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Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*)

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Abstract We conducted playback experiments to examine how parent tree swallows (*Tachycineta bicolor*) use nestling begging calls to distribute feedings to individuals within broods. In a first study, we used a paired-choice test to determine if parents discriminated between the taped begging calls of nestlings deprived of food and those of nestlings that had been recently fed. Our results showed that parents directed their first feeding attempt towards model nestlings near speakers playing deprived calls significantly more often than to models near speakers playing fed calls. They also made more feeding attempts overall to models with deprived calls. In the second study, we varied call rate and amplitude to examine which call features parents might use to discriminate begging calls. Parents directed significantly more first feeding attempts and more feeding attempts overall towards non-begging nestlings near speakers playing high call rates than to nestlings near speakers playing low call rates. They did not, however, discriminate between calls differing in amplitude. Previous studies have shown that parent birds use begging calls to regulate overall feeding rates to the brood. Our results suggest that parent tree swallows also use begging calls when feeding individual nestlings and, in particular, prefer calls associated with increased levels of nestling hunger.

Keywords Begging calls · Signalling · Tree swallows · Nestlings

Introduction

Nestling birds solicit resources from parents using a begging display that includes visual (e.g. posturing and

gaping) and vocal components. This signalling between nestling birds and their parents has become a model for testing ideas on parent-offspring conflict (e.g. Godfray 1995a), honest signalling of need (e.g. Godfray 1995b) and the evolution of complex displays (Kilner et al. 1999).

Much of the empirical research on this communication system supports the idea that begging displays are honest indicators of offspring need that are used by parents to allocate resources (Godfray 1995b). That is, the intensity of visual and vocal signals increases with nestling hunger (e.g. Kacelnik et al. 1995; Price and Ydenberg 1995; Leonard and Horn 1998; Kilner et al. 1999) and with poor physical condition (e.g. Hussell 1988; Price et al. 1996; Iacovides and Evans 1998; Lotem 1998). Parents generally respond to these signals by directing feedings to the most intensively begging nestling in their brood (e.g. Kilner 1995; Price et al. 1996; Kölliker et al. 1998; but see Cotton et al. 1999) and by increasing their provisioning rate to the brood as a whole (Hussell 1988; Leonard and Horn 1998; Ottosson et al. 1997; Kilner et al. 1999). Physical competition amongst nestlings for access to parents also influences feeding decisions (e.g. McRae et al. 1993; Kilner 1995; Kölliker et al. 1998; Cotton et al. 1999), with the most intensively begging nestlings usually occupying optimal feeding locations (but see Cotton et al. 1999). Thus, nestlings solicit resources from parents using a complex suite of visual and vocal signals and physical competition for space.

Most studies examining the relationship between begging and parental response have focussed on how this suite of signals and physical competition influences parental feeding decisions. This approach is informative in that it links the behaviour of the nestlings to a parental response. However, it does not identify the relative impact of each factor in influencing parental feeding decisions. Isolating the role of features such as gape colour and begging calls which, unlike physical competition, have presumably evolved as signals, is important for understanding the evolution of begging. To date, the only studies to experimentally isolate different signal compo-

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nents have focussed on manipulations of gape colour (Götmark and Ahlström 1997; Kilner 1997; Noble et al. 1999).

Here we conducted the first manipulation of the vocal component of the signal to examine how parents might use the begging call to distribute feedings within broods. Previous studies have shown that playback of recorded begging calls increases parental provisioning rates to broods (e.g. Ottosson et al. 1997; Burford et al. 1998; Price 1998; Kilner et al. 1999; but see Clark and Lee 1998). However, there is no information on whether the call influences the allocation of food within broods. The vocal component of begging is particularly interesting because calls can attract predators to nests (Leech and Leonard 1997; Dearborn 1999; Haskell 1999) and so may account for the main cost of begging. The costs of begging are thought to prevent escalation of the signal and enforce its honesty. Thus, determining the influence of the vocal components of begging on parental feeding decisions is useful for understanding the evolution of this display.

The purpose of our study was to determine whether parent tree swallows (*Tachycineta bicolor*) use nestling begging calls to distribute feedings within broods. We conducted two experiments to address this question. We used a paired-choice test to examine whether parents discriminated between the begging calls of nestlings deprived of food and those that had recently been fed. We then varied the rate and amplitude of calls to determine whether these features might be used in discrimination. In both experiments, we also examined whether responses to playback differed between male and female parents, because earlier work on this population suggested that the sexes might differ in their responses to begging (Leonard and Horn 1996).

In tree swallows, both large and small nestlings increase the rate and duration of their calls with increasing food deprivation and large nestlings also increase the amplitude of their calls (Leonard and Horn, in press). Thus, begging calls potentially carry information on nestling hunger and size that could be used by parents to make feeding decisions.

Methods

We conducted this study in the Gaspereau Valley of Nova Scotia, Canada, in June and July of 1998 and 1999. A description of the study sites is included in Leonard and Horn (1996). Tree swallows at these sites bred in wooden nest boxes and first egg and hatching dates were determined by checking boxes every 2 days. Adult females were marked on the head with a small dot of non-toxic paint to allow us to recognize male and female parents on videotapes.

Choice experiment

We played taped begging calls (see below for details) to parents at 13 nests in 1998 and 34 nests in 1999. Technical difficulties (8 trials) and failure of parents to return to the nests within our allotted time (6 trials) reduced the final sample size to 8 successful trials in

1998 and 25 (12 rate and 13 amplitude) successful trials in 1999. The average age of the broods at the time of the experiments was 7.6 days (range 6–8 days) in 1998 and 7.3 days (range 6–10 days) in 1999. We describe protocols for each year separately because questions and methodology differed between years.

Begging calls and parental discrimination

In 1998, we presented parents with recorded begging calls of nestlings that had been deprived of food for 20 min (i.e. fed) and the same nestlings after they had been deprived for 100 min (i.e. deprived) to determine if the parents discriminated between the calls.

Twenty-four hours before each trial, we opened the hinged side of the nestbox and placed a Plexiglas plate in the opening. We then wrapped a dark plastic bag around that side of the nestbox. This kept the nestbox dark and let parents habituate to the bag that would eventually cover a videocamera. The next day, we placed two InterTan 33-8396 earphone speakers in the box and attached them by an 18-m cable to a Sony WM D6 "Professional" cassette recorder. The speakers were secured to the nesting material midway along the length of the nest on the left and right edges. Both speakers were oriented upward toward the nestbox opening. We then placed a Panasonic PV-900-K VHS videocamera on a tripod facing the open side of the box and covered it with the plastic bag. We moved away from the nest and waited until at least one parent fed a minimum of three times to verify that parents were feeding normally after our initial disturbance.

Following these feeding visits, we quickly removed the resident nestlings and put them in a container with a hot-water bottle. We then placed one of two identical, plasticene model nestlings directly ahead of each speaker. The models were the approximate size and colour of 7-day-old tree swallow nestlings and were in a begging posture with open gapes oriented toward the nest opening. When parents returned to the nestbox to feed, the begging calls of fed and deprived nestlings were played simultaneously and continuously from each speaker. The volume of the playback was adjusted to natural levels and kept constant and equal throughout the study. Across trials we alternated the fed and deprived calls between the left and right speaker; however, the position of the models and the speakers was consistent across trials. Trials continued until male and female parents made at least one feeding visit each or 0.5 h had elapsed. At the end of the trial, resident nestlings were fed and returned to their nestbox.

Stimulus tapes

We used recordings of the begging calls of four 7-day-old nestlings made during an experiment examining how begging vocalizations changed with food deprivation (Leonard and Horn, in press). The taped calls were digitized at 44 kHz and 16 bits using Canary 1.2 software (Charif et al. 1995). They were then re-recorded with a Sony WM D6 "Professional" cassette recorder onto Sony metal SR cassette tapes in a stereo program consisting of 3 s of begging calls, delivered at natural rates as they were recorded, with fed calls in one channel and deprived calls in the other, and then looped continuously. In total, we created four stimulus tapes, each with the begging calls of an individual nestling experiencing fed (i.e. 20 min without food) and deprived (i.e. 100 min without food) conditions. Parent tree swallows do not discriminate between the calls of their own nestlings and those of other pairs (Leonard et al. 1997a), so their response to the experiment should not be influenced by the identity of the nestling on the stimulus tape.

Video analyses

An observer blind to the treatment watched the videotapes and noted (1) the number of feeding attempts by each parent to the right and left model and (2) the time spent by each parent adjacent to the right and left model. We considered that a feeding attempt

had occurred when the parent placed its bill, with food, into or above a model's open gape. Parents were considered to be "adjacent" to a model if they were facing the model while standing in the same half of the nestbox. Parents made an average of 1.60 feeding visits to nests during the trials (range 0–7). When they made multiple visits, we included information from the first two visits only because we assumed that these first visits would best reflect their preference.

Call features and parental discrimination

In 1999, we presented parents with pairs of begging calls that differed in either rate or amplitude to examine some of the features potentially used in discrimination.

Twenty-four hours before each trial, we removed the nest and young from the home nestbox and replaced the nestbox with an experimental box. Experimental boxes were identical to home nestboxes except for a 10×10 cm opening cut in the back wall (i.e. wall opposite the nest opening) of the box and the presence of two InterTan 33-8396 earphone speakers attached midway along the length of the box on the left and right sides. The speakers were level with the top of the nesting material when the nest was in place and oriented toward the nest opening. The boxes were attached to the nest poles at the same height and with the hole oriented in the same direction as the original box. After securing the experimental box, we returned the nest and young and covered the back of the box with a dark plastic bag.

The next day we attached the speakers to an 18-m cable that we connected to a Sony TCD-D100 DAT recorder. We also placed a Panasonic PV-900-K VHS videocamera on a tripod pointed through the opening at the back of the box and covered it with the plastic bag. We then removed the resident nestlings and placed them in a container with a hot-water bottle. We fed the two nestlings closest in weight to satiation, by stimulating them 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. These nestlings were then returned to the experimental box and each was placed adjacent to a speaker with their heads oriented toward the nestbox opening. In 31 of the original 34 trials, satiated nestlings were silent and maintained non-begging postures throughout the trial. In the remaining 3 trials, one of the nestlings begged in response to a parent. These trials were not included in the analyses.

Begging calls were played simultaneously and continuously from each speaker when a parent entered the box. Across trials we alternated the high- and low-rate or high- and low-amplitude calls between the left and right speakers which remained consistent across all trials. We also alternated rate and amplitude playbacks across trials. Trials continued until male and female parents made at least one feeding visit each to the nest or 0.5 h had passed. At the end of the trials, experimental boxes were replaced with the original nestbox and all nestlings were fed and returned to their home nestboxes.

Stimulus tapes

We have previously shown that tree swallow begging calls increase in rate, amplitude and duration with increasing periods of food deprivation (Leonard and Horn, in press). In the current study we presented parents with calls that differed in either rate or amplitude. We chose to manipulate these features because, unlike duration, they can be altered without changing other aspects of call structure (Beeman 1998).

Playback tapes were recorded and digitized as described above. Call rate treatments were continuous loops of 3 s of begging calls, delivered at natural rates as recorded (low rate, 80 calls/min) and 3 s of calls in which the inter-call intervals were halved (high rate, 160 calls/min). Call amplitude treatments were continuous loops of 3 s of begging calls amplified at either a low intensity of 65 dB or a high intensity of 71 dB. The background

sounds that occurred in inter-call intervals were digitally silenced before the amplification, so that treatment effects could not be attributed to background noise. In both experiments, the high and low treatment calls reflected the mean (i.e. low) and 1.5 standard deviations above the mean (i.e. high) rates and amplitudes for 20, 6- to 7-day-old nestlings deprived of food for 45 min (Leonard and Horn, in press). Thus, our treatments reflected rates and amplitudes within the natural range. In total, we created three stimulus tapes for each treatment.

Video analyses

An observer blind to the treatments watched the videotapes and noted (1) the number of feeding attempts by each parent to right and left nestlings and (2) the time spent by each parent adjacent to the right and left nestling (as measured above). We considered that a feeding attempt had occurred when the parent thrust its bill, with food, toward a nestling. Parents made an average of 1.74 feeding visits to nests during the trials (range 0–8). When parents made multiple visits, we used information from the first two visits only.

Statistical analyses

Because parents are expected to use begging signals to assess offspring need, we predicted they would show a preference for the calls that reflected an increased need for food. We therefore expected a preference for deprived calls in the 1998 experiment and for high-rate and high-amplitude calls in the 1999 experiments. We thus refer to responses to these stimuli as correct responses.

In each experiment, we compared the frequency of first feeding attempts to the correct (i.e. deprived) model or correct (i.e. high rate/amplitude) nestling to chance using binomial and χ^2 -tests. We also measured the strength of parental response by comparing the total number of feeding attempts and the total amount of time spent adjacent to correct and incorrect models or nestlings. Time spent is a less direct measure of parental preference than our other measures, but correlates with the proportion of feeding attempts ($r_s=0.91$, $df=24$, $P=0.0001$) suggesting that time spent is a reasonable measure of preference in trials in which feeding attempts did not occur. We used parametric tests to examine strength of preference when data met the assumptions of these tests. Otherwise we used non-parametric equivalents. We arcsin-transformed proportions and conducted power tests for medium effect sizes (Cohen 1977) on results with $0.05 < P < 0.20$.

Results

Sex differences in response to playback

We tested for differences between the sexes by combining the results of the three experiments and examining whether females and males differed in their responses overall. The proportion of trials in which the first feeding attempts were directed toward the correct model/nestling did not differ significantly between the sexes (females 18/25 trials, males 20/23 trials, $\chi^2=1.62$, $df=1$, $P=0.20$, power=0.54). In addition, the proportion of total feeding attempts and the proportion of time spent with correct models/nestlings did not differ significantly between male and female parents (feeding attempts: females 0.71 ± 0.09 , males 0.73 ± 0.09 , paired t -test, $t=1.65$, $df=10$, $P=0.13$, power=0.20; time spent: females 0.59 ± 0.09 , males 0.58 ± 0.09 , paired t -test, $t=0.41$, $df=19$, $P=0.68$).

In the following analyses of first feeding attempts, we omitted trials in which the sexes differed in where they directed their first feeding attempt. For all other analyses we summed male and female responses in each trial for our measures of preference strength.

Begging calls and parental discrimination

Parents attempted to feed model nestlings in seven of the eight trials. Significantly more first feeding attempts were directed toward the model with the playback of deprived calls (six of six trials in which preferences of males and females matched, binomial test, $P=0.016$, Fig. 1; or five of five trials, $P=0.031$ with outlier removed – see below). In six of the seven trials with feeding attempts, parents directed more feedings to models with calls of deprived nestlings than to models with calls of fed nestlings (Fig. 2). The one exception to this pattern showed a strong bias towards the fed model, but also had an unusually high rate of feeding attempts for this data set (Fig. 2). When this apparent outlier was included in the data set, the total number of feeding attempts did not differ significantly between deprived and fed models (Wilcoxon signed-ranks test, $Z=1.19$, $n=7$,

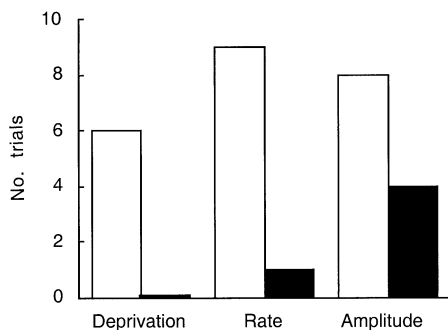


Fig. 1 Number of trials in which the first feeding attempt by parent tree swallows was directed toward a playback representing higher (open bars) or lower (filled bars) levels of food deprivation, call rate, or call amplitude

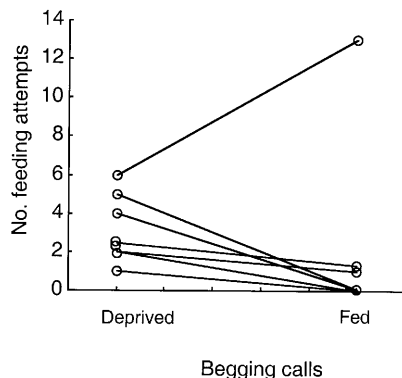


Fig. 2 Number of feeding attempts by parent tree swallows directed to models with begging calls of food-deprived and fed nestlings. Lines connect points from the same trials

$P=0.23$). However, when it was excluded, significantly more feeding attempts were directed to deprived than to fed models ($Z=2.23$, $n=6$, $P=0.026$). The time spent adjacent to models with deprived and fed playbacks did not differ significantly (deprived: 12.12 ± 5.39 s, fed: 6.38 ± 3.68 s, paired t -test, $t=1.25$, $df=7$, $P=0.25$).

Call features and parental discrimination

Parents attempted to feed nestlings in 10 of 12 rate trials and 12 of 13 amplitude trials. In rate trials, significantly more first feeding attempts were directed to nestlings with playbacks of the high call rate (9/10 trials, binomial test $P=0.01$; Fig. 1). Similarly, significantly more total feeding attempts were to the playback of high call rates (Wilcoxon signed-ranks test, $Z=2.72$, $n=10$, $P=0.007$). The time spent near each nestling did not, however, differ for high and low call rates (high rate: 61.40 ± 18.88 s, low rate 27.80 ± 8.88 s, paired t -test, $t=1.74$, $df=9$, $P=0.12$, power=0.18).

During amplitude trials, parents showed no significant preference for high amplitude calls in terms of either first feeding attempts (8/12 trials, binomial test $P=0.19$, power=0.15; Fig. 1) or total feeding attempts (Wilcoxon signed-ranks test, $Z=0.67$, $n=11$, $P=0.50$). Parents also did not differ in the amount of time spent near nestlings with playbacks of high- and low-amplitude calls (high: 34.54 ± 10.10 s, low: 31.23 ± 12.67 s, paired t -test, $t=0.16$, $df=12$, $P=0.87$).

Discussion

The results of this study showed that both male and female tree swallows preferred the begging calls of food-deprived nestlings to those of recently fed nestlings and calls given at high rates to those given at low rates. Previous studies have emphasized the role of calling in regulating parental provisioning to the brood (e.g. Kilner et al. 1999). However, to our knowledge, this is the first study to show that begging calls, independently of other cues, could influence parental choice within broods.

Parents responded to our taped calls by attempting to feed models or nestlings placed by the speakers, suggesting that our experimental paradigm was an adequate simulation of the natural situation. Our experimental situation was, however, unrealistic in some respects, which makes us cautious in interpreting our results. For example, nestlings rarely call at the levels that we presented in these experiments without simultaneously reaching and gaping, so the combination of the inactive nestlings and calling found in the second study was unusual. Furthermore, calling occurs in brief bouts immediately after the parents' arrival, with sporadic calling after feeding (M.L. Leonard and A.G. Horn, unpublished data). In our playbacks, calling continued as long as a parent was in the nest. For this reason, the first attempts at feeding are likely to be our best measure of response.

Role of calling in feeding

The begging calls of a variety of species, including tree swallows, appear to vary with both long- and short-term need (Hussell 1988; Price et al. 1996; Iacovides and Evans 1998; Kilner et al. 1999) and, in some species, increases in call rate and amplitude have been associated with increases in the likelihood of a feeding to individual nestlings (e.g. Price and Ydenberg 1995). However, calls have not been isolated either statistically or experimentally from the visual components of the begging signal, so their independent influence on the distribution of food within broods is unknown.

