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Marty L. Leonard · Andrew G. Horn

Dynamics of calling by tree swallow (*Tachycineta bicolor*) nestmates

Abstract The begging display of nestling passerine birds has become a model for examining the evolution of animal signals. A particular problem for nestlings when transmitting begging signals to parents may be interference from nestmates. The strategies used by nestlings to reduce signal interference have not been studied, yet potentially contribute to the design of these complex displays. In this study, we recorded the begging calls of nestling tree swallows (*Tachycineta bicolor*) when alone and with a begging nestmate, to determine whether nestlings changed the output, structure or timing of their calls in ways that would reduce acoustic interference. We found that nestlings increased their call rate in the presence of a begging nestmate, but did not alter the length, amplitude or frequency of their calls. They also appeared not to adjust the timing of their calls to avoid those of nestmates. Contrary to expectation, nestling calls became more similar in some aspects when nestmates called together. An increase in call rate in the presence of a begging nestmate should increase the likelihood that a parent detects an individual's calls. However, if all nestlings increase their calling rate in response to competitors, then the overall level of acoustic interference across the brood is potentially increased, an effect exacerbated by the tendency for call similarity to increase when calling together. We discuss how increasing call rate may improve detectability despite this effect and we also examine how an increase in rate and call similarity may serve to produce a strong brood signal.

Keywords Begging · Nestmate interactions · Tree swallows · Nestlings · Animal communication

M.L. Leonard (✉) · A.G. Horn
Department of Biology, Dalhousie University, Halifax,
Nova Scotia, B3H 4J1, Canada
e-mail: mleonard@is.dal.ca

Introduction

A problem encountered by signallers in many communication systems is interference from competing signals. This may be especially relevant for acoustic signals, which seem to be particularly susceptible to masking effects (Greenfield 1994). Perhaps not surprisingly then, the vocal displays of a variety of species seem designed to circumvent acoustic interference. For example, insects, frogs and birds of several species alternate rather than overlap their calls or songs with nearby conspecifics (Gerhardt 1994; Greenfield 1994; Todt and Naguib 2000) and sympatric species of frogs that call at the same time of day tend to produce calls at different frequencies (e.g. Narins and Zelick 1988). Thus, selection to reduce signal interference seems to play a role in shaping acoustic displays.

Begging by nestling passerine birds has become a model for examining the design of animal signals (Godfray 1995). The acoustic component of this display involves the production of loud calls given by nestlings when parents arrive with food. These begging calls contain information on nestling hunger levels and condition (e.g. Hussell 1988; Price and Ydenberg 1995; Kilner et al. 1999) and they also appear to be used by parents when making feeding decisions (e.g. Price and Ydenberg 1995; Kilner et al. 1999).

One of the main obstacles to effective acoustic transmission by calling nestlings is thought to be interference from nestmates (Choi and Bakken 1990; Dawkins and Guilford 1997). Loud concurrent calls from several begging offspring are thought to mask one another and obscure the individual call characteristics that parents could use when selecting which nestling to feed (Choi and Bakken 1990). Previous work on insect and frog calls (e.g. Greenfield 1990; Klump and Gerhardt 1992) suggests several ways in which nestlings might alter their calling to reduce these masking effects. For example, they could increase call output, such as loudness, length or rate and, thus, increase the likelihood that parents detect their call. Nestlings could also change structural fea-

tures such as frequency, so that calls are distinguishable from those of nestmates. Finally, they could time the delivery of their calls to avoid or minimise overlap with nestmate calls.

The strategies used by nestling birds to reduce interference from nestmates have not been studied, yet may be relevant to the large body of research that attempts to explain why begging appears to be unnecessarily conspicuous (Godfray 1995; Kilner and Johnstone 1997). For example, if nestlings attempt to overcome interference by increasing the loudness or rate of their calls, some of the conspicuousness of begging signals may be explained by selection for effective signal transmission.

The purpose of our study was to determine if nestling tree swallows, *Tachycineta bicolor*, alter the output, structure or delivery of their begging calls in response to the calls of nestmates and, if so, whether these responses vary with nestling age and size. We examine the effect of age because call structure changes dramatically with age (Leonard et al. 1997a), so strategies to reduce masking might also be expected to change. Similarly, the size of a nestling relative to its nestmates might also influence calling strategies.

Tree swallows are ideal for such a study because their begging calls provide information on the hunger and thermal needs of individual nestlings (Leonard and Horn 2001a) and parents attend to these signals when making feeding decisions (Leonard and Horn 2001b). Thus, the effective transmission of individual begging calls should be important in this species. Furthermore, because three to four nestlings typically call on each feeding visit in average-sized broods of five (Leonard and Horn 1996), individual calls are potentially susceptible to masking effects.

