Age-Related Changes in Signalling of Need by Nestling Tree Swallows (*Tachycineta bicolor*)

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Abstract

Despite a large literature on the ontogeny of behaviour, few studies have examined how the function of juvenile behaviour changes during development. One of the most widespread and important juvenile behaviours is begging, the display used by young animals to solicit food from their parents. Begging signals generally vary reliably with offspring need for food and have served as models for understanding the evolution of honest signalling. Little is known, however, about whether the relationship between begging and need varies over the period of rapid juvenile development. Here, we examine whether tree swallow, *Tachycineta bicolