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Nest acoustics and begging call structure in nestling tree swallows

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Acoustic signals are altered by the environment during transmission, and, as a result, many show features that overcome this constraint. This phenomenon is well documented for long-distance signals used for mate attraction and territorial defence, but is relatively unexplored for short-distance signals such as the begging calls of young animals. We used the cavity-nesting tree swallow, *Tachycineta bicolor*, to examine whether the acoustic environment of the nest affected the structure and transmission of begging calls. We found that begging calls were longer and minimum call frequency was lower in smooth-walled than rough-walled nests, and that minimum call frequency decreased with increasing cavity diameter. Begging call features did not, however, vary with reverberation and frequency response within nests, even though calls were more degraded in nests with a more variable frequency response. Our results show that begging call structure varies with the structure of nest cavities and that the acoustic environment of nest cavities affects call transmission. Thus, some of the variation in begging calls currently attributed to factors such as evolutionary conflicts of interest or predation might be partially attributable to the acoustic environment of the nest. More generally, selection for effective transmission deserves more attention as a factor affecting the structure of short-range acoustic signals.

The transmission of acoustic signals can be significantly impacted by the environment. For instance, as signals move through the environment their amplitude (Brumm & Slabbekoorn 2005), frequency or temporal structure may be disrupted by wind (Richards & Wiley 1980; Lengagne et al. 1999) and vegetation (Wiley & Richards 1978; Richards & Wiley 1980; Forrest 1994). In turn, acoustic signallers may structure signals to overcome these transmission constraints, and thus ensure that information is transferred effectively (Boncoraglio & Saino 2007; Ey & Fischer 2009).

The effects of the acoustic environment on the long-distance signals used by adult animals for mate attraction and territorial defence have been well studied (reviewed in Ey & Fischer 2009). Its effects on short-range signals, such as begging calls, however, have received little attention, possibly because there are seemingly few obstacles to the effective transmission of short-distance signals (Horn & Leonard 2002).

Recent evidence suggests, however, that the acoustic environment may affect short-range begging calls much as it does long-distance signals (Leonard & Horn 2005, 2008). For instance, in higher levels of ambient noise, parent tree swallows, *Tachycineta bicolor*, do not discriminate between nestlings calling at different rates, as they do at lower noise levels (Leonard & Horn 2005). Nestlings will, in turn, adjust begging calls in noise in ways that apparently help parents to distinguish between calls (Leonard & Horn 2005, 2008). Thus, the acoustic environment appears to impede the transmission of short-range begging signals and select for changes in call structure that improve transmission and discrimination.

Another potential constraint on the effective transmission of avian begging calls is the nest itself. Reflection and absorption of sound waves by nest walls could alter begging call structure through reverberation (the elongated decay of sounds caused by repeatedly reflected sound waves), resonance (amplification of certain frequencies by constructive interference of reflected waves) and attenuation (loss of amplitude due to absorption, scattering and destructive interference), all properties that should vary with the size and structure of the nest. These acoustic properties may be particularly important for cavity- and burrow-nesting species, whose begging calls are given within small, enclosed spaces (Horn & Leonard 2002).

Indeed, research in other communication systems suggests that the acoustics of small spaces can alter sound transmission and that burrow- and cavity-dwelling animals adjust their signals to the acoustic properties of their enclosed calling locations. Various taxa amplify their calls by matching call frequency to the resonant frequencies of the space (frogs: Lardner & bin Lakim 2002) and by building (crickets: Bennet-Clark 1987; Bailey et al. 2001) or using (frogs: Penna & Solís 1996; Penna 2004; Penna & Marquez 2007) resonant burrows to amplify incoming calls. Some species also call

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at low frequencies to avoid high-frequency attenuation within their burrows (subterranean rodents: Schleich & Busch 2002; Lange et al. 2007). Together these responses suggest that the acoustics of the environment may be a key force shaping communication of animals living in small spaces, and the begging calls of nestling birds should be no exception.

The overall goal of our study, therefore, was to determine whether the begging calls of nestling birds varied in relation to the acoustic environment of the nest. If so, this would suggest that constraints on transmission, which are known to shape the long-range acoustic signals of adult animals (Boncoraglio & Saino 2007; Ey & Fischer 2009), also contribute to the structure of short-range acoustic signals, specifically those given by young animals. This would raise the possibility that some of the variation in short-range signals within and between species that is usually attributed to evolutionary conflicts of interest (e.g. Kilner & Hinde 2008) might instead be attributable to selection for effective transmission.

Here, we used the cavity-nesting tree swallow as a model to examine whether the acoustic environment of the nesting cavity affects the structure and delivery of nestling begging calls. This species is well suited for a first test of such a relationship, because acoustic effects should be especially pronounced in cavity nests, compared to more open nests (Horn & Leonard 2002). Also, tree swallows are secondary cavity nesters, which means they nest in cavities created by a range of other species. Thus, cavity structure varies widely across different nests (e.g. Rendell & Robertson 1989), which might in turn yield wide variation in their acoustic properties.

We first asked whether call features varied with nest structure, hypothesizing that nestlings might have different calls depending on the type of cavity in which they are raised. We then asked whether two acoustic properties generally known to affect sound transmission in enclosed spaces, reverberation and frequency response (e.g. Kuttruff 2009; Davies 2010), varied with cavity structure and, if so, could help to explain any relationships between begging calls and nest structure. Finally, we asked whether the transmission of nestling calls within nest cavities was affected by these acoustic properties.

METHODS

Study Sites

This study was conducted between May and July 2008 and 2009 using tree swallows nesting in tree cavities in flooded open forest swamps near Wolfville, Nova Scotia, Canada (45°05′N, 64°32′W; for details on study sites, see Fairhurst 2010). Research was conducted under protocols approved by Dalhousie University's Committee on Laboratory Animals (Protocol 08-041).

To locate nests, we surveyed study sites every 2–3 days for signs of nesting activity. Once nest sites were located, we checked the cavity with an infrared camera mounted on a pole (modified from Boland & Phillips 2005) to determine when the clutch was complete and incubation was initiated. Nests were not disturbed again until 2 days before the anticipated hatch date, when they were checked daily to determine hatch date and brood size. Nests were in narrow, high, partly decayed snags in deep water and therefore were generally inaccessible or so fragile that extracting nestlings risked destroying nests.

Begging Call Features

We recorded begging calls at 18 nests in situ when nestlings were 10 days old. We placed a Sennheiser EW 312 G2 wireless lapel microphone at the top of each cavity entrance approximately 10–15 cm from the nestlings and then connected it to a Marantz PMD 671 solid-state digital recorder. Input levels were calibrated against sounds of known levels in an acoustic free field (described below) and were kept constant across recordings. To help standardize hunger levels across nests and allow parents to acclimate to the microphone, we allowed parents to feed for 1 h after we set up the equipment and we then recorded begging calls at 16 bits with a sampling rate of 44.1 kHz during the next five parental feeding visits.

We measured the first five nonoverlapping calls made during each of the five parental visits. Most nestlings within a brood would have contributed to our sample for any given brood, because on an average visit three to four nestlings beg, and only 15–20% of their calls are overlapped by calls of other nestlings (Leonard & Horn 2001b). The sampling was sufficient for analysing variation in call structure among different broods, given the large variance in call structure between relative to within broods (Leonard et al. 1997).

For each call, we measured several call features that signal nestling hunger (Leonard & Horn 2006) and are likely to affect call transmission (Horn & Leonard 2002). Specifically, we measured call length (ms) in Raven's waveform view (Raven Pro 1.4; Charif et al. 2010), and minimum and maximum frequency (kHz) in the spectrogram view (Hamming window, 289 Hz filter bandwidth, displaying 2 s of recording in the sound window). We also calculated call bandwidth (maximum–minimum frequency; kHz). Frequency features of calls were not highly correlated ($r = -0.68$ to 0.25), so all are included in the analyses.

Measurements of any acoustic signal from spectrograms can be strongly affected by amplitude and reverberation, because greater amplitudes make more of the call visible above background noise and reverberation can smear the beginning and end of calls as they appear on the spectrogram (Zollinger et al. 2012). In our sample, however, the spectrogram amplitude floor was set above constant background noise, and no call features were collinear with call amplitude ($r = -0.22$ to 0.47). Also, the starts and ends of calls were clearly distinguishable from their echo tails (when such tails were present), as sharp falloffs in spectrogram amplitude (>30 dB within 2–3 ms).

Nest Structure

To determine how nest structure influenced call features, we described the structural features of each nest cavity, including internal height, internal diameter, whether it was closed on both ends or open at one end, whether its walls were smooth or rough, and the diameter of the cavity entrance (see Table 1 for description).

Table 1
Definitions of structural features measured in tree swallow nest cavities

Structural feature	Definition
Internal height	Distance (cm) from the center of the nest cup to the cavity ceiling in closed nests, or to the end of the cavity wall above the nest cup in open nests
Internal diameter	Distance (cm) from the wall beside the nest entrance to the wall directly opposite
Openness	Whether cavity was closed (both ends of cavity closed to the external environment) or open (one end of cavity closed)
Wall texture	Whether cavity's internal walls were smooth (with ridges, crevices and lumps extending no more than 1–2 cm above or below the main wall surface) or rough (larger ridges, crevices and lumps >2 cm above or below the main wall surface)
Entrance diameter	Vertical diameter (cm) of nest entrance hole