Methods

We conducted this study between 1 May and 31 July 1999 in the Gaspereau Valley of Nova Scotia, Canada, using a population of box-nesting tree swallows (study sites described in Leonard and Horn 1996).

First-egg dates and hatching dates were determined by checking nestboxes every 2 days until the predicted hatching date. Nests were then checked daily until hatching was complete. When nestlings were 7 or 8 days old (hatch=day 1), we removed the nestlings from 26 broods (mean±SE brood size=5.38±0.18) and weighed each to the nearest 0.1 g. We then placed the largest (15.25±0.36 g), smallest (11.47±0.38 g) and two middle-ranked (13.69±0.36 g) nestlings by weight into a heated container and drove them to the laboratory. If the entire brood was required for the experiment, we temporarily transferreded two nestlings of the same age from a nearby nest, so that parents would continue to feed at the original nestbox. In the laboratory, we standardised hunger levels by stimulating nestlings to beg with parental contact calls (Leonard et al. 1997b) and feeding them moistened Hartz's egg biscuit for birds until they no longer begged in response to the calls. We did this so that differences in begging during the experiment were less likely to be caused by nestlings' short-term feeding histories.

We performed two trials on each brood, one in which the large and small nestlings were recorded singly and together (i.e. unmatched trials) and another in which the two middle-sized nes-

tlings were recorded under the same conditions (i.e. matched trials). Recordings took place in a nestbox lined with a soft cloth and maintained at approximately 37°C. A cardboard partition separated the right and left sides of the box and prevented visual or physical contact between nestlings. Begging calls were recorded with two lapel microphones (Genexxa 33-3003 lapel) secured to opposite sides of the nestbox and connected to each channel of a stereo digital-audio tape recorder (Sony DM-100). We also videotaped each trial with a Panasonic PV-900-K VHS videocamera placed against a Plexiglas plate that replaced one side of the box.

One hour after the feeding, we placed the nestlings in the nestbox and stimulated them to beg by playing six repetitions of a sequence of two parental contact calls that began 1 s apart and were repeated every 5 s. We then videotaped and recorded their responses when alone and with the other nestling. The location (i.e. left or right side) of the first nestling tested alone was initially selected at random and then alternated in remaining trials, as was trial order (nestlings matched or unmatched in size) and whether the large or small nestling was used first in unmatched trials (always random for matched nestlings). We also randomly selected the sequence of testing (i.e. alone, alone, together) for the first trial, but then cycled through the other combinations in the remaining trials. In all cases we waited for 1 min after moving nestlings into the nestbox before beginning the playback. We fed nestlings at the end of trials and returned them to their home boxes. Nestlings were away from their nestboxes for an average of 1.5 h.

The entire procedure was also repeated using large (23.65± 0.48 g), small (20.60±0.57 g) and mid-sized (22.38± 0.49 g) nestlings from 16 broods of 13-day-old nestlings. Eight of these broods had also been tested as younger nestlings. With the following exceptions, the protocols used in these trials were identical to those described above. We conducted trials on older nestlings at room temperature rather than at 37°C because nestling tree swallows are endothermic by 13 days post-hatch (Marsh 1980). We also had a 2-h acclimation period before beginning each trial and waited between 5 and 10 min after nestlings were moved into the nestbox before playing parental contact calls. This latter change in protocol was necessary because older nestlings take longer than younger nestlings to settle following handling. Thus, older nestlings were away from their home nestbox for approximately 3 h. We recorded no mortality of nestlings that could be attributed to being used in these experiments.

Acoustic analyses

To quantify changes in call structure in response to our treatments, we digitised all calls at 44 kHz and 16 bits using Canary 1.2 software (Charif et al. 1995). When two nestlings were calling in the same recording session, we used the amplitude of the calls on the time waveform (oscilliscopic) display to distinguish between the calls of each nestling (e.g. the nestling on the left side of the nestbox was louder in the left channel of the recording). We excluded calls from the analysis if the identity of the caller was ambiguous (less than 1% of calls). Both nestlings had to call when they were alone and when they were placed with their nestmates for a trial to be included in the analyses.

From spectrographs of the calls (filter bandwidth 699 Hz, grid resolution 3 ms×22 Hz), we took the following measurements of call output: call rate (total number of calls in response to the six parental calls, calls/5 s), call amplitude (root mean square pressure of the whole call, in dB, ref. 0.02 mPa, calibrated as in Leonard and Horn 2001a) and call length (ms). We also took the following measures of call structure: frequency range (highest frequency minus lowest frequency, in Hz) and peak frequency (the frequency with the highest amplitude in the call, in Hz). All call features, except for call rate, were averaged across the sequence of six parental contact calls. Correlations between different call features were low (Leonard and Horn 2001a), so all were included in our analyses.

