



Effect of ambient noise on parent–offspring interactions in tree swallows



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Many recent studies suggest that increased ambient noise can disrupt acoustic communication in animals and might ultimately decrease their reproductive success. Most of these studies have focused on long-distance signals used in mate attraction and territory defence, but close-range acoustic interactions between parents and offspring may also be disrupted by noise and are closely linked to reproductive success. To test the effect of noise on parent–offspring interactions, we experimentally applied white noise (65 dB SPL) to the nests of tree swallows, *Tachycineta bicolor*, when nestlings were 3–6 days old. At experimental nests, parents gave fewer provisioning calls, which are used to stimulate begging, but otherwise we detected no difference in provisioning behaviour between experimental and control nests. More nestlings begged for food at experimental nests, using calls that were higher in amplitude and minimum frequency, than at control nests. When we played back nestling begging calls during parental visits to stimulate higher feeding rates, parents increased their feeding rates at control nests, but not at experimental nests. Our results show that noise can alter parent–offspring interactions and interfere with parental responses to begging calls. Nestlings may be able to compensate for moderate increases in noise by enhancing the conspicuousness of their begging signal, although at higher noise levels these adjustments may prove ineffective or the extra begging effort may be physiologically costly.

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Human-generated noise has become widespread across the globe as a result of activities such as transportation, recreation and resource extraction (Barber, Crooks, & Fristrup, 2010). This noise is known to have various effects on animals across a wide range of taxa, including distraction (Chan, Giraldo-Perez, Smith, & Blumstein, 2010), increased stress (Kight & Swaddle, 2011) and interference with acoustic communication (Brumm, 2013). Such effects may ultimately reduce reproductive success and fitness (Halfwerk & Slabbekoorn, 2013; McGregor, Horn, Leonard, & Thomsen, 2013), although noise might have positive consequences in some cases, if it deters or confounds predators, for example (Francis, Kleist, Ortega, & Cruz, 2012).

Much of the research examining the effects of ambient noise on acoustic communication, in particular, has focused on signals used in mate attraction and territory defence (Brumm, 2013). Acoustic signals are also used in a variety of other communication systems, however, including communication between parents and their

young, a system that has been particularly well studied in passerine birds (Kilner & Hinde, 2008; Wright & Leonard, 2002).

Nestling passerine birds produce an elaborate display known as begging when their parents come to the nest with food (Wright & Leonard, 2002). The display includes calling, posturing and scrambling for positions close to the parent. The intensity of the display varies with nestling hunger levels and condition, and parents use the display to allocate resources to individual nestlings and to regulate the overall feeding rate to the brood (Horn & Leonard, 2008; Wright & Leonard, 2002). Individual nestlings calling at the highest rate, posturing most intensively and positioned closest to the parent are most likely to be fed on a given visit (Leonard, Horn, & Parks, 2003; Wright & Leonard, 2002). Similarly, when broods call at higher rates and for longer durations, they generally receive more frequent food deliveries than when they call at lower rates and durations (Horn & Leonard, 2008; Kilner & Hinde, 2008; Leonard, Horn, & Dorland, 2009).

A growing body of evidence suggests that increased noise reduces breeding success in birds (Habib, Bayne, & Boutin, 2007; Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011; Kight, Saha, & Swaddle, 2012; Schroeder, Nakagawa, Cleasby, & Burke, 2012; but see Crino, Johnson, Blickley, Patricelli, & Breuner, 2013). The reasons for the reduced success are not well understood, however

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(Francis & Barber, 2013; Kight & Swaddle, 2011). In some species, adults make fewer visits (Naguib et al., 2013; Schroeder et al., 2012) and nestlings beg proportionally less (Naguib et al., 2013) in nests exposed to noise compared to quiet control nests. Nestlings at noisier nests may also beg less readily to acoustic cues of the parents' arrival at the nest (Leonard & Horn, 2012). Taken together, these studies suggest that noise could disrupt feeding interactions and communication between parents and young.

The goal of our study was to determine how ambient noise affects feeding interactions between parent tree swallows, *Tachycineta bicolor*, and their young. Specifically, we examined how ambient noise affects the allocation of food to individual nestlings and overall feeding rates to the brood. We did this by playing low levels of noise inside nests, and then comparing parent–offspring feeding interactions at these nests with those of control (no added noise) nests. We also played back nestling begging calls during parental visits to experimental and control nests, and compared overall feeding rates to the brood.

We expected noise might affect parent–offspring interactions in several ways. Previously, we found that nestlings exposed to increased noise often fail to beg to playback of acoustic cues associated with the arrival of parents at the nest (Leonard & Horn, 2012). In natural situations, nestlings have other cues to detect the arrival of a parent, but if noise masks the acoustic cues, then feedings might take longer, feeding rate might decline and/or parents might have to increase the number of provisioning calls they use to stimulate begging (Leonard, Horn, Brown, & Fernandez, 1997). We also predicted that missing the arrival of the parent in noise might result in fewer nestlings begging, which, in turn, could affect competitive interactions among nestmates. If so, this could disrupt the tendency of parents to feed nestlings that were posturing more intensively or closer than their nestmates, because parents would face a smaller range of choices.

If these effects occur because noise masks the acoustic cues that underlie many parent–offspring interactions, then parents or nestlings might avoid some of these effects by altering their acoustic signals. Specifically, many animals, including nestling tree swallows (Leonard & Horn, 2005, 2008), make their calls stand out in noise by increasing call amplitude or raising the minimum frequency of the call away from the low frequencies that predominate in most ambient noise (Brumm, 2013). Thus we tested for such changes in both parental provisioning calls and nestling begging calls.

Finally, to test more directly whether noise interferes with how begging affects parental feeding rates to the brood, we played back the begging calls of whole broods at experimental and control nests, during parental visits to the nests. We used brood calls because they are the main signal most parent songbirds, including tree swallows (Horn & Leonard, 2008; Leonard et al., 2009), use to regulate overall feeding rate.

METHODS

We conducted this study in the Gaspereau Valley of Nova Scotia, Canada between May and July 2013 (study sites described in Leonard & Horn, 1996) using a population of box-nesting tree swallows. The protocols of this study were approved by the Dalhousie University Committee on Laboratory Animals (Protocol 13-041).

Application of Noise

We checked nestboxes daily around the anticipated hatching date to determine nestling age and then every other day to determine brood size and fate. At hatch, we matched pairs of broods for

the field or the orchard that their nest was in and for their age and brood size. We then randomly assigned each to either an experimental (white noise added) or a control (no noise added) treatment. There were no significant differences between treatments in average brood size (mean \pm SE here and throughout; experimental: 5.5 ± 0.25 nestlings, control: 4.9 ± 0.26 nestlings; $F_{1,23} = 2.35$, $P = 0.14$) or mean nestling weight at day 6–7 post-hatch (experimental: 10.7 ± 0.65 g, control: 10.4 ± 0.68 g; $F_{1,23} = 0.06$, $P = 0.81$). Nestlings from all broods fledged.

When broods were 3 days old (hatch day = day 1), at both experimental and control nests we placed a pair of Sony (Toronto, ON, Canada) 8n8 series earbud speakers facing upward in the nest material along the side of the nest rim, midway between the front and back of the nestbox. We hid the speakers in the nest material so that parents would not attempt to remove them. The speaker wires led to two plastic bags tacked to the underside of the nestbox, which contained a Sony Hip Street HS-T29 2 GB MP3 player at experimental nests and nothing at control nests. We changed the MP3 player batteries daily in the experimental treatment, and mimicked the battery changes in the control treatment to control for disturbance. The speakers and MP3 player were removed following filming on day 6 post-hatch (see below).

Beginning on day 3, we played computer-generated white noise at a resolution of 16 bits, a sampling rate of 44.1 kHz, and in wav format using Audacity version 2.1 (Audacity Team, <http://audacityteam.org/>) through the speakers in the experimental treatment. The noise ranged from 0 to 22 kHz, which encompasses the frequency range of nestling calls (2–10 kHz) and was played at 65 dB SPL (measured in the box as described below; reference level 20 μ Pa here and throughout), which is at the upper end of the amplitude range (41–67 dB SPL) of ambient noise measured inside nestboxes in the field (Leonard & Horn, 2005).

We used white noise, rather than noise from a specific source or that emphasized particular frequencies, to test for effects that noise might have across the whole range of biologically relevant frequencies, including masking within the frequency range of nestling calls and disturbance outside that frequency range (Naguib et al., 2013). White noise is also easily characterized and replicated, and its use here eases interpretation of our results in the context of our previous experiments, all of which used white noise. Although most ambient noise varies over time and emphasizes particular frequencies (usually low frequencies), the continuous application of white noise used here is similar in duration, frequency range and sound level to that produced by some common noise sources, such as flowing water, rain and ventilation systems.

Sources of higher levels (>60 dB SPL) of ambient noise at our study sites include birds, wind, vehicles and a river (Leonard & Horn, 2005), with some nestboxes near the river experiencing sustained levels of noise similar to the experimental noise used here. Compared to the natural ambient background sounds within control nestboxes, the playback raised spectrum levels by about 10 dB, and produced more sustained and even spectrum levels (\pm 6 dB) (spectra in Leonard & Horn, 2008; McIntyre, Leonard, & Horn, 2013). The reverberations of sustained noise within an enclosure, such as a nestbox, also results in a more even sound pressure level throughout the enclosure ('diffuse sound field'; Raichel, 2006). Thus nestlings at different positions in the nest, as well as parents when they entered the box, probably experienced similar sound levels. Ambient sound levels measured just before parental feedings (measured through the microphone, as described below) were 65 ± 0.8 dB at experimental nests ($N = 20$) and 55 ± 0.8 dB at control nests ($N = 18$). The noise was uploaded to the MP3 player as a 24 h track that was reset each morning when the batteries were checked, so that the noise played continuously between days 3 and 6 post-hatch.

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