to diminish the efficacy of its signal. This, in turn, can interfere with many aspects of the animal's life history;

in birds, for instance, acoustic communication is used for mate attraction, territorial defense, foraging, and antipredatory tactics (Marler and Slabbekoorn 2004, Brumm and Slabbekoorn 2005, Patricelli and Blickley 2006). Additionally, vocal signals are an important element in chick begging displays and have often been reported as an honest but costly signal of nestling status (Kilner 2001, Sacchi et al. 2002, Villaseñor and Drummond 2007). Because effective parent–offspring communication is vital to maximizing fitness gains for both the adults and juveniles of many altricial bird species, disruptions in this signaling process could have long-term negative effects.

One potential source of disruption is anthropogenic environmental noise (Patricelli and Blickley 2006, Warren et al. 2006, Slabbekoorn and Ripmeester 2008). Anthropogenic noise pollution potentially leads to modifications in avian signaling strategies (Slabbekoorn and Peet 2003, Brumm 2004b, Fernández-Juricic et al. 2005, Wood and Yezerinac 2006), mate association (Habib et al. 2007, Swaddle and Page 2007), song learning (Katti and Warren 2004, Leader et al. 2005, Brumm and Slater 2006), and avian community structure (Bayne et al. 2008, Francis et al. 2009). However, it is relatively unknown whether there are notable fitness costs associated either with reductions in signaling efficacy or alterations to signaling behaviors (but see Habib et al. 2007, Bayne et al. 2008, Kight 2010, Halfwerk et al. 2011).

Another relatively overlooked question is how ambient environmental noise affects juvenile birds. To date, most noise studies have focused on adult life stages (Brumm and Slabbekoorn 2005, Patricelli and Blickley 2006, Warren et al. 2006, Slabbekoorn and Ripmeester 2008). However, it is clear that many adult birds have the capacity to relocate to less disturbed areas (Brown 1990, Bowles 1995, Delaney et al. 1999), and many appear to have a sufficiently large repertoire of vocalizations to adjust quickly to noise (Halfwerk and Slabbekoorn 2009). Although relocation of adults could alter species composition in relatively noisy areas (Francis et al. 2009), it may not have particularly notable consequences for

individual or population fitness if suitably quiet alternative habitats are available nearby. Hence, we recommend emphasizing life stages in which birds are relatively immobile and cannot simply flee from noise pollution.

To our knowledge, only two published studies have reported the effects of ambient environmental noise on nestlings; both investigated parent–offspring communication and provisioning in Tree Swallows (*Tachycineta bicolor*), which nest in secondary cavities (Leonard and Horn 2005, 2008). In an elegant experimental study, Leonard and Horn (2005) demonstrated that nestling Tree Swallows can increase the amplitude of their begging calls in response to increases in ambient noise level; furthermore, the nestlings' vocal manipulations are extreme enough to improve signal-to-noise ratio (SNR), thus making the calls more audible to parents and inducing increases in parental feeding rates. Surprisingly, in a second study (Leonard and Horn 2008), chicks in noisy and control nests were fed at similar rates; as a result, there were no noticeable differences in growth rate or body size across the two treatments. However, chicks in the noise treatment produced calls with different frequency characteristics (higher minimum frequency, lower maximum frequency), and these differences remained, to varying degrees, even after the ambient noise was removed. This result suggests that natal acoustic environment could influence vocal development in birds, which may affect their ability to communicate effectively as adults. Furthermore, the contrasting results in these two studies indicate that multiple aspects of ambient noise (e.g., timing, length, and intensity) will interact to determine whether and how chicks modify their begging calls; this, in turn, will influence parental responses. Thus, alterations in communication can have important fitness consequences for both parents and their offspring.

To explore whether other avian species are similarly affected by environmental noise, we designed a two-part study focused on nestling Eastern Bluebirds (*Sialia sialis*). Like Tree Swallows, Eastern Bluebirds nest in secondary cavities; their nestlings, which are flightless until ~16 days posthatch, cannot escape the ambient noise environment surrounding their nest boxes (Gowaty and Plissner 1998). Hence, we predicted that this species would be particularly sensitive to changes in noise conditions during this life stage. In the first part of our study, we conducted field observations along an acoustic gradient to evaluate the impact of ambient noise on the structure of chick begging calls. In the second part of the study, we investigated how variations in popular bluebird nest-box designs influenced the propagation of sounds that enter and exit the box. This is especially important given the increasing use of nest boxes not only by Eastern Bluebirds (Gowaty and Plissner 1998) but also by a variety of other species, including Tree Swallows, Carolina Chickadees (*Poecile carolinensis*; Mostrom et al. 2002), and House Wrens (*Troglodytes aedon*; Johnson 1998). For Eastern Bluebirds at least, nest boxes aided the successful recovery of the population in the eastern United States as the availability of natural secondary cavities dwindled dramatically (Gowaty and Plissner 1998). Cumulatively, this research was intended to broaden our understanding of how human noise and materials influence nestling life stages of a secondary cavity nester exposed to noisy natal environments such as those found along many managed nest-box trails.

Methods

Study Species and Research Site

Eastern Bluebirds are small, brightly colored thrushes found from Ontario to Mexico (Gowaty and Plissner 1998). Where possible, they nest in naturally occurring secondary cavities originally excavated by other animals, but across much of their range they depend on manmade nest boxes (Gowaty and Plissner 1998). Since 2002, our research group has maintained a large (>500-box) network of these boxes around Williamsburg, Virginia, where they are situated along a previously documented noise-disturbance gradient (Kight 2005, 2010; LeClerc et al. 2005; Kight and Swaddle 2007). The boxes are constructed of pine and mounted at a standardized height at the top of metal poles fitted with a cylindrical snake baffle (Kight 2005, LeClerc et al. 2005).

At the study site, Eastern Bluebird breeding pairs begin forming in early spring; nest building typically occurs during late February and early March. Pairs commonly lay multiple clutches within a single breeding season, with the first eggs hatching as early as late February and the last broods hatching as late as the end of August. Young Eastern Bluebirds are altricial at hatching and solicit parental care with stereotypical

opened-beak calls and up-stretched necks. Parents typically feed nestlings adult and larval invertebrates (mostly insects and spiders) and maintain nest sanitation by removing fecal sacs excreted by the chicks. In our study population, parents visited nests as regularly as every 10–15 min or as sparsely as every 30–45 min (C. R. Kight unpubl. data). Prior to opening their eyes, nestlings emit short, high-pitched peep calls in response to the noise of parents arriving at the nest (Gowaty and Plissner 1998).

Experiment 1: Nestling Vocalizations along a Noise-disturbance Gradient

We sought to understand the impact of ambient environmental noise on parent–offspring communication in Eastern Bluebirds. We hypothesized that nestling vocalizations would vary along an ambient noise gradient in a manner that decreased the masking of calls by ambient noise. That is, as ambient noise increased in the environment, we expected nestlings to increase the amplitude (loudness, so that parents are more likely to hear them), frequency (pitch, to get above the frequency of background noise), duration (so that parents are more likely to hear calls), and rate of their calls (again to increase likelihood of parents hearing begging calls). This would result in the maintenance (or possibly even improvement) of SNR along the environmental noise gradient. We investigated these hypotheses in the field by recording nestling vocalizations simultaneously inside and outside nest boxes located along a noise-disturbance gradient.

Study site.—We recorded sounds at 19 active nests, all with a brood size of three nestlings at the times of measurement, between May and July 2007. In order of approximately loudest to quietest, two of the boxes were next to roads; one was adjacent to a park's parking lot; three were on a college campus; three were on local golf courses; one was next to an active recreational field; six were located at the borders of fields and wooded areas on a hospital campus; two were adjacent to rarely used open fields; and one was in a remote area of a state park. We chose these sites to represent maximal variance in noise characteristics among nest boxes and made sound recordings at times of day that captured typical noise profiles for these locations (Kight 2010).

Recording sounds at nest boxes.—We recorded the begging calls of nestling Eastern Bluebirds at

two locations: from within the nest box (hereafter "internal recordings") and outside the box (hereafter "external recordings"). Internal recordings were collected using a Sennhesier e608 microphone (*Sennheiser* Electronic GmbH, Wedemark, Germany), which was small enough to fit unobtrusively within the nest box and was anchored to the roof with tape so that the microphone pointed down directly at the chicks. External recordings were collected using a Sennheiser ME67 shotgun microphone positioned 1.5 cm directly above the nest box, and 15 m away from the nest box in each of the four compass directions, at a height of 1.6 m (i.e., the approximate height of the nest box entrance hole). We chose the 15-m recording distance because preliminary observations at 20 nests indicated that parental birds commonly perch ~15 m from their boxes during chick vocalizations. Prior to data collection, both microphones were calibrated in a soundproof booth so that we could calculate the "true" amplitude of recordings made in the field; hereafter, "amplitude" refers to measurements that have been calibrated to reflect actual, real-world values. For both sets of recordings, data were collected with and stored in a Marantz PMD660 solid-state recorder.

At most nest sites we encountered obstacles, including buildings, roads, dense vegetation, and bodies of water, at several of the 15-m recording positions. In these instances, we moved to a new location within 5 m of the intended point of recording. After setting up the recording equipment, field personnel retreated to a distance of 20–40 m in order to observe the nest without further disturbing the parents. At each recording point, observations and recordings were continued until a parent fed the chicks or until 40 min elapsed. Each nest was visited when nestlings were 7 and 10 days of age, for a total of two visits per box.

In order to control for the potentially confounding effects of local weather conditions, we used a Kestrel 4000 weather meter (Nielsen-Kellerman, Boothwyn, Pennsylvania) to record ambient air temperature (measured to 0.1°C precision) and humidity (to 0.1% precision) at each nest box location. Because of competing field-work demands, the weather meter was not available on every recording day; thus, when necessary, we used temperature and humidity data collected at a local weather station ($n = 6$ recordings).

Chick call analyses.—Using RAVEN PRO, version 1.2, acoustic analysis software (Cornell Lab

of Ornithology, Ithaca, New York), we visualized recordings and measured the following call parameters: root mean square (RMS) amplitude (i.e., mean square of the call waveform, in dimensionless kU), lowest frequency of the call (Hz), highest frequency of the call (Hz), frequency range (difference between highest frequency and lowest frequency, in Hz), and call duration (in seconds). Within a sequence of begging by chicks in a box, we measured all parameters from every consecutive 5-s section until the sequence was completed, then averaged these measurements to get a single value per begging sequence. To measure ambient environmental noise levels, we averaged the amplitude of noise recorded during the 5 s immediately preceding and following each begging sequence. We also calculated SNR (call amplitude/ambient noise amplitude) and call rate (number of individual calls/duration of entire begging sequence). Finally, we averaged measurements at each location to obtain one value per distance for each day of recording.

Statistical analyses.—We used SPSS, version 17.0 (SPSS, Chicago, Illinois), to construct generalized linear mixed models, each of which included the following explanatory variables: site, as an among-subjects factor; age and distance, as within-subjects factors; temperature inside the box; humidity inside the box; outside temperature; outside humidity; and amplitude of ambient noise. Dependent variables included RMS amplitude, minimum frequency, maximum frequency, frequency range, call duration, call rate, and SNR per begging sequence.

EXPERIMENT 2: EFFECTS OF NEST-BOX CONSTRUCTION MATERIALS ON SOUND DEGRADATION

We hypothesized that the materials used to construct nest boxes influence how sounds (i.e., nestling vocalizations, ambient environmental noise, and parental vocalizations) travel through the box, both from outside to inside and from inside to the external environment. Therefore, we conducted an experimental playback-recording study in which standardized test sounds were broadcast from nest boxes and recorded externally, and vice versa. This technique was repeated for nest boxes built from four different construction materials of varying acoustic hardness. We predicted that higher-frequency and lower-amplitude sounds would be attenuated

most easily when traveling through denser materials (e.g., hardwoods and plastics vs. softwoods).

Construction and location of experimental nest boxes.—Following recommendations made by the North American Bluebird Association (see Acknowledgments), we constructed nest boxes suitable for Eastern Bluebirds out of four of the most popular materials used in bluebird nest-box trials: cedar, pine, plywood, and PVC. Nest boxes constructed from the three wood materials (cedar, pine, plywood) had identical internal dimensions (10 × 13 × 27 cm) and 2-cm-thick walls; however, the PVC box was constructed from a 2-cm-thick PVC tube with internal dimensions of 10.5 cm diameter and 27 cm length, capped on the top and bottom with 2-cm-thick PVC plates. The nest entrance hole was the same diameter (3.7 cm) for every nest box.

All nest boxes were mounted on a standardized pine pole positioned upright in a bucket of gravel so that the nest box's entrance hole was 120 cm from the ground. This allowed us to present nest boxes in a standardized orientation during playback and recording trials. The wooden pole holding the nest box was fitted with a platform adjacent to the box so that a microphone could be positioned at the same height as the nest box. By placing one microphone on this external platform, along with a second microphone inside the nest box, we could simultaneously collect internal and external recordings while the microphones were equidistant from a single broadcasting speaker. In keeping with the first experiment, we separated the broadcasting speakers and receiving microphones by 15 m in order to approximate the distance between perched adult Eastern Bluebirds and their vocalizing offspring.

The experimental playback and recording trials were conducted in a quiet open-field site where Eastern Bluebirds are known to breed. We were careful to choose an environment with large amounts of short mown grass and without vertical structures; additionally, it was located >200 m from any source of anthropogenic noise. Related work in this field site found that these habitat characteristics minimize masking caused by ambient noise and reduce environmental degradation of playback tones (Kight 2010).

Generation, playback, and recording of tones.—Using NCH tone generator software (NCH Software, Canberra, Australia), we produced pure tones at three different frequencies: 2, 4, and 6 kHz. These are representative of the average frequencies of

vocal communications produced by common secondary cavity-nesting species (Gowaty and Plissner 1998, Johnson 1998, Mostrom et al. 2002). RAVEN PRO was used to produce two amplitude conditions for each of the three frequency tones: 42 and 52 dB sound pressure level (SPL) at 1.5 m from the microphone, as calibrated in a soundproof room when played from a SanDisk m200 series MP3 player at a standardized volume setting. Each playback segment consisted of 5 s of tone followed by 5 s of silence, stepping from 2 kHz through to 6 kHz with the quieter tone before the louder tone. The entire sequence of 2–6 kHz tones was repeated three times in each playback segment.

Playback–recording trials were conducted during July 2008 at times when ambient noise was minimized at our field site. Tones were broadcast through a KYE Systems Corporation SP-1200 portable speaker mounted on a pole so that it was positioned at the same height as the nest entrance hole. Recordings were collected with a Sennheiser ME67 shotgun microphone (for out-of-box recordings) and Sennheiser e608 microphones (for in-box and adjacent-box recordings) connected to Marantz PMD660 solid-state recorders. Two setups were used for the playback experiments: (1) the speaker was placed 15 m from the nest box and the two recording microphones were positioned inside and adjacent to the box (e.g., simulating the transmission trajectory of environmental noise and sounds made by the parents as they enter the box from outside); and (2) the speaker was placed inside the nest box, one microphone was mounted on the platform outside the box, and the other microphone was mounted at the same height 15 m from the nest box (e.g., simulating offspring vocalization reception by parents perched on top of and near the nest box, respectively). All microphones were oriented toward the broadcasting speakers.