We used cross-correlation analyses (Charif et al. 1995) to examine the overall similarity between calls given when nestlings

were alone versus when they were with a nestmate. Cross-correlation yields an overall measure of the similarity between two calls by aligning the pair of sonagrams along the time axis at the point where the calls show the most overlap, and then measuring the correlation between the amplitudes of the two calls for each point in the frequency versus time plane. The cross-correlation value is the correlation between the amplitude of the calls at every point on the sonagram and, thus, is a measure of how well the sounds coincide in the distribution of their energy across the sonagram (Charif et al. 1995). We calculated the cross-correlation between the last call delivered by each nestling when calling alone and when calling together. We selected the last calls to allow the nestlings as much time as possible to adjust their call structure to that of their nestmates. Amplitudes were normalized before cross-correlation (Charif et al. 1995), so that variation in overall amplitude of calls would not affect cross-correlation values.

Cross-correlation used to measure call similarity has drawbacks for some applications. For example, two bird songs that follow exactly the same pattern in frequency with time can have a low cross-correlation if one song is given at a slightly slower tempo or at a higher frequency than the other (Charif et al. 1995). In our case, however, cross-correlation is appropriate because we were interested in how much nestling calls overlapped one another in frequency and time, which is exactly what cross-correlation measures.

Statistical analyses

We tested whether the response of nestlings to the calls of nestmates varied with age or size of their competitor by first calculating, for each nestling, the difference between the value of the call feature (e.g. rate) when it was alone and when it was with its nestmate. We averaged these differences for the two nestlings in each trial, to produce one datum per trial. We entered these data into two one-way ANOVAs: one testing for an effect of nestling age (young or old) and another testing for an effect of relative size (matched or unmatched). Our intention when designing the experiment was to test for age and size effects using nests as blocks. However, obtaining complete blocks in which each of four nestlings called when both alone and together proved to be difficult. To avoid pseudoreplication in the current analyses, trials conducted on the same brood (e.g. cases where matched and unmatched trials on the same brood were successful) were weighted so that each brood contributed only one degree of freedom to the analysis, and the error term was based on variation among broods, rather than among trials or nestlings (Winer 1971).

We also tested whether call similarity when alone or together varied with age or relative size using the method described above, except that we used cross-correlation values rather than differences. Because averaging differences for large and small nestlings in unmatched trials could obscure size effects, we also tested whether differences between large and small nestlings varied, using paired t-tests. Finally, we used paired t-tests to compare whether call features when nestlings were alone differed from features when they were with a nestmate.

We conducted power tests to calculate the minimum proportion of variation in the dependent variable that each of the above tests could detect, if a significant effect had existed (ω^2, a measure analogous to R^2; Hays 1988). Using a power of 0.80 and an alpha level of 0.05 (Cohen 1977), the minimum proportion of detectable variation for each test was – ANOVAs on age and relative size: 0.20; paired t-tests for large versus small nestlings: 0.23; paired t-tests for nestlings alone versus together: 0.13.

We examined whether nestlings timed their calls in relation to the calls of nestmates. We calculated the time interval between the start of successive calls by each nestling (i.e. A_A) and between the start of its call and its nestmate's next call (i.e. A_B). We used only intervals in which the first nestling did not call again before its nestmate's call (i.e. the sequence A_B_A) and we did not use intervals in which a parental contact call from the stimulus tape intervened between either type of interval. We then determined whether nestmates called in or out of phase with one another, by first calculating the phase angles between their calls using the equation

$$\frac{360 \times A\_B}{A\_A}$$

For each nestling, we then tested whether its phase angles were concentrated around a particular angle by calculating the Rayleigh statistic, r, which varies from 0 (i.e. timing of call is random with respect to the call of another nestling) to 1 (i.e. timing is non-random with respect to the call of another nestling; Klump and Gerhardt 1992; Zar 1999). For example, nestlings calling simultaneously with their nestmate would have a distribution of phase angles that was concentrated at 360°, while nestlings that placed their calls exactly between their nestmate's calls would have phase angles that were concentrated at 180°. In either case, the more the phase angles were concentrated at a particular angle (i.e. the less variation about the mean phase angle), the closer r would be to 1. Rayleigh statistics were then tested for significance for each nestling following Zar (1999).