In earlier work, we found that nestling tree swallows that reached higher, gaped sooner and were closer to the parent had an increased chance of receiving food (Leonard and Horn 1996). The current study suggests that nestling vocalizations could also influence parental feeding decisions, independently of visual cues. We are now investigating the relative impact of the visual and vocal components of begging on food allocation within broods.

In general, signals with multiple components, especially those in different sensory modalities, are thought to improve detection and discrimination by receivers (Rowe 1999). Indeed, a recent study on multiple begging signals in reed warblers (*Acrocephalus scirpaceus*) showed that visual and vocal components of the signal provided more information together than either did alone (Kilner et al. 1999). Some preliminary evidence from our study system suggests a weak correlation between the vigour of visual and vocal aspects of begging (Leonard and Horn, in press). Thus, in natural begging situations, calls may add to the redundancy of the display and thereby enhance detection and discrimination.

Features used in discrimination

Parent tree swallows in our study showed a preference for begging calls delivered at higher rates. Because nestling call rate increases with hunger, this preference would generally ensure that the “neediest” offspring receives food. This conclusion is, of course, complicated by the fact that parental feeding decisions are influenced by more than nestling begging calls (see above).

Call rate could, however, influence parental feeding decisions in two ways. If call rate contains information about nestling hunger, then parents could use this feature to actively discriminate amongst several begging nestlings, ultimately choosing the nestling with the greatest need for food. Alternatively, calling at a high rate may simply attract parental attention (Wiley 1994). That is, hungry nestlings calling at high rates would be noticed first and, therefore, would be more likely to be fed. Whatever the case, a parental preference for high calling rates should result in adaptive feeding choices by parents.

Interestingly, parents did not discriminate between calls differing in amplitude. Several possibilities might

explain this result. The first, and most obvious, is that our ability to detect a difference in amplitude was limited by low power. Another possibility is that call amplitude is not a particularly reliable indicator of nestling need. Indeed, in our earlier experiment, only large nestlings showed a relationship between call amplitude and hunger level (Leonard and Horn, in press). Thus parents may be less responsive to features that are not highly correlated with nestling condition. Finally, certain combinations of call features may interact in different ways. For example, parents may only attend to call amplitude when calls are below a particular rate or duration threshold. A more refined experimental protocol may allow simultaneous and systematic variation in a number of call features to tease apart their various contributions.

Sex differences

We found no evidence for sex differences in response to our treatments. In an earlier study on this population, males preferentially fed larger nestlings and females preferentially fed smaller nestlings (Leonard and Horn 1996). At that time, we found no differences in begging behaviour between these size classes of nestling. However, more recently, we have found evidence of differences in calling that could serve as cues for differential feeding (Leonard and Horn, in press). Thus, sex differences possibly do exist and might be found using another experimental playback paradigm.

Implications for signal design

Previous workers assumed that the calls of hungry nestlings would mask one another, making it impossible for parents to use individual call characteristics when selecting which nestlings to feed (e.g. Choi and Bakken 1990). Various mechanisms can, however, provide release from call masking (Klump and Gerhardt 1992). Studies of auditory masking in birds, for example, suggest that the reception of calls may be substantially enhanced by slight spatial separation between callers or by delivery of calls in silent intervals (Klump 1996).

If parents use calls as a guide to feed individual nestlings, then the selective pressures on call structure and delivery to overcome masking by nestmates may be considerable. Far from being a cohesive nest in which all nestlings call for food with one voice, the nest may instead be seen as a potentially complex communication network (McGregor and Dabelsteen 1996). The structural features of begging signals, especially begging calls, may be designed to optimally avoid or exploit the costs and benefits of signalling in such a network. In particular, the apparently excessive conspicuousness of the begging display, which has attracted so much theoretical attention, may in fact be necessary in the face of the noise produced by multiple signallers.

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