



Acoustic signalling of hunger and thermal state by nestling tree swallows

MARTY L. LEONARD & ANDREW G. HORN
Department of Biology, Dalhousie University

(Received 8 November 1999; initial acceptance 28 February 2000;
final acceptance 21 June 2000; MS. number: A8629)

The begging displays used by altricial nestling birds to solicit care from parents include vigorous movements and loud calling. These begging signals have attracted considerable interest, mainly because their intensity seems excessive for the function of transmitting information about nestling need to parents. However, how information on need is encoded in the various components of the signal, especially its acoustic components, is poorly understood. We examined how begging calls of large and small nestling tree swallows, *Tachycineta bicolor*, changed during a short period of food deprivation and cooling, as a first step in determining the role that various call characteristics played in advertising nestling need. In contrast to previous studies, we examined several call variables, and related them not only to need for food but also need for warmth. When nestlings were deprived of food, their calls increased in rate and length. Large nestlings also increased the amplitude of their calls. When nestlings were cooled during food deprivation, they decreased the frequency of their calls and their call rate. The latter trend was especially evident in small nestlings. Our results suggest that begging calls carry information not only on the overall hunger level of broods, as emphasized in previous studies, but also on the size, hunger and thermal need of individual nestlings. Further tests are needed to determine whether parents use this information and whether begging calls are optimally designed to convey it.

© 2001 The Association for the Study of Animal Behaviour

The conspicuous begging displays of young animals have become models for studies on the evolution of animal signals (reviewed by Kilner & Johnstone 1997). A particular focus of these studies has been to understand why begging signals appear so intense. For example, altricial nestling birds expose brightly coloured gapes, flap their wings and call loudly when begging for food from parents. This apparently vigorous display seems unnecessary given the proximity of parents and young during signalling. Furthermore, in many cases, intense begging has predation costs (e.g. Leech & Leonard 1997; Dearborn 1999; Haskell 1999).

Several theoretical approaches have been taken to suggest why nestlings signal their needs so conspicuously. Parent–offspring conflict theory suggests that seemingly exaggerated begging is a result of selection on offspring to manipulate parents into providing more resources than parents have been selected to provide (e.g. Godfray 1995). Honest signalling models, on the other hand, suggest that begging reliably conveys aspects of offspring need (e.g. hunger) that parents cannot assess directly. Begging is

Correspondence: M. L. Leonard, Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada (email: mleonard@is.dal.ca).

more intense than seems necessary because the costs associated with increased intensity keep the signal honest (Godfray 1991, 1995). A more recent, and largely untested, explanation is that begging is conspicuous to increase the likelihood that receivers (i.e. parents) detect the signal in the noisy environment of nests (Dawkins & Guilford 1997). The perceptual difficulty of quickly determining the needs of individual offspring, in the face of competing displays from several offspring, may select for begging signals with increased detectability, such as louder or longer begging calls (Wiley 1983; Dawkins & Guilford 1997).

These theoretical approaches are difficult to evaluate, however, without more detailed information on the structure and function of the various components of begging displays, especially on which components encode information on nestling need. Recent research has started to tease apart the roles of the various visual components of begging, especially gape colour (Kilner 1999). The acoustic components of begging, however, have not been studied as intensively, so the role of different call features in signalling the need of individual nestlings is unclear. Yet the ease with which begging calls can be measured and manipulated, combined with the

groundwork provided by extensive studies of the design of other acoustic signals (e.g. bird song: [Catchpole & Slater 1995](#)), make begging calls ideal for studying the design of begging signals.

The purpose of this study was to examine how information on nestling need is encoded in the structure of begging calls given by nestling tree swallows, *Tachycineta bicolor*. In contrast to previous studies, we examine several call variables, and relate them not only to need for food but also need for warmth. Advertisement of thermal need has been overlooked in passerine birds (but see [Choi & Bakken 1990](#)), even though brooding is a critical component of parental care for their initially ectothermic nestlings (e.g. [Clark & Ricklefs 1988](#)), and advertisement of thermal need is well documented in several nonpasserine species (e.g. [Evans 1994](#); [Iacovides & Evans 1998](#)).

