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

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## ARTICLE INFO

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

### Application of Noise

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: $5.5 \pm 0.25$ nestlings, control: $4.9 \pm 0.26$ nestlings; $F_{1,23} = 2.35$, $P = 0.14$) or mean nestling weight at day 6–7 post-hatch (experimental: $10.7 \pm 0.65$ g, control: $10.4 \pm 0.68$ 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 µPa 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 $65 \pm 0.8$ dB at experimental nests ($N = 20$) and $55 \pm 0.8$ 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.

*Recording Parent–Offspring Feeding Interactions*

When broods were 5 days old, we opened the hinged side of the nestbox (the left side, when looking into the nest entrance) and individually marked each nestling on their heads with dots of nontoxic white paint (Leonard & Horn, 1996). We then placed a Plexiglas plate in the opening and covered that side of the nestbox with a dark plastic bag. This mimicked the experimental set-up used to record feeding interactions and allowed both parents and nestlings to acclimate before recordings were made the next day.

The following day, we removed and weighed the nestlings, and suspended a Genexxa 33-3003 microphone (RadioShack, Fort Worth, TX, U.S.A.) 10 cm over the nest cup. The microphone was attached to a Zoom H1 recorder that had a sampling rate of 44.1 kHz and a bit depth of 16 bits. The input level of the recorder was set so that it would adequately register nestling calls without overloading. The level was calibrated by using the set-up just described to record a 1 kHz tone while measuring the sound pressure level with a SPL meter (RadioShack 33-2005, C-level weighting). It was then kept constant for all recordings. We also placed a second set of speakers behind the speakers already placed in the experimental and control treatments, for use in the playback experiment described further below.

We then returned the nestlings to the nest, replaced the Plexiglas plate with a higher-quality plate for filming, and mounted a GoPro (Vancouver, BC, Canada) HERO3: White Edition video camera on a small cardboard box placed on the opened side door of the nestbox. The camera was placed a standard distance from the nest so that the base of the nest entrance appeared in the top right corner of the field of view. We then covered the entire side of the box including the camera with a plastic bag, and video and audio recorded feeding visits by parents and begging by the nestlings for 2 h. Trials were completed between 0630 and 1230 hours Atlantic Daylight Time (ADT) for 35 nests (17 experimental and 18 control). For eight nests (4 experimental and 4 control), trials were completed between 1230 and 1830 hours ADT, because weather was poor or equipment was unavailable on some mornings.

We used QuickTime™ version 7.7 (Apple Inc., Cupertino, CA, U.S.A.) to record the number of feeding trips to the nest and on each visit (1) the time (s) between a parent entering the box and the first feeding (i.e. latency to feed), (2) the number of provisioning calls given by a parent between landing at the nestbox entrance and the first feeding, (3) the number of nestlings that begged, (4) the maximum postural begging intensity of each nestling that begged, (5) the duration of each nestling's begging and (6) which nestling was fed. Postural begging intensity was ranked on the following scale: (1) head down, gaping, sitting on tarsi; (2) head up, gaping and sitting; (3) same as (2) plus neck stretched upward; (4) same as (3) but body lifted off tarsi; and (5) same as (4) but wings waving (observed at only one nest).

*Measurement of Parental and Nestling Calls*

We imported the audio recordings into RavenPro 1.4 (Charif, Waack, & Strickman, 2010) and created a spectrogram (Hann window, 248 Hz bandwidth) of the first two adult provisioning calls and the first three nonoverlapping nestling begging calls given in each of the last five feeding visits. We used the last feeding visits to minimize any effects that setting up the equipment may have had on parents or nestlings (and thus their calls). For each call, we measured the following six call features: call length (ms), amplitude (dB, minus amplitude of background sounds via transformation to linear measurements as described in, e.g. Raichel, 2006), minimum frequency (Hz), maximum frequency (Hz) and centre frequency (Hz). We also measured the amplitude of background sounds, free of swallow calls, for 2 s before the parent arrived for each feeding visit, so that background sound levels could be subtracted from measured call amplitudes. To minimize bias in measurements in relation to background sound levels (Zollinger, Podos, Nemeth, Goller, & Brumm, 2012), we kept the parameters of the spectrogram display, including the minimum amplitude displayed, constant across recordings and used robust measurements of frequency and time features (from the fifth percentile of call energy; Charif et al., 2010). All these measurements were taken by visually selecting the beginning and end, and the highest and lowest frequency of each call on a spectrogram. However, the analysis program selected the robust measurements based on analysis of all the spectral slices that made up that spectrogram (details in Charif et al., 2010).

Frequency variables were strongly intercorrelated ($r > 0.60$ for adults, $r > 0.90$ for nestlings), so only data for minimum frequency, the frequency variable most often measured in studies of bird sounds in noise (Brumm & Zollinger, 2013), are presented here.

*Testing Parental Responses to Brood Calling*

To test whether noise interfered with the parents' reception of the brood-level signal that regulates feeding trips to the nest, we used a playback approach known to increase feeding rates (Horn & Leonard, 2008; Leonard et al., 2009) and then asked whether the response of the parents to playback differed in the presence of noise. Specifically, immediately after the 2 h filming period described above, we attached the second set of speakers placed in both experimental and control nests just before filming began (see above) to an MP3 player attached to a 20 m cable. For the next hour, an observer 20 m from the nest played back 30 s of nestling begging calls at natural levels (55 dB, as measured by recordings calibrated similarly to those described above, in Leonard & Horn, 2006) every time a parent came to the nest.

Each playback tape ($N = 4$) included the begging calls of a brood of 6-day-old nestlings given in response to a parental feeding visit, recorded on the study site in the previous year. Parent tree swallows do not discriminate between the calls of their own nestlings and those of other pairs (Leonard et al., 1997), so playing back the calls of foreign nestlings should not affect the results. We alternated playback tapes between experimental and control nests. We found no interactions between recording replicate and any treatment effect or interaction with treatment (analysed by adding recording replicate as a main effect and as an interaction term to the general linear models described below; all $Ps \geq 0.15$), suggesting that our results were not attributable to a particular recording.

We videorecorded parental feeding trips and nestling begging, as described above, during the 1 h playback period and for a further 1 h without the playback (i.e. post-playback period). We used the second hour of the 2 h recording period described in the previous experiment as a pre-playback period. Including both a pre- and a post-playback period allowed us to identify whether parents increased their pre-existing feeding rates after the onset of playback and resumed those rates once playback ceased (Leonard et al., 2009).

We uploaded the video footage as described above and recorded the number of feeding trips made by the parents during the pre-playback, playback and post-playback periods. We excluded the first 10 min of the playback period to account for any disturbance associated with our visiting the nest to attach the speakers to the MP3 player just before the playback period. To ensure the other periods were treated the same way, we also excluded the first 10 min of the pre-playback and post-playback periods. We also recorded the number of nestlings begging on each feeding trip, and the postural intensity and duration of their begging. We did this

because nestlings can be stimulated to beg by the begging calls on the playback tapes (Leonard et al., 2009), and if noise reduced that effect, then nestlings in the noise treatment might beg less intensively than nestlings in the control treatment, thus sending a weaker signal to parents. Because the goal of this study was to determine how noise affected the reception of the overall signal by the parents, we needed to ensure that the signals in each treatment were comparable. We measured visual signals rather than acoustic signals because nestling calls were obscured by the taped calls and therefore difficult to measure. Nevertheless, visual begging signals effectively reflect the amount of calling, because when nestlings at this age beg visually, they usually call as well (Leonard et al., 2003).

*Statistical Analyses*

Sample sizes vary across analyses because some situations did not occur at all nests. In particular, of the 43 nests that were videorecorded, 18 nests were omitted from analyses of parent–offspring feeding interactions within the nest because either the females brooded throughout most of the feeding visits ($N = 11$), the views of the nestlings were blocked by feathers ($N = 5$), or there were no feeding visits during the recording period ($N = 2$), despite the parents being present and entering the nest. Of the remaining 25 nests used in the analyses of parent–offspring feeding interactions, 21 nests ($N = 10$ experimental and 11 control) were filmed on day 6 post-hatch, while four nests ($N = 2$ experimental and 2 control) were filmed on day 7 because of inclement weather on day 6.

We tested for the effects of noise on feeding interactions by applying general linear models to mean values for each nest, so that each nest contributed one datum to each analysis. Most tests were simple one-way comparisons, with treatment (experimental versus control) as the fixed effect. To analyse treatment differences in how parents allocated food, however, we included nestling status (fed versus unfed), as well as treatment as fixed effects, and nest as a random effect. Similarly, to test for the effects of noise on responses to playback of begging calls, we included playback period (pre-playback, playback, or post-playback) and treatment as fixed effects, with nest as a random effect.

For all tests, we examined residuals to confirm assumptions of equal variances and normal distributions. In one case (latency to feed), we transformed data to achieve normality, and in two other cases (number of provisioning calls and postural begging intensity) we could not find an appropriate transformation and instead tested for treatment effects using a nonparametric test (Wilcoxon two-sample test). All analyses were conducted using JMP 11 (SAS Institute Inc., Cary, NC, U.S.A.). Means are reported ± SE.

**RESULTS**

*Does Noise Alter Parent–Offspring Feeding Interactions?*

The time between a parent's arrival at the nest and when it fed a nestling did not differ significantly between treatments (experimental: $3.69 \pm 0.126$ s, control: $4.46 \pm 0.126$ s; $F_{1,22} = 1.14$, $P = 0.30$), nor did overall feeding rates (experimental: $15.5 \pm 1.98$ feeds/h, control: $14.9 \pm 1.84$ feeds/h; $F_{1,26} = 0.05$, $P = 0.82$). Parents gave significantly fewer provisioning calls before feeding nestlings at experimental nests compared to control nests (experimental: $1.01 \pm 0.201$, control: $1.45 \pm 0.201$; $Z = 2.51$, $N = 24$, $P = 0.012$).

Significantly more nestlings begged in the experimental than in the control treatment (experimental: $3.02 \pm 0.215$, control: $2.24 \pm 0.224$; $F_{1,23} = 6.34$, $P = 0.019$; Fig. 1). The postural begging intensity of the nestlings that begged did not, however, differ
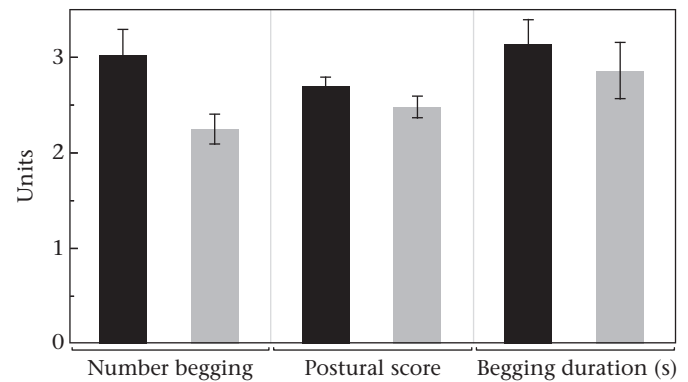


**Figure 1.** Mean ± SE number of tree swallow nestlings that begged, their postural begging intensity score and the duration of their begging in experimental (black) and control (grey) treatments.

between treatments (experimental: $2.69 \pm 0.100$, control: $2.47 \pm 0.104$; $Z = 1.66$, $N = 25$, $P = 0.10$), nor did the duration of their begging (experimental: $3.13 \pm 0.273$ s, control: $2.85 \pm 0.283$ s; $F_{1,23} = 0.49$, $P = 0.49$; Fig. 1).

The relationship between begging behaviour and the likelihood of being fed did not differ significantly between treatments. Fed nestlings had significantly higher postural begging intensity and were closer to parents than unfed nestlings (begging intensity: $F_{1,21} = 62.66$, $P < 0.0001$; distance to parent: $F_{1,22} = 67.02$, $P < 0.0001$), in both treatments (interaction begging intensity: $F_{1,21} = 1.75$, $P = 0.20$; Fig. 2a; interaction distance to parent: $F_{1,22} = 0.14$, $P = 0.71$; Fig. 2b).

*Do Parents or Nestlings Alter Their Calls in Noise?*

The structure of parental provisioning calls did not differ significantly between treatments, although there was a tendency for calls in the experimental treatment to be longer and higher in amplitude than calls in the control treatment (Table 1). The structure of nestling begging calls did, however, differ significantly between experimental and control treatments, with begging calls in the experimental treatment having higher amplitudes and minimum frequencies than calls in the control treatment (Table 1).

*Does Noise Interfere with Parental Responses to Brood Calling?*

The response of parents to playback of begging calls differed between experimental and control nests (playback effect: $F_{2,78} = 2.82$, $P = 0.06$; noise effect: $F_{1,39} = 0.23$, $P = 0.63$; noise∗ playback period interaction: $F_{2,78} = 6.22$, $P = 0.003$; Fig. 3). Specifically, at experimental nests, feeding rates did not differ significantly across the three periods (post hoc contrast: $F_{1,78} = 0.07$, $P = 0.79$), while at control nests, feeding rates were significantly higher during the playback period than during the pre- and post-playback periods (post hoc contrast: $F_{1,78} = 13.23$, $P = 0.0005$; Fig. 3).

The number of nestlings that begged did not change significantly in response to playback (playback effect: $F_{2,78} = 1.86$, $P = 0.16$) for either treatment (noise∗ playback interaction: $F_{2,78} = 0.25$, $P = 0.78$). More nestlings begged across all playback periods in the experimental treatment than in the control treatment (noise effect: $F_{1,39} = 6.39$, $P = 0.015$; Fig. 4a).

The postural begging intensity of the nestlings that begged did not change significantly in response to playback overall (playback effect: $F_{2,75} = 1.68$, $P = 0.19$), but there was a significant treatment∗ playback interaction ($F_{2,75} = 3.67$, $P = 0.03$; Fig. 4b). Specifically, at experimental nests, nestlings begged with higher postural intensity
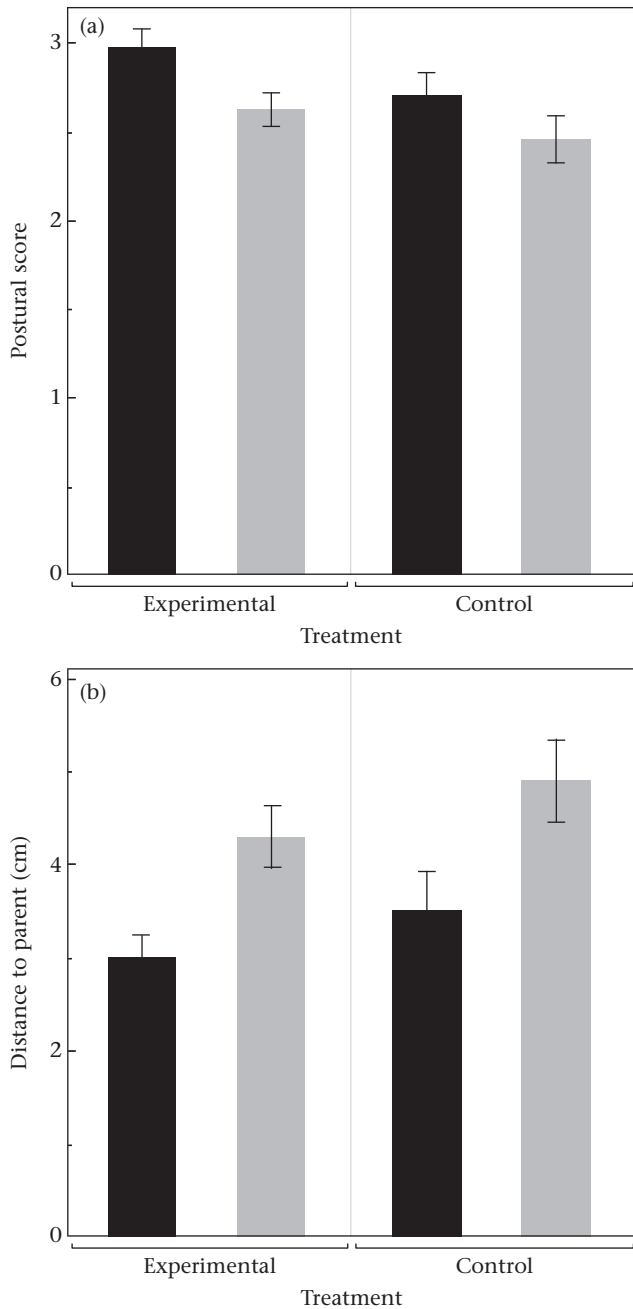
Figure 2. Mean ± SE (a) postural begging intensity score and (b) distance to parents (cm) for tree swallow nestlings that were fed (black) or not fed (grey) by parents in experimental and control treatments.
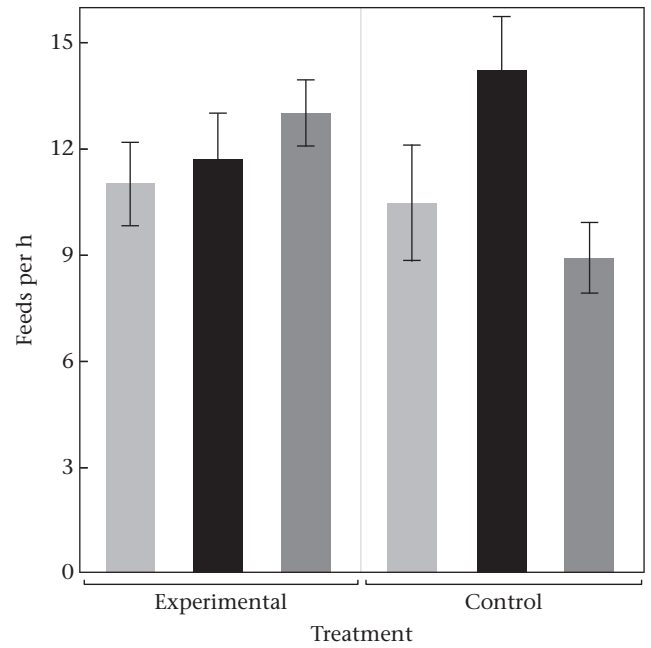


Figure 3. Mean number of feeding visits by tree swallow parents during the pre-playback (light grey), playback (black) and post-playback (dark grey) periods in experimental and control treatments.

**Table 1**
Features of adult provisioning calls and nestling begging calls at experimental and control tree swallow nests

|  | Experimental | Control | ANOVA |
|---|---|---|---|
| **Parental call feature** |  |  |  |
| Length (ms) | 114±8.8 | 87±6.5 | $F_{1,30}=3.70, P=0.06$ |
| Amplitude (dB) | 80±1.0 | 77±1.0 | $F_{1,30}=3.46, P=0.07$ |
| Minimum frequency (kHz) | 1.47±0.071 | 1.50±0.054 | $F_{1,30}=0.26, P=0.62$ |
| **Nestling call feature** |  |  |  |
| Length (ms) | 36±2.6 | 32±3.0 | $F_{1,33}=1.32, P=0.26$ |
| Amplitude (dB) | 63±0.8 | 60±1.1 | $F_{1,33}=6.27, P=0.018$ |
| Minimum frequency (kHz) | 5.31±0.137 | 4.70±0.158 | $F_{1,33}=8.54, P=0.0062$ |

Values are means ± SE.

during the playback period than during the pre- and post-playback periods (post hoc contrast: $F_{1,75} = 6.92$, $P = 0.010$), but at control nests they did not (post hoc contrast: $F_{1,75} = 1.09$, $P = 0.30$; Fig. 4b). The postural intensity of nestlings over all periods combined showed no difference between experimental and control nests ($F_{1,38} = 2.04$, $P = 0.16$).

## DISCUSSION

We found that low-level white noise affected parent–offspring interactions in tree swallows in several ways, but not all effects were as we predicted. Most notably, noise did not appear to affect how parents delivered and distributed food to nestlings, even though the playback experiment suggested that noise does disrupt parental responsiveness to brood begging calls.

### Does Noise Alter Parent–Offspring Feeding Interactions?

Noise changed parent–offspring interactions, but not in the ways we predicted. We found no evidence that noise affected the time it took parents to feed or the number of overall feedings. Noise also did not affect the provisioning rules that parents used when deciding which nestling to feed. It did appear to alter some parental and nestling behaviours, however. Specifically, at experimental nests, parents gave fewer provisioning calls and more nestlings begged than at control nests.

Parents might give fewer provisioning calls, which stimulate begging, at experimental nests, if more nestlings are begging when they arrive to feed (Leonard et al., 1997). It is not immediately clear, however, why more nestlings begged in the noise treatment, particularly given our previous demonstration that noise interferes with nestlings' detection of the parents' arrival at the nest (Leonard & Horn, 2012). Presumably this interference would lead to fewer nestlings begging in noise.
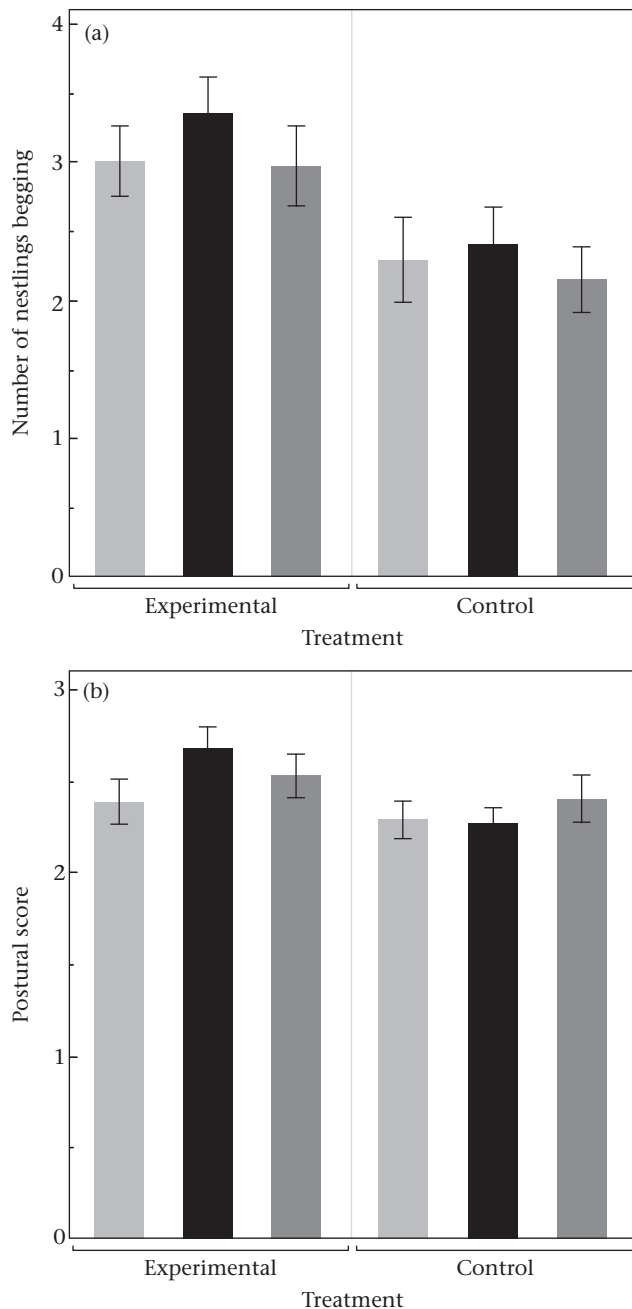
**Figure 4.** Mean ± SE (a) number of tree swallow nestlings that begged and (b) postural begging intensity score of nestlings that begged during the pre-playback (light grey), playback (black) and post-playback (dark grey) periods in experimental and control treatments.

One explanation for an increase in the number of begging nestlings in noise is that nestlings in this treatment were hungrier than those in the control treatment. This seems unlikely, though, because feeding rates and nestling weights were similar between treatments (see Methods). Another possibility is that, when noise is sustained, nestlings might compensate by intensifying their responsiveness to the parents, or by attending to other cues of the parent's arrival. The previous study presented noise for 80 min and used only acoustic stimuli, whereas the present study lasted days, and nonacoustic cues of the parent's arrival, such as the darkening of the nest hole and the vibration from the parent's landing, were available to nestlings. Moreover, the results of the present study's playback of begging calls, discussed below, suggest that nestlings

might be more responsive to one another in noise, which would further enhance the likelihood of begging at the parent's arrival.

### Do Parents or Nestlings Alter Their Calls in Noise?

We predicted that parents and offspring might change their acoustic signals in ways that aid reception in noise. Parents showed no significant changes in the structure of their calls, but nestlings did change their begging calls as predicted, increasing the amplitude and minimum frequency of their calls. Both of these responses to noise have been seen in a wide range of taxa, including tree swallow nestlings (Horn & Leonard, 2008; Leonard & Horn, 2005) and may serve to enhance call reception by parents in noise (Brumm & Zollinger, 2013). We showed in a previous study that parents failed to distinguish between the calling rates, and hence hunger levels, of individual nestlings in noise, but that discrimination was restored when nestlings increased the amplitude of their calls (Leonard & Horn, 2005). In the present study, nestlings not only increased the amplitude but also the minimum frequency of their calls, two responses we have also documented in previous laboratory and field studies (Leonard & Horn, 2005, 2008). Unlike increasing amplitude, raising minimum call frequency would be ineffective in white noise, but may be effective in the low-frequency noise that normally prevails (Pohl, Slabbekoorn, Klump, & Langemann, 2009), and/or may narrow the bandwidth of key call components or simplify call structure overall (Lohr, Wright, & Dooling, 2003). Together with the increase in the number of nestlings begging discussed above, changes in call structure might have compensated for the increased noise, and thus might account for the absence of effects on feedings by parents.

### Does Noise Interfere with Parental Responses to Brood Calling?

Although noise had relatively little effect on how parents allocated food, it did appear to affect the response of parents to the enhanced brood signal, which typically increases feeding rate (Leonard et al., 2009). Specifically, parents in noise did not increase their feeding rates in response to the playback of nestling calls, while parents in the control treatment did. Since the same calls were played back at experimental and control nests, at experimental nests the calls lacked any adjustments in call structure that real nestlings might have made to compensate for the noise. The absence of such adjustments might explain why noise disrupted parental feeding rates during playback of the calls we provided, but not when parents were interacting freely with their own nestlings.

Interestingly, nestlings increased their postural begging intensity in response to recorded begging calls in experimental nests but not in control nests. This result again suggests that nestlings increase the intensity of their begging display in noise. How they do so (by begging more often, with different call structure, or more intensely) appears to vary across different circumstances, however. For example, our present results show a sustained increase in the number of begging nestlings at experimental nests and an increase in postural intensity at those nests when we played back begging calls. These two changes may function in baseline and short-term signalling, respectively, but the causes and functions, if any, of the nestlings' varied responses to noise needs more study.

### Consequences of Noise for Reproductive Success

Anthropogenic noise is attracting increasing attention as a conservation concern (McGregor et al., 2013). In particular, several studies have suggested that the reproductive success of songbirds is lowered in noise (reviewed in Introduction). So far, however, only one study has directly linked this decrease to parent–offspring

interactions. Specifically, house sparrows, *Passer domesticus*, nesting near a noisy electric generator had lower parental feeding rates, nestling growth rates and recruitment of nestlings into the breeding population than sparrows nesting at quieter locations (Schroeder et al., 2012). Other evidence suggests that the lowered fitness in noise is not attributable to disrupted mate choice or a reduction in territory quality, which are the other main factors proposed to explain why noise reduces fitness in songbirds (Schroeder et al., 2012).

In the present study, however, noise altered parent–offspring interactions, but did not alter food allocation or feeding rates. Similarly, in a previous study we played noise through almost the entire nestling period (day 3 to day 15) and found effects on the call structure of nestlings, but not on their mass or wing growth (Leonard & Horn, 2008). Thus, we have good evidence that noise disrupts parent–offspring interactions in tree swallows, but no evidence that this disruption lowers reproductive success.

Reproductive success might be unaffected by noise because nestlings successfully compensate for the noise, by increasing their responsiveness to their parents and each other and by raising the amplitude and changing the structure of their calls. In the short term, these adjustments are probably not costly, because growth is unaffected and because begging in this species is energetically cheap (Leonard, Horn, & Porter, 2003). We applied moderate levels of noise in this study, however. As noise levels increase, these adjustments are likely to become increasingly ineffective and costly.

In particular, although begging may be energetically cheap, higher begging levels can increase physiological stress (e.g. Moreno-Rueda, Redondo, Trenzado, Sanz, & Zúñiga, 2012), which would compound any stress the noise can cause via other mechanisms (e.g. Blickley et al., 2012). In turn, chronically elevated stress during the nestling period may introduce long-term costs, such as disruptions in auditory development (e.g. Amin, Gastpar, & Theunissen, 2013), whose consequences may not be apparent until well after the young have left the nest.

## Acknowledgments

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