All means are presented ±1 SE and significance levels were set at P=0.05. We checked residuals for departures from normality (Shapiro-Wilk test) and homogeneity (Brown Forsythe tests; SAS 1995). In all cases, departures were due to one to three outliers and distributions were otherwise symmetric. We repeated these analyses with the outliers removed and also with non-parametric tests and achieved similar results. Including the outliers in parametric tests yielded the most conservative results, so we present those results here.

Results

Age and size

We found no significant effect of age or relative size on the differences in call features or cross-correlation values when nestlings were alone versus when they were together (age: all $F_{1,25}$<4.05, P>0.10; size: all $F_{1,25}$<2.94, P>0.18). The differences in call features of large and small nestlings when calling alone and together also did not differ significantly (all t<1.35, df=13, P>0.20), except that amplitude differences were less for large than for small nestlings (paired t-test, t=–2.40, df=13, P=0.03; Table 1). In the remaining analyses, we pool trials at different ages and sizes and, with the exception of amplitude of different-sized nestlings, use the average value for nestlings from each trial when alone and together. Amplitude measurements for large and small nestlings were analysed separately. In cases where more than one trial on a brood was successful, we average the values for nestlings when alone and together across the different trials.

Table 1 Mean (±SE) call rate, amplitude, length, frequency range, peak frequency and cross-correlation values for tree swallow nestlings calling alone and together with a nestmate. Means were compared using paired t-tests (df=25 for all comparisons)

Variable	Alone	Together	t	P
Rate (calls/5 s)	5.11±0.51	7.44±0.90	4.48	0.001
Amplitude (dB)	73.1±0.94	73.7±0.91	1.08	0.23
Length (ms)	47.2±4.04	44.9±3.64	–1.57	0.13
Frequency range (kHz)	1.70±0.11	1.67±0.13	–0.36	0.72
Peak frequency (kHz)	5.12±0.11	5.07±0.10	–0.85	0.40
Cross-correlation (r)	0.47±0.02	0.56±0.02	4.03	0.001

Call output, structure and timing

With one exception, call output and structure did not change significantly when nestlings called alone versus when they called with a nestmate (Table 1). The exception was call rate, which increased significantly when nestlings were together (Table 1). Small nestlings tended to increase the amplitude of their calls when placed with their larger nestmate (alone: 70.2±1.70 dB; together: 73.1±0.97 dB; paired *t*-test, *t*=2.11, *df*=13, *P*=0.06). However, large nestlings did not change their call amplitude significantly when placed with a smaller nestmate (alone: 71.9±1.00 dB, together: 71.6±0.68 dB, paired *t*-test, *t*=–0.39, *df*=13. *P*=0.70). Cross-correlation values changed significantly when nestlings were together, with begging calls becoming more similar, in terms of spectral overlap over time, when nestlings were with a nestmate (Table 1).

Finally, the calls of nestmates showed no tendency to be in or out of phase with one another. Rayleigh coefficients were low (*r*=0.30±0.03, *n*=74 nestlings) and were only significant for 4 of 74 nestlings. According to this analysis, the timing of nestmate calls is independent, so calls will overlap at chance levels determined by call length and intercall interval. Using our mean values for these variables (Table 1), in an average-sized brood of five nestlings, on average, 15–20% of a nestling's calls would be overlapped by the calls of a nestmate (assuming three to four nestlings begging on most visits; Leonard and Horn 1996).

Discussion

We have previously shown that features of tree swallow begging calls increase with hunger (Leonard and Horn 2001a) and that parents preferentially direct feeding attempts toward playbacks of calls of hungry nestlings (Leonard and Horn 2001b). Given these observations, we predicted that nestlings might change the output, structure or timing of their calls to avoid acoustic interference from calling nestmates and ensure that parents receive their calls. In the current study, we found that nestlings increased their call rate when their nestmates called. Surprisingly, we also found that the begging calls of nestmates became more, rather than less, similar when nestlings called together. We also found no effect of age or size differences in responses to nestmates, although these analyses had lower power than those testing for overall effects of nestmates. We did find that small nestlings tended to increase the amplitude of their calls when with a larger nestmate. The effect was, however, relatively weak.

Call rate

Perhaps the most fundamental way to increase the redundancy of a signal, and hence the ease with which it is received, is by repeating it (Wiley 1983). This may be one reason why increases in signal rate are a common response to acoustic interference in a variety of communication systems (e.g. advertising orthopterans, frogs, birds; Gerhardt 1994; Greenfield 1994; Todt and Naguib 2000). By increasing calling rate in the face of interference from nestmates, individual tree swallow nestlings may increase the likelihood that parents detect their calls. This could happen in two ways. Nestlings that increase their call rate may simply swamp the airspace with their calls and, thus, increase the chances they are heard by parents. Another possibility is that by increasing call rate, a nestling increases the probability that its call is the first a parent hears when it arrives at the nest. In many communication systems, receivers are differentially attracted to the first signal they detect in a group of closely timed signals (Greenfield 1994). Thus, a nestling calling at a high rate may increase the chances that it is detected before its nestmates.

If all signallers increase their rate simultaneously, however, detection of individual signals may become more, rather than less, difficult. This effect may be overcome, however, if parents also incorporate information from visual signals (e.g. gaping) when making feeding decisions. In addition, if parental choice is based on which nestling they hear first, rather than on call rate per se, the advantage of increasing call rate may persist even when nestmates are calling at high rates.

An interesting aspect of the response of nestlings to the calling of nestmates relates to the conspicuousness of begging signals. That is, if each signaller responds to the calls of its nestmates by increasing its own rate, then the intensity of the signal in general is likely to be greater than if they, for example, shifted the frequency of the signal to overcome interference. Thus, if nestlings mainly rely on increasing call rate to reduce masking, then some of the conspicuousness and costliness of begging signals, now attributed to attempts by nestlings to exaggerate their needs or to costs required to enforce honesty (Godfray 1995), may instead be explained by selection for effective signal transmission.

Call convergence

Interestingly, we found that the calls of nestmates became more similar, as measured by cross-correlation, when nestmates were placed together. How call convergence is achieved is not clear from our current data. Inspection of sonograms did not reveal any single set of features which converged (Fig. 1). Post hoc analyses of call measurements did, however, indicate that call lengths were more similar when nestmates were together than when they were apart (paired *t*-tests on absolute differences between nestmates when alone and together: *t*=3.99, *df*=25, *P*=0.001). None of the other variables we measured became more similar when nestmates called together (all *P*>0.05). So call length, or, perhaps, some variable not measured in this study, may account for the increase in cross-correlation scores. We also could not

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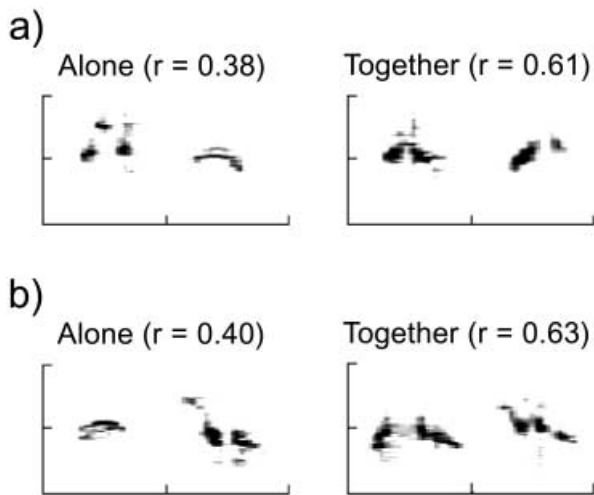
Fig. 1 Sonagrams of calls of two 7-day-old (**a**) and 13-day-old (**b**) nestmates when recorded alone and together (cross-correlation coefficient, *r*, for each pair in parentheses). *Tic marks* are at 5-kHz intervals on y-axis, 100-ms intervals on x-axis; filter bandwidth is 350 Hz

determine, from sonagrams or analyses of call length, whether convergence occurred by one nestling matching the other's call structure or by both nestlings converging on an intermediate call structure. Further experiments are clearly needed to determine how call convergence is achieved.

The convergence in call structure was contrary to our expectation that nestlings would attempt to avoid interference by making their calls more distinctive. It is interesting to speculate on why this might occur. One possibility is that several similar calls convey a stronger overall signal to parents than several different calls and ultimately are more effective in increasing the overall feeding rate to the brood. Thus nestlings may benefit by matching, to some degree, the calls of nestmates. At the same time, by calling at a high rate they may also increase the chances that parents detect their signal.

Calling and other components of begging

In the present experiment, we examined how changes in call output and structure might reduce acoustic interference. However, other aspects of begging might influence the ease with which parents discriminate amongst begging nestlings. For example, small spatial separation among nestlings could substantially reduce masking effects (Klump 1996), so the calls of nestlings sitting on opposite sides of the nest might not interfere with one another. Similarly, the distinctiveness of nestling gapes in the parent's visual field may increase the ability of parents to discriminate among calling nestlings. For animal signals in general, visual and acoustic components can interact in a number of ways that may enhance reception (Rowe 1999), many of which deserve closer scrutiny in the case of begging.

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