Both setups were repeated with the entrance hole of the nest box facing directly toward either the external speaker (configuration 1) or the external microphone (configuration 2). Further, both setups and both configurations were repeated using nest boxes made from each of the four construction materials. Finally, we also repeated every possible combination of trials under two different weather conditions (a cool morning and a typically hot afternoon, which we averaged for analyses), so as to capture a representative range of microclimate values. This fully factorial experimental design allowed us to investigate the independent effects of construction material, tone frequency, tone amplitude, and orientation of nest entrance hole on the propagation of sound into and out of each nest box.

Acoustic analyses.—To minimize the influence of extraneous noises on our analyses, we band-pass filtered all recordings 50 Hz above and below the original tone frequency. Using the same general methods described above, we employed RAVEN PRO to measure 1-s samples of each tone (selected from the middle of each tone section) to generate metrics of RMS amplitude (averaged across three repeat measurements for each of the three 1-s samples for each tone). As before, we converted the dimensionless RMS amplitude values into dB SPL. To isolate the effects of the box on sound degradation of each tone, we examined the difference in RMS amplitude as measured by the internal and external (immediately adjacent to the nest box) microphones (described in more detail below)—which was our measure of attenuation (dB SPL).

Statistical analyses.—We used SPSS to construct analysis of variance (ANOVA) models with box material (cedar, pine, plywood, or PVC) as an among-subjects variable and tone (2, 4, 6 kHz), amplitude (low, high), and orientation of nest hole (toward and away) as within-subject variables, with attenuation as the dependent variable in each model. In the first model, we examined the difference in tone amplitude when the broadcasting speaker was 15 m away and one microphone was inside the box while the other was adjacent to the box (i.e., configuration 1). This analysis assessed how box material, tone frequency, tone amplitude, and nest-hole orientation affected attenuation of tones as they entered the box from the outside environment. In the second model, we examined the difference in amplitude measured when the broadcasting speaker was inside the box and the microphone was 15 m away (i.e., configuration 2) and when the broadcasting speaker was outside the box and 15 m away (i.e., part of configuration 1) and the microphone was adjacent to the box. In other words, this analysis explored the influence of box materials, tone frequency, tone amplitude, and nest-hole orientation on the attenuation of signals that originate from inside the nest box and are received in the environment 15 m away.

In both ANOVA models, we inspected model main effects of construction materials, tone frequency, tone amplitude, and nest-hole orientation, as well as two-way interactions of material and tone frequency, material and tone amplitude, and

TABLE 1. Summary of estimated marginal means of nestling call features and 95% Wald confidence intervals (CI) for 7 and 10 days of age. Asterisk indicates $P < 0.05$.

Call feature	Age	Mean	95% Wald CI	
			Lower	Upper
SNR*	7	3.62	–1.47	8.71
	10	19.84	15.25	24.44
Call amplitude (kU)*	7	2.29	1.39	3.19
	10	4.60	3.42	5.79
Call rate (calls s⁻¹)*	7	2.61	2.43	2.79
	10	1.81	1.66	1.96
Call bought length	7	44.23	35.89	52.57
(s)*	10	2.22	–7.70	12.14
Frequency range	7	1,455.97	1,279.86	1,632.08
(Hz)	10	1,354.76	1,162.19	1,547.34
Lowest frequency	7	4,860.90	4,251.25	5,470.55
(Hz)	10	5,138.75	4,188.59	6,088.91
Highest frequency	7	6,316.87	5,739.35	6,894.38
(Hz)	10	6,493.52	5,541.84	7,445.20

material and orientation; these allowed us to examine how nest-box construction materials influenced the attenuation of particular frequencies and amplitudes and whether they altered the effect of nest-hole orientation on attenuation. We used post hoc Tukey tests to examine differences among the four categories of nest box material and the three categories of tone frequency. All data were inspected for normality and log-transformed where necessary. We employed two-tailed tests of probability throughout.

RESULTS

EXPERIMENT 1

Call amplitude and SNR increased with age, whereas rate and duration of calls decreased with age (Table 1). Mean detected SNR, amplitude of calls, rate of calling, and duration of calls were higher inside the next box than 15 m away (Table 2). In other words, chick calls were more difficult to detect farther from the box, as expected. Ambient noise recorded inside the box was predominantly <1.5 kHz at an average amplitude of ~51 dB SPL. External ambient noise was also predominantly below 2 kHz, but was louder at an average amplitude of ~64 dB SPL.

More importantly, the SNR of nestling calls decreased significantly as the ambient noise level increased at the nest site (β = –7.44, df = 1, P = 0.001). Further, we found no significant associations between any other call feature and ambient noise (Table 3). Cumulatively, these results show that the nestlings did not adjust their calls according to environmental noise conditions, although it is unclear whether this is because they could not detect changes in environmental noise, were unable to manipulate their vocalizations, or were able to make adjustments but simply chose not to.

TABLE 2. Summary of estimated marginal means of nestling call features and 95% Wald confidence intervals (CI) for inside the nest box and at 15 m. Asterisk indicates $P < 0.05$.

Call feature	Distance (m)	Mean	95% Wald CI	
			Lower	Upper
SNR*	0	19.03	15.49	22.58
	15	4.43	1.25	7.60
Call amplitude (kU)*	0	6.36	5.54	7.17
	15	0.53	–0.34	1.41
Call rate (calls s⁻¹)*	0	2.38	2.27	2.49
	15	2.03	1.82	2.25
Call bought length (s)*	0	31.12	27.37	34.88
	15	15.33	10.62	20.03
Frequency range (Hz)*	0	1,887.67	1,731.27	2,044.07
	15	923.07	832.37	1,013.77
Lowest frequency (Hz)	0	4,633.60	4,320.59	4,946.62
	15	5,366.05	4,811.62	5,920.47
Highest frequency (Hz)	0	6,521.27	6,161.48	6,881.07
	15	6,289.11	5,806.42	6,771.81

TABLE 3. Summary of the direction of associations between chick begging-call features and increases in ambient noise amplitude, air temperature inside and outside the box, and relative humidity inside and outside the box (+ signifies a positive relationship at $P < 0.05$; – signifies a negative relationship at $P < 0.05$; NS signifies $P > 0.05$).

Call feature	Ambient noise amplitude	Ambient air temperature		Ambient relative humidity	
		Calls inside	Calls outside	Calls inside	Calls outside
SNR	–	+	–	NS	NS
Call amplitude	NS	+	–	NS	NS
Call rate	NS	+	–	+	–
Call bout length	NS	NS	NS	+	–
Frequency range	NS	NS	–	NS	NS
Lowest frequency	NS	NS	NS	NS	NS
Highest frequency	NS	NS	NS	NS	NS

Interestingly, we found significant associations between nestling call features and ambient temperature and humidity (Table 3). Specifically, for calls recorded outside the nest box (15 m away), amplitude ($\beta = -1.14$, df = 1, $P < 0.001$), frequency range ($\beta = -92.54$, df = 1, $P = 0.035$), SNR ($\beta = -5.32$, df = 1, $P < 0.001$), and rate ($\beta = -0.184$, df = 1, $P < 0.001$) all decreased significantly as the ambient temperature increased. On the other hand, for calls recorded inside the nest box, we observed increases in amplitude ($\beta = 0.985$, df = 1, $P < 0.001$), SNR ($\beta = 0.631$, df = 1, $P = 0.035$), and rate ($\beta = 0.209$, df = 1, $P < 0.001$). Similarly contrary patterns were observed for relationships between ambient humidity and call parameters. Among calls recorded outside the nest box, bout length ($\beta = -1.623$, df = 1, $P = 0.015$) and call rate ($\beta = -0.048$, df = 1, $P < 0.001$) decreased as humidity increased. However, among calls recorded inside the next boxes, both bout length ($\beta = 2.587$, df = 1, $P = 0.003$) and call rate ($\beta = 0.071$, df = 0.88, $P < 0.001$) increased with the same increases in ambient humidity.

Interior and exterior call recordings were made simultaneously, across the same range of environmental conditions. Thus, our interpretation is that although nestlings increase the intensity of their calling (in terms of amplitude, rate, and length) on hot and humid days, these same weather conditions reduce signal transmission and make it more difficult for parents to hear their offspring calling. In other words, the physical environment mediates a contradiction between the actual calling response of the signaler and perception of those calls by receivers.

EXPERIMENT 2

Tone traveling from outside to inside the box.—Orientation of the nest hole to the source of the sound had little influence on attenuation when the sound was received inside the nest box ($F = 0.218$, df = 1 and 4, $P = 0.665$). However, there was a notable box material × orientation interaction term ($F = 9.71$, df = 3 and 4, $P = 0.026$). This relationship was driven by a notable increase in attenuation in pine and PVC boxes when the nest hole was oriented away from the source of the sound (Fig. 1).

Tone frequency significantly influenced attenuation of sounds traveling from outside to inside
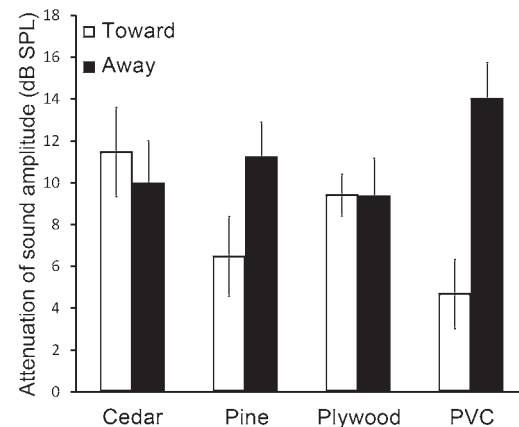

FIG. 1. Mean (± SD) attenuation of sound amplitude inside nest boxes constructed of four materials (cedar, pine, plywood, or PVC) when the nest hole was oriented toward (hollow bars) or away from (filled bars) the external source of noise.
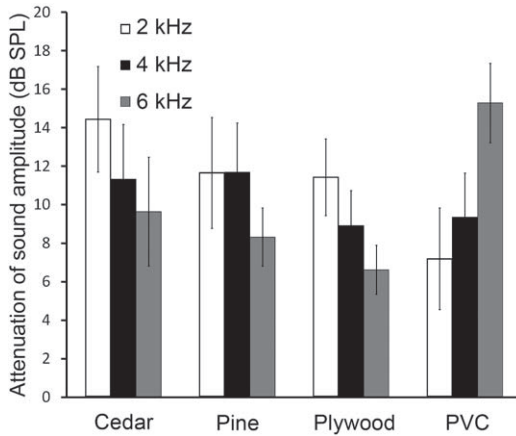
FIG. 2. Mean (± SD) attenuation of sound amplitude of three pure tones (2, 4, and 6 kHz) inside nest boxes constructed of four materials (cedar, pine, plywood, or PVC) when the tones were played outside in the environment and received inside the boxes.
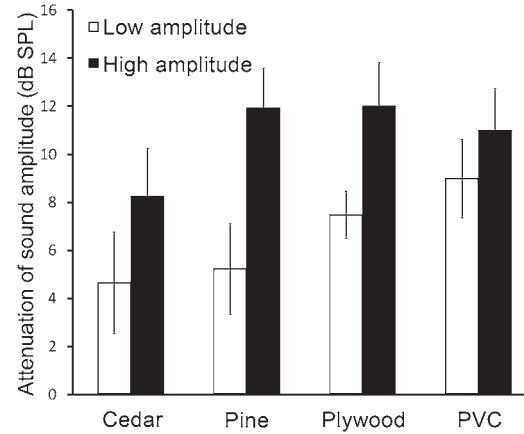

FIG. 3. Mean (± SD) attenuation of sound amplitude of three pure tones (2, 4, and 6 kHz) inside nest boxes constructed of four materials (cedar, pine, plywood, or PVC) when the tones were played outside in the environment and received inside the boxes.

the box ($F = 14.71$, df = 2 and 8, $P = 0.002$). Specifically, attenuation was higher for lower-frequency tones (Fig. 2). These patterns were also somewhat related to nest-box material, as indicated by a marginal material × tone frequency interaction term ($F = 2.84$, df = 6 and 8, $P = 0.087$). For the cedar, pine, and plywood boxes, attenuation was higher for lower-frequency tones; however, the inverse occurred among PVC boxes, in which degradation decreased for lower-frequency tones (Fig. 2).

There was a positive relationship between attenuation and amplitude among sounds traveling from outside to inside the nest box ($F = 10.69$, df = 1 and 4, $P = 0.031$). This was not affected by box material ($F = 0.582$, df = 3 and 4, $P = 0.658$).

Except for the box material × orientation and material × tone frequency interactions noted above, there did not appear to be a strong relationship between box material and overall tone attenuation ($F = 0.657$, df = 3 and 4, $P = 0.620$), which indicates that construction materials did not impede the transmission of sound from the outside environment into the nest box.

Tone traveling from inside to outside the nest box.— Tones were somewhat less attenuated when the nest hole from which the sound was emanating pointed directly toward the receiving speaker ($F = 6.18$, df = 1 and 4, $P = 0.068$); however, this minor attenuation by nest-hole orientation was not generally influenced by box construction material ($F = 3.80$, df = 3 and 4, $P = 0.115$)

Contrary to our findings in the previous experiment, tone frequency did not affect attenuation of signals traveling from inside to outside the nest box ($F = 1.82$, df = 2 and 8, $P = 0.223$). We also did not detect a nest-box material × tone frequency interaction term ($F = 1.75$, df = 6 and 8, $P = 0.226$).

As before, higher-amplitude tones attenuated more than lower-amplitude tones ($F = 8.83$, df = 1 and 4, $P = 0.041$; Fig. 3). The differential degradation of louder and quieter tones was affected by box material ($F = 14.00$, df = 3 and 4, $P = 0.014$); specifically, the attenuation of louder tones was particularly evident in the pine and plywood boxes, but much less so in the cedar and PVC box (Fig. 3).

The main effect of box material on overall tone attenuation was not significant ($F = 0.341$, df = 3 and 4, $P = 0.798$). However, as noted above, box materials appeared to interact somewhat with tone amplitude to differentially affect attenuation (Fig. 3).

DISCUSSION

EXPERIMENT 1

Our results show that chick call parameters are influenced by a variety of factors. These include variables that have previously been shown to affect nestling signaling, such as age (Leonard

and Horn 2006) and temperature (Evans 1994), and others that have not, to our knowledge, been addressed in the literature (e.g., humidity and distance from receiver). Surprisingly, we did not find evidence supporting our main prediction (based on reports of nestling Tree Swallows; Leonard and Horn 2005, 2008), that Eastern Bluebirds would increase their amplitude in response to increased ambient noise levels, thus preserving or even improving their SNR. Further, chick call features attenuated surprisingly rapidly as local temperatures and humidity levels increased. Cumulatively, these results suggest that chicks signaling in noisy environments may have a particularly difficult time communicating effectively during the latter months of the breeding season, when both temperature and humidity peak.

For older chicks, calls were louder, had better SNR, were shorter, and were delivered at a lower rate. These observations are consistent with previous reports on the ways in which chick begging calls vary throughout the nesting period (Jurisevic 1999, Leonard and Horn 2006, Anderson et al. 2010, Marques et al. 2010, Wright et al. 2010). Therefore, it is important to account for nestling age when assessing the effects of noise on this life stage—older nestlings may be better able to make themselves heard over background noise.

We documented a dramatic difference in the parameters of calls recorded within the nest (e.g., the original signal) and those received 15 m away (e.g., the degraded signal heard by the adults). Specifically, the detected SNR, amplitude, duration, and rate of calling were all lower at 15 m than they were inside the box. Many previous studies have documented environmental effects on signal transmission (Brumm and Slabbekoorn 2005); among other things, vegetation (Dabelsteen et al. 1993, Blumenrath and Dabelsteen 2004), wind turbulence (Madsen et al. 2006, Rabin et al. 2006), and both "natural" and anthropogenic ambient noise (Lohr et al. 2003, Lugli and Fine 2003, Foote et al. 2004, Slabbekoorn and den Boer-Visser 2006, Luther 2009) are known to affect signal efficacy. Given that these are common features at our sites, we expected to observe some signal degradation; however, we did not anticipate that it would be so notable over such a relatively short distance (15 m). Most other studies of sound degradation have reported effects over much larger distances, with little change over the short distance we measured here. The effects of environment on

duration and rate are perhaps most perplexing; these results suggest that particularly quiet call features are completely lost during call transmission, leading the receiver to hear shorter, more widely spaced notes than those that are actually produced.

The efficacy of chick signaling was also influenced by local climate conditions. Chicks (as recorded within the nest box) increased the intensity of their calling in response to both rising temperature and humidity levels. However, this is the opposite of what was recorded 15 m away, where the calls sounded less intense. This unexpectedly dramatic effect is likely a result of the fact that higher temperatures allow the atmosphere to hold more moisture, which generally absorbs more sound waves, resulting in the loss of sound pressure (Bradbury and Vehrencamp 1998). Thus, our system appears to provide an interesting example of how systematically increased temperatures could mediate parent–offspring conflict in communication. If Eastern Bluebird parents have difficulty hearing nestling vocalizations, they are more likely to underestimate chick need, because chick begging is often an honest indication of chick hunger and condition (Sacchi et al. 2002, Villaseñor and Drummond 2007). It is also interesting to consider why chicks increased call intensity in response to higher temperatures and humidity levels. It is possible that the changes in call parameters reflect greater energetic demands. Models and among-species empirical support suggest that the energetic costs of birds' calling will increase with temperature (Gillooly and Ophir 2010, Ophir et al. 2010), though, to our knowledge, there are no reports linking changes in weather, metabolism, and nestling begging behavior within a species. These vocal adjustments may also be an innate response designed to improve acoustic communication (at the nest box, though not 15 m away) in situations where atmospheric conditions would otherwise decrease sound transmission.

In addition, variations in signal efficacy could affect predator–prey interactions in a number of ways. For instance, poor signal transmission (whether related to weather conditions or ambient noise) could reduce depredation by animals that use phonotaxis to locate their prey. At the same time, nestlings might also have difficulty using alarm calls to alert adults to nest invasions occurring while the parents are not in visual contact with the nest box. It would be possible to test this latter hypothesis by monitoring parental

responses to simulated nestling playbacks under different noise, temperature, and humidity conditions.

Perhaps our most notable finding was that, unlike nestling Tree Swallows (Leonard and Horn 2005), Eastern Bluebird chicks do not adequately adjust their vocalizations to increasing noise and, therefore, experience reduced SNR. This lends further support to the growing notion that background noise is a major constraint on acoustic signaling (Slabbekoorn et al. 2007). Complementary studies of the same Eastern Bluebird population revealed that adult males are capable of adjusting both the frequency (pitch) and amplitude of their songs in response to increases in ambient noise levels (Kight 2010). Because Eastern Bluebird chicks significantly increased their call amplitude and SNR in response to changing weather conditions, it is unlikely that the disparity between adult and juvenile responses to ambient noise levels resulted from a physical inability to call more loudly. Rather, it seems probable that their relatively less developed sensory system (Kubke and Carr 2000) prevents them from detecting the increase in ambient noise level. It is also possible, and perhaps more likely, that their nest box filters out much of the ambient noise (see below), leaving the chicks unaware that call adjustments are warranted.

Experiment 2

Contrary to our hypothesis, nest-box material did not have a major impact on the attenuation of signals being transmitted between nest boxes and the outside environment, except indirectly, when it interacted with nest-box orientation and call frequency and amplitude. Instead, the variables that had the greatest influence were related to the signals themselves (e.g., frequency and amplitude) and to the direction in which the signals were traveling (e.g., originating outside the box and propagating inward, or vice versa).

Nest-box orientation did not affect attenuation at all when the tone was played toward the box, and was only weakly associated with attenuation of tones exiting the box. Unsurprisingly, in the latter case, tones were less attenuated when the entrance hole was pointing toward the microphone (i.e., when there was no box wall between the speaker and the microphone). As we expected, the effect of the material × orientation interaction term seems to be driven by differences in the

densities of the four nest-box materials (PVC = 1.38 g/cm³, pine ≈ 0.545 g/cm³, plywood ≈ 0.5 g/cm³, cedar = 0.38 g/cm³); the densest materials, PVC and pine, attenuated sound waves the most.

We were surprised by the interactions between frequency and attenuation for signals originating from both outside and inside the box. In general, lower-frequency tones attenuate more slowly than higher-frequency tones, so we did not expect to find that lower-frequency tones attenuated more rapidly during transmission into the nest box. To further explore these issues, it will be necessary to more rigorously explore the acoustic properties of these and other nesting materials in a more controlled environment (e.g., a soundproof room). In contrast to the relationship between frequency and attenuation found for sounds originating outside the box, we found no associations between these variables for sounds originating inside the box; further, there were also no material × frequency interactions. The differences in these two sets of results may be related to when the sound waves meet the box wall. In the first experimental setup, the tones have already undergone attenuation due to spherical spreading by the time they interact with the nest-box material; thus, they must transmit through the box when they are already relatively weak. In the second experimental setup, however, the tones have only just been broadcast from the speaker and, therefore, pass through the box wall when they are much stronger. Among signals originating both outside and within the nest box, attenuation increased with increasing amplitude. These findings were unexpected, given that higher-amplitude sounds should attenuate more slowly than lower-amplitude sounds (Bradbury and Vehrencamp 1998, Berg and Stork 2004). There was a material × amplitude interaction for tones broadcast from within the nest box, such that louder tones degraded more in boxes made from pine and plywood, but less in boxes made from PVC and cedar. This does not appear to be related to the density of the construction materials or the thickness of the box wall, given that these factors are evenly distributed across the two reactions (e.g., pine and PVC are most dense, whereas pine and cedar are thickest). Thus, this relationship probably results from interactions between multiple physical characteristics of the nest-box construction materials (e.g., a thickness × density effect) and their effects on acoustic processes such as scattering and reverberation.

We did not find a significant association between attenuation and box construction material, regardless of whether the tone was played toward the box or emerged from within it. This is fairly conclusive evidence that, under these environmental conditions and in these nest-box shapes, signal persistence is not affected by construction material alone. In nature, however, secondary cavity nests are not as uniform in size and shape as they were here. The varying acoustic properties of different nest-box materials are likely to become more obvious when they are compounded by changes in characteristics such as external and internal dimensions, as well as the location of the hole in relation to the nest (e.g., the location of the chicks that would be both producing signals and receiving them); in fact, these variations are likely to influence not just attenuation, but other aspects of signal propagation as well. Cumulatively, the results of this experiment indicate that, in the absence of other complicating factors such as fluctuations in temperature, humidity, and ambient noise, signals are better preserved when they originate from within a nest box and propagate out into the environment. Although this is likely to be beneficial for begging chicks and incubating females producing begging or alarm calls, it may also increase the likelihood that nests will be discovered by passing predators.

General Discussion

In many respects, nest boxes appear to act as acoustic filters. This would explain why, unlike Tree Swallow chicks studied previously, the nestling Eastern Bluebirds observed in our first experiment failed to respond to increasing levels of ambient noise. In the Tree Swallow experiments (Leonard and Horn 2005, 2008), ambient noise stimuli did not pass through the walls of the nest box, but instead were played directly through the entrance hole or an open side of the box. In other words, the noise that reached the Tree Swallow chicks was undiluted, whereas the noise in the Eastern Bluebird experiment seems to have been muffled by the box walls. Indeed, the results of our second experiment clearly show that nest-box materials attenuate noises originating from the outside environment; the strength of this effect appears to be dependent on the density of the construction material. Overall, common nest boxes appear to be particularly good at filtering out sounds that are lower-frequency and higher-amplitude.

Interestingly, these are the very same traits that characterize anthropogenic noise (Patricelli and Blickley 2006, Warren et al. 2006, Slabbekoorn et al. 2007). If, indeed, nest boxes act as a sort of buffer to noise disturbance, they may actually protect chicks from some negative effects of chronic noise exposure, such as high levels of stress hormones and reduced immune function (Stansfeld and Matheson 2003, Goines and Hagler 2007, Chloupek et al. 2009, Barber et al. 2010). Of course, these potential benefits may also be outweighed by the fact that the filtering effect could negatively affect chicks' ability to communicate with their parents (as discussed above).

Historically, secondary cavity-nesters such as the Eastern Bluebird have likely been selected to communicate effectively in their chosen nesting territories. Thus, their signals may be particularly well adapted to deal with the acoustic pressures imposed by cavities. However, historical Eastern Bluebird nests (e.g., snags and, later, fence posts; Gowaty and Plissner 1998) probably have very different acoustic properties than manmade nest boxes. It would be interesting to make a comparison of these cavities in order to evaluate the extent to which the acoustics at current nest sites differ from those for which the birds are adapted; this might facilitate predictions about whether we could expect to see adaptative evolution of communication behaviors in anthropogenic areas, or whether these relatively new acoustic conditions fall within the range of those previously experienced by Eastern Bluebirds.

On the whole, our results highlight the vulnerability of young birds to environmental conditions—particularly ambient noise—outside the nest. Chicks are at a disadvantage for three main reasons. First, unlike their parents, chicks are not able to move away from the source of noise. Second, they may be relatively physiologically constrained in how they can adjust their vocalizations in response to changing environmental conditions, as appears to be the case in Eastern Bluebirds. Third, unlike adults (outside of molt), nestlings are undergoing physiological development; both directly and indirectly, ambient noise has the potential to reduce parental care and increase general developmental stress, possibly leading to long-term physical abnormalities (Mooney et al. 1985, Gest et al. 1986, Siegel and Mooney 1987, Nowicki et al. 2002, Spencer and MacDougall-Shackleton 2011, Swaddle 2011). Hence, further quantification of the influence of noise on bird populations may

benefit from focusing on the behavioral, physiological, and later-life fitness consequences of living in noisy sites. Finally, our results also indicate that the effects of physical materials on sound propagation may have positive as well as negative effects. We encourage researchers and managers alike to explore whether creative use of both absorbent and reflective materials may enable us to improve the acoustic space of breeding birds in human-modified habitats by reducing the impacts of anthropogenic noise while simultaneously promoting the propagation of avian signals.

Acknowledgments

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