We also examine if the relationship between calling and nutritional or thermal need varies with nestling size. We examine the influence of size because large and small nestlings may differ in how much food or warmth they require after a set period of deprivation, and therefore may differ in how or when they call for care from parents. Also, large and small nestlings may differ in their abilities to advertise their needs effectively ([Cotton et al. 1999](#)), so smaller nestlings, for example, may have more difficulty producing longer or louder calls at high rates. Whatever the case, differences in calling by large and small nestlings could also provide parents with information on size.

METHODS

Subjects

Tree swallows are cavity-nesting passerines with altricial nestlings. Nestlings hatch over 1–3 days, resulting in size differences between the first- and last-hatched nestling that are maintained throughout the nestling period ([Leonard & Horn 1996](#)). Young are fed by both parents throughout the 20-day nestling period. Nestling tree swallows cannot regulate their own body temperature before 7–8 days of age ([Marsh 1980](#)) and so must be brooded by the female until approximately 10 days after hatching (unpublished data).

Study Sites

We conducted this study in the Gaspereau Valley of Nova Scotia, Canada between 1 May and 15 July 1998. A description of the study sites is included in [Leonard & Horn \(1996\)](#). Tree swallows at these sites breed in wooden nestboxes measuring 30 × 15 × 15 cm. First egg dates and hatching dates were determined by checking nestboxes every 2 days until 2 days before the predicted hatching date, after which nests were checked daily until hatching was complete. In the present study, nestlings were defined as 1 day old on the day that they hatched, and the age of the first-hatched nestling was considered to be the age of the brood.

General Methods

When first-hatched nestlings were 6–7 days old, we weighed them, measured their wing and tarsus length, and then removed the largest (13.6 ± 0.35 g), smallest (10.7 ± 0.35 g) and middle-ranked (12.49 ± 0.35 g) nestlings, by weight, from each of 28 broods of four to seven nestlings (four nestlings, $N=6$; five nestlings, $N=11$; six nestlings, $N=10$, seven nestlings, $N=1$). We then took them to the laboratory in a small cooler containing a hot-water bottle. This transfer took less than 10 min, during which the nestlings were not fed.

In the laboratory, we placed each nestling in an artificial nest inside one of three identical tree swallow nestboxes. One side of each box was replaced with Plexiglas, so we could see the nestlings. A heating pad beneath each nest maintained the temperature in the box at 37°C, which is approximately the mean temperature in the centre of the nest cup in natural broods at this age (38.4°C, $N=16$ broods).

We suspended a Genexxa 33-3003 lapel microphone 10 cm above the centre of each nest and attached it to a Marantz PMD-222 portable cassette recorder. We kept the sound recording level constant across each box, at a level found during pilot trials to be low enough to prevent clipping of the loudest calls, but high enough for the quietest calls to be detectable against background noise. In the first trial, we randomly assigned the large, middle and small nestlings to one of the three boxes. In subsequent trials, we cycled through the remaining combinations.

To standardize hunger levels, we fed the nestlings to satiation approximately 10 min after they were placed in the nestboxes. We stimulated them to beg by playing parental contact calls ([Leonard et al. 1997](#)) through a personal stereo headphone placed in the opening of the nestbox. If a nestling gaped (i.e. opened its mouth) we gave it a forceful of moistened Hartz egg biscuit for birds. This was repeated until nestlings no longer gaped in response to the contact call. Thus the nestling's begging behaviour, rather than the amount of food we gave the nestling, provided our measure of satiation; we did not measure how much food we gave each nestling.

The first experiment began 30 min following the feeding of the last nestling. In both experiments, we stimulated begging by playing a sequence of six pairs of parental contact calls to each of the three nestlings, proceeding from box 1 to box 3, and recorded the begging calls that the parental contact calls stimulated. Throughout this paper, 'test period' refers to one playback of the sequence of parental contact calls, and 'trial' refers to a complete set of playbacks to all nestlings from a particular brood.

Experiment 1: Call Structure and Deprivation

The purpose of this experiment was to examine how the structure of nestling begging calls varies with food deprivation. During each trial we stimulated the large and small nestlings to beg and recorded their begging calls every 10 min for 80 min, for a total of nine test periods.

At the end of each trial, we fed the nestlings to satiation as described above.

Experiment 2: Call Structure and Cooling

The purpose of this experiment was to examine how the structure of nestling begging calls varies with thermal state. Thirty minutes after ending experiment 1, we stimulated nestlings to beg and recorded their calls. At this time, we also measured their skin temperature using a Fisher glass bulb thermometer placed against the skin of the nestling, between the abdomen and leg. Following this procedure, we turned off the heating pad in the nestbox of the large and small nestlings, and opened the top and side of the box for 1 min.

In every other trial (i.e. for every second set of broodmates tested), the medium-sized nestling served as a control. Controls were necessary for this experiment because nestlings were being deprived of food as they cooled. Controls that were deprived, but not cooled allowed us to separate these effects, and pilot trials suggested that including controls in only half the trials would provide an adequate sample size. In these trials, we also turned off the heating pad in the nestbox of the medium nestling, but then immediately turned it on again. In a similar way, we opened and then immediately closed the top and side of the box. During experiment 1, these nestlings had been treated in the same way as small and large nestlings, but their calls were not recorded. We used medium-sized nestlings from the same brood as controls, rather than matching the size of small or large nestlings with nestlings from other broods. We reasoned that size effects between large and medium or small and medium would be negligible compared to the potential effects from mixing broods. The few differences between large and small nestlings that we observed (see Results) suggest that this decision would not have introduced any confounding variables that were due to nestling size.

The sequence of recording, measuring skin temperature, and opening and closing the box was repeated every 5 min until the skin temperature of the large or small nestling reached 30°C (55.5 ± 1.35 min). The skin temperature of large and small nestlings, but not of control nestlings, decreased rapidly with time. Small nestlings cooled faster than large nestlings, so that by the time 40 min had elapsed, small nestlings were significantly cooler than large nestlings (large $33.0 \pm 0.36^\circ\text{C}$, small $31.8 \pm 0.36^\circ\text{C}$; $t_{52}=2.41$, $P=0.02$). By comparison, the minimum temperature reached by each control nestling was $36.7 \pm 0.20^\circ\text{C}$ ($N=14$), and controls showed an average change of temperature across the trial of $+0.8 \pm 0.72^\circ\text{C}$ ($N=14$). The temperature change in large and small nestlings simulated a situation in which nestlings were starting to cool and would presumably need to be brooded, but were not physiologically stressed (Marsh 1980). The rate of cooling was approximately one-third the cooling rate of lone nestlings and the maximum cooling rate of broods of three to four nestlings in natural broods at similar ages measured by Dunn (1979). At the end of experiment 2, all nestlings were fed to satiation

and returned to their home nest, having been away from their nest for a maximum of 4 h.

Analysis of Call Structure

We measured several features of nestling begging calls during each experiment. We counted nestling calls using a Unigon Model 4500 spectrum analyser, and digitized the first call in every other test period ($N=350$) at 44 kHz and 16 bits using Canary 1.2 software (Charif et al. 1995) to measure several features of individual calls. Call rate was considered to be the total number of calls given to each set of parental contact calls, converted to calls per min. The features we measured from individual calls were: call length (ms), sound pressure level (RMS pressure, in dB, re 0.02 mPa), peak frequency (the frequency with the highest amplitude in the call, in Hertz), and frequency range of the fundamental frequency (a measure of the frequency change in the call: highest frequency minus lowest frequency, in Hertz). We took all time measurements and amplitude measurements from a wave form display of the call, and all frequency measurements from a spectrograph with an analysis bandwidth of 699 Hz and display resolution of 22 Hz and 3 ms. We calibrated sound pressure level (SPL) by recording test tones (1–8 kHz, at 1-kHz intervals) played from a speaker placed in the nest rim, using the same recording settings as used to record the nestlings, and taking simultaneous SPL measurements beside the microphone using a CEL-480 logging SPL meter. We had also measured the highest and lowest frequencies in the call, but these measurements were strongly correlated ($r \geq 0.70$) with either peak frequency or frequency range, so we did not include them in the analysis. Correlations between the remaining variables were low ($r \leq 0.56$).

Statistical Analyses

We examined variation in call features over time in two steps. First, we regressed call features against time elapsed since the start of the playbacks, for each nestling. Second, we entered their regression parameters in t tests to test for significant changes over time or for differences between large and small nestlings. Specifically, we first performed separate regressions for each individual nestling in each experiment. We calculated the slope and intercept of the line regressing the variable of interest (e.g. call rate, call length) as the dependent (y) variable and time elapsed as the independent (x) variable. For call rate, the time elapsed was measured from the beginning of playbacks to that nestling, while the remaining call features were measured from the time that calling began. Plots of the data suggested that quadratic regressions (i.e. regressions of the form $Y = \beta_0 + \beta_1 X - \beta_2 X^2$) were appropriate for call rate, with a positive linear component (β_1) to describe an initial increase in call rate and a negative quadratic component (β_2) to describe a subsequent levelling off of call rate. Therefore both components of the relationship were calculated. Graphs of the remaining variables showed that linear models were adequate.

Second, we compared the slopes of the regression lines to zero using one-sample t tests, with the slope from each trial on an individual nestling representing one datum. To determine whether the calls of large and small nestlings changed in different ways over time, we compared the slopes of their regressions using two-sample paired t tests, with trials as blocks. We also tested whether the calls of large and small nestlings showed pre-existing differences before our treatments (deprivation and/or cooling) were applied by comparing the intercepts of their regressions using two-sample paired t tests, with trials as blocks.

We used this individual regression approach, rather than a more conventional repeated measures analysis of variance (ANOVA), because it accommodated missing data and allowed comparisons of overall patterns of change without use of complex interaction terms.

Data for some analyses were not normally distributed (Shapiro–Wilk tests, $P < 0.05$). However, the parametric tests we used are robust to deviations from normality (Zar 1999) and nonparametric tests on the slopes and intercepts yielded similar results to the parametric tests reported here. We present parametric statistics mainly because they yield clearer and more concise summaries of the data. All statistical tests are two-tailed. We used a significance level of $P < 0.05$. We did not apply a correction for the number of comparisons (e.g. the Bonferroni test), mainly because of the low power and arbitrariness of such corrections; instead we allow evaluation of significant results by providing graphs and exact P values (Stewart-Oaten 1995). Means are reported \pm SE. To avoid pseudoreplication, we used trials, rather than nestlings or test periods, as our unit of analysis, so all degrees of freedom are in terms of number of trials. Although all nestlings completed the experimental treatments we have described, sample sizes vary, because for some trials, nestlings did not call for a minimum of three alternating test periods, as our regression analyses required.

RESULTS

Call Structure and Size

Pairwise comparisons of intercepts between small and large nestlings ($df=13$ for experiment 1, $df=9$ for experiment 2) were not significant (two-sample t tests: NS), indicating that we could not statistically distinguish between their calls before deprivation and/or cooling began.

With two exceptions, the slopes of the regression lines for call features over time did not differ between large and small nestlings (two-sample t tests: NS). The slope of call amplitude during the deprivation experiment did, however, differ between large and small nestlings ($t_{13}=2.56$, $P=0.02$), as did the slopes of call rate during cooling (linear component $t_{26}=2.55$, $P=0.017$; quadratic component: $t_{26}=-2.03$, $P=0.05$). For this reason, we separate large and small nestlings in analyses of call amplitude in experiment 1 and call rate in experiment 2. For the

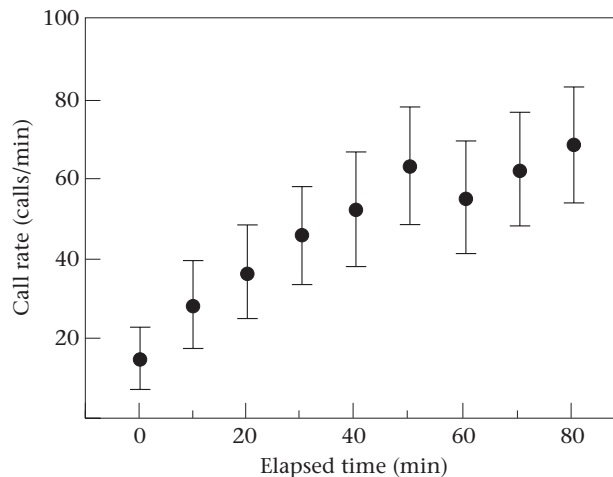


Figure 1. Mean \pm SE call rate for tree swallow nestlings (averaged for large and small nestlings) versus time elapsed during deprivation trials.

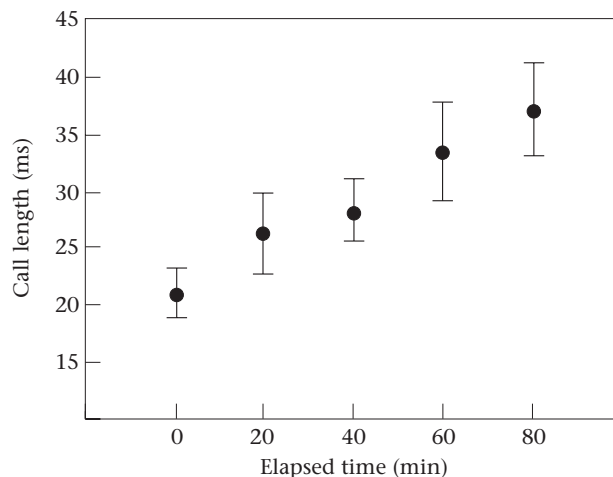


Figure 2. Mean \pm SE call length for tree swallow nestlings (averaged for large and small nestlings) versus time elapsed since calling began during deprivation trials.

remaining analyses we average the values for large and small nestlings.

Experiment 1: Call Structure and Deprivation

Both the linear and quadratic components of variation in call rate with deprivation time differed significantly from zero (linear component: $t_{27}=3.74$, $P=0.001$, quadratic component: $t_{27}=-2.51$, $P=0.018$), indicating an increase in call rate that gradually levelled out after about 60 min (Fig. 1). Call length also increased with the duration of deprivation ($t_{21}=2.72$, $P=0.013$; Fig. 2).

Call amplitude during deprivation showed different patterns for large and small nestlings. Large nestlings significantly increased their call amplitude during deprivation ($t_{14}=4.13$, $P=0.001$), but small nestlings did not ($t_{22}=0.61$, $P=0.45$; Fig. 3). Frequency measures did not vary significantly with deprivation time ($P > 0.88$).

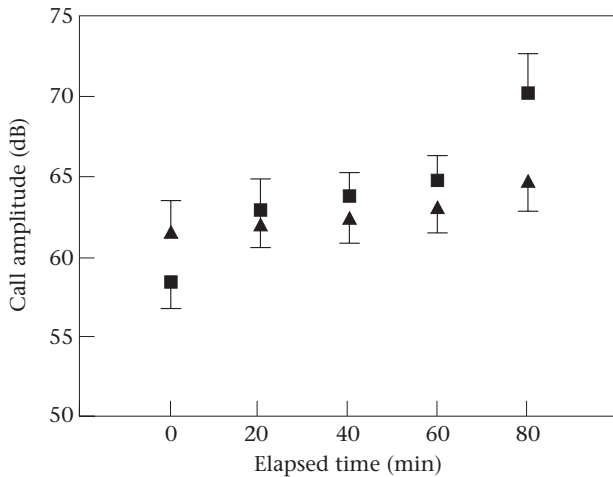


Figure 3. Mean±SE call amplitude for tree swallow nestlings versus time elapsed since calling began during deprivation trials (■: large nestlings; ▲: small nestlings).

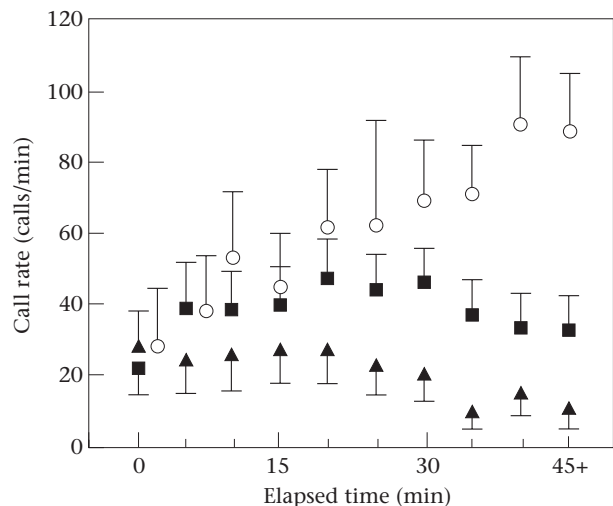


Figure 4. Mean±SE call rate for tree swallow nestlings versus time elapsed during cooling trials (○: control nestlings; ■: large nestlings; ▲: small nestlings).

Experiment 2: Call Structure and Cooling

Large and small nestlings showed different patterns in their call rates when cooled during deprivation, as indicated by significant regression coefficients for large nestlings (linear component: $t_{26}=3.03$, $P=0.005$; quadratic component: $t_{26}=-2.77$, $P=0.010$), but not small nestlings (linear component: $t_{26}=0.06$, $P=0.96$; quadratic component: $t_{26}=-1.03$, $P=0.86$). Large nestlings showed an initial increase in call rate, followed by a decrease, whereas small nestlings did not show a significant change in call rate during this time (Fig. 4). Both patterns contrasted with that of controls, which increased their call rate linearly throughout the period (linear component: $t_{14}=2.64$, $P=0.019$; quadratic component: $t_{14}=1.43$, $P=0.15$; Fig. 4).

The slope of peak frequency over time also differed significantly from zero, with calls showing an overall

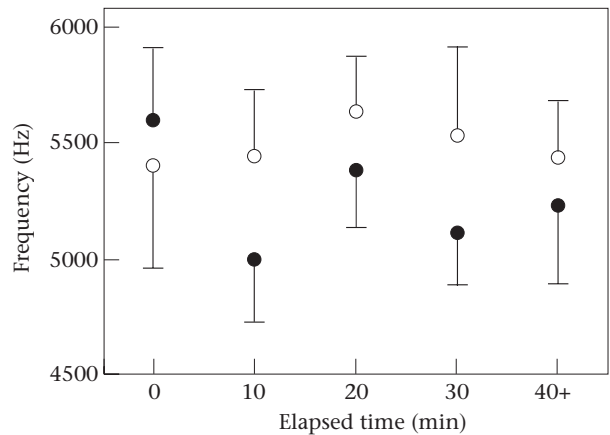


Figure 5. Mean±SE peak call frequency for tree swallow nestlings versus time elapsed since calling began during cooling trials (○: control nestlings; ●: average of large and small nestlings).

weak decline in peak frequency with cooling ($t_{15}=-2.38$, $P=0.03$; Fig. 5). Peak frequency did not, however, change significantly for control nestlings ($t_9=1.52$, $P=0.16$; Fig. 5). The remaining variables (call length, amplitude and frequency range) did not vary significantly with cooling (NS).

DISCUSSION

Information Encoded in Begging Calls

Size

We found some evidence that large and small nestlings called differently in response to our manipulation of both hunger and temperature. Large nestlings, but not small nestlings, increased the amplitude of their calls during deprivation and their call rate (at least temporarily) during cooling. These results may reflect differences in the ability of nestlings of different size to produce loud, frequent calls, and raise the possibility that, in some situations, large nestlings may outcompete small nestlings for feedings by making their calls easier for parents to detect. Previously, we had found no size-related differences in visual aspects of begging (Leonard & Horn 1996, unpublished data), although we do have limited evidence that male and female parents preferentially feed larger and smaller nestlings, respectively (Leonard & Horn 1996), and competitive asymmetries in begging have been found in other passerines with brood size hierarchies (reviewed by Cotton et al. 1999).

Hunger

Our results show that information about hunger is encoded in the rate, length and, for large nestlings, amplitude of begging calls. Previous studies on other passerines have found that call rate increases with food deprivation and have emphasized the role of calling in regulating the rate at which parents provision the brood as a whole (e.g. Burford et al. 1998; Price 1998; Kilner et al. 1999; but see Clark & Lee 1998). Fewer studies, however, have tested whether features of individual calls,

such as length or amplitude, also change with food deprivation, or have related call features to the need of individual nestlings (but see Redondo & Castro 1992; Price et al. 1996). Our results show that nestling calls provide information that could enable parents not only to regulate their provisioning rate to the brood, but also to choose which nestling to feed once they are at the nest. Preliminary results of two-speaker playbacks of nestling calls to parents at the nest suggest that they do use calls in this way (unpublished data).

Our experimental design used repeated stimulation of the nestlings without a food reward, raising the possibility that nestlings changed their begging calls at least partly in response to the repeated stimulation, rather than to deprivation per se. Here the role of this factor was probably minor, because nestlings deprived of food for similar lengths of time as in this experiment, but without repeated stimulation, show levels of begging postures and calls similar to those of nestlings in the present experiment (unpublished data). None the less, in natural situations, parents feed only one nestling on any given visit, so the other nestlings often beg for several parental visits in a row before being fed. Thus the rate at which nestlings are rewarded for begging may be an important factor affecting begging intensity, and deserves further study.

Thermal state

We found that the rate and peak frequency of calls decreased in nestlings that were cooled during food deprivation, relative to nestlings that were deprived of food but kept warm. Both decreases might arise from a decrease in muscular performance with cooling temperature (Choi & Bakken 1990), especially if production of high-frequency calls requires tension of the syrinx or forceful expiration of air (Vicario 1991). However, whether these patterns arise from physiological constraints or have been selected to serve as signals, parents could still use them to assess the thermal needs of the nestlings.

Call frequency may be a useful cue for conveying thermal need, despite the weakness of its relationship to cooling (Fig. 5), because of the manner in which call rate varies with both hunger and cooling. A nestling calling at a low rate sends an ambiguous message: either it is satiated and warm or it is hungry and cold. Encoding thermal state in call frequency, as well as in call rate, however, may resolve this ambiguity: a nestling calling at a low rate is warm and satiated if its calls are high, but it is cool and hungry if its calls are low.

Signalling of thermal need has been largely overlooked in studies of begging by passerines (for the one exception see Choi & Bakken 1990), even though it is well documented in several species of nonpasserines (e.g. Evans 1994; Iacovides & Evans 1998). Playback experiments are needed to confirm that parents are using the information on thermal state that appears to be encoded in begging calls. Such playback experiments have shown that heat solicitation by calling is an important component of thermal regulation for nonpasserine embryos and hatchlings (Evans 1992).

Selective pressure for a similar system in young passerine nestlings should be strong, because the trade-off between foraging and brooding is a key component of nesting success (Clark & Ricklefs 1988; McCarty & Winkler 1999). Nestlings may help parents optimize the balance by vocally advertising their relative needs for food and warmth. Such information may be especially useful during the transition from ectothermy to homeothermy (i.e. approximately the age of our subjects for the present study; Marsh 1980). At this time, the parental care that cool nestlings should solicit presumably shifts from brooding to provisioning of more food for thermoregulation, so vocal signals that differentiate between these needs would be adaptive.

Detectability and Design of Begging Calls

The relationships we found between call structure and need have implications for how begging calls might be designed for effective transmission to parents. If a parent arriving at the nest is to use the information that is apparently encoded in nestling calls, it must differentiate among the calls of several offspring that are calling at once. From the nestling's point of view, the calls of nestmates are a source of noise that must be overcome for effective transmission of the signal (Wiley 1994; Dawkins & Guilford 1997). Nestlings might overcome this acoustic interference by producing individually distinctive calls, by calling during the silent intervals between the calls of their nestmates, or by producing calls that are faster, longer, louder, or distinctive in frequency characteristics, relative to the interfering calls of nestmates. If they use the latter strategy, then at least some of the apparently needless intensity of begging displays may in fact be needed for efficient signal transmission, despite the proximity of parents and young during signalling (Dawkins & Guilford 1997). We are now conducting observations and experiments to examine the mechanisms of call interference and its avoidance in more detail.

Acknowledgments

We thank J. Campbell, T. Michaud and L. Rendell for invaluable help in field and laboratory. J. McCarty, P. McGregor, L. Rendell, D. Sherry and D. Weary kindly read drafts of the manuscript. This study was supported by an NSERC research grant awarded to M.L.L. The research presented here was described in Animal Utilization Proposal Nos 95-031, 95-032 and 97-040 approved on May 1995, April 1996 and May 1997, respectively, by the Dalhousie University Animal Research Ethics Board.

References

- Burford, J. E., Friedrich, T. J. & Yasukawa, K. 1998. Response to playback of nestling begging in the red-winged blackbird *Agelaius phoeniceus*. *Animal Behaviour*, **56**, 555-561.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University.

- Charif, R. A., Mitchell, S. & Clark, C. W. 1995. *Canary 1.2 User's Manual*. Ithaca, New York: Cornell Laboratory of Ornithology.
- Choi, I.-H. & Bakken, G. S. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. *Physiological Zoology*, **63**, 965–986.
- Clark, A. B. & Lee, W.-H. 1998. Red-winged blackbird females fail to increase feeding in response to begging call playbacks. *Animal Behaviour*, **56**, 563–570.
- Clark, L. & Ricklefs, R. E. 1988. A model for evaluating time constraints on short-term reproductive success in altricial birds. *American Zoologist*, **28**, 853–862.
- Cotton, P. A., Wright, J. & Kacelnik, A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *American Naturalist*, **153**, 412–420.
- Dawkins, M. S. & Guilford, T. 1997. Conspicuousness and diversity in animal signals. *Perspectives in Ethology*, **12**, 55–72.
- Dearborn, D. C. 1999. Brown-headed cowbird nestling vocalizations and risk of nest predation. *Auk*, **116**, 448–457.
- Dunn, E. H. 1979. Age of effective homeothermy in nestling tree swallows according to brood size. *Wilson Bulletin*, **91**, 455–457.
- Evans, R. M. 1992. Embryonic and neonatal vocal elicitation of parental brooding and feeding responses in American white pelicans. *Animal Behaviour*, **44**, 667–675.
- Evans, R. M. 1994. Cold-induced calling and shivering in young American white pelicans: honest signalling of offspring need for warmth in a functionally integrated thermoregulatory system. *Behaviour*, **129**, 13–34.
- Godfray, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature*, **352**, 328–330.
- Godfray, H. C. J. 1995. Evolutionary theory of parent–offspring conflict. *Nature*, **376**, 133–138.
- Haskell, D. G. 1999. The effect of predation on begging-call evolution in nestling wood warblers. *Animal Behaviour*, **57**, 893–901.
- Iacovides, S. & Evans, R. M. 1998. Begging as graded signals of need for food in young ring-billed gulls. *Animal Behaviour*, **56**, 79–85.
- Kilner, R. 1999. Family conflicts and the evolution of nestling mouth colour. *Behaviour*, **136**, 779–804.
- Kilner, R. & Johnstone, R. A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, **12**, 11–15.
- Kilner, R. M., Noble, D. B. & Davies, N. B. 1999. Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature*, **397**, 667–672.
- Leech, S. M. & Leonard, M. L. 1997. Begging and the risk of predation in nestling birds. *Behavioral Ecology*, **8**, 644–646.
- Leonard, M. L. & Horn, A. G. 1996. Provisioning rules in tree swallows. *Behavioral Ecology and Sociobiology*, **38**, 341–347.
- Leonard, M. L., Horn, A. G., Brown, C. R. & Fernandez, N. J. 1997. Parent–offspring recognition in tree swallows, *Tachycineta bicolor*. *Animal Behaviour*, **54**, 1107–1116.
- McCarty, J. P. & Winkler, D. W. 1999. Relative importance of environmental variables in determining the growth of nestling tree swallows *Tachycineta bicolor*. *Ibis*, **141**, 286–296.
- Marsh, R. L. 1980. Development of temperature regulation in nestling tree swallows. *Condor*, **82**, 461–463.
- Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. *Animal Behaviour*, **56**, 571–577.
- Price, K., Harvey, H. & Ydenberg, R. 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behaviour*, **51**, 421–435.
- Redondo, T. & Castro, F. 1992. Signalling of nutritional need by magpie nestlings. *Ethology*, **92**, 193–204.
- Stewart-Oaten, A. 1995. Rules and judgements in statistics: three examples. *Ecology*, **76**, 2001–2009.
- Vicario, D. S. 1991. Contributions of syringeal muscles to respiration and vocalization in the zebra finch. *Journal of Neurobiology*, **24**, 488–505.
- Wiley, H. R. 1983. The evolution of communication: information and manipulation. In: *Animal Behaviour*. Vol. 2: *Communication* (Ed. by T. R. Halliday & P. J. B. Slater), pp. 156–189. Oxford: Blackwell Scientific.
- Wiley, H. R. 1994. Errors, exaggeration, and deception in animal communication. In: *Behavioural Mechanisms in Evolutionary Ecology* (Ed. by L. A. Real), pp. 157–189. Chicago: University of Chicago Press.
- Zar, J. H. 1999. *Biostatistical Analysis*. 4th edn. Upper Saddle River, New Jersey: Prentice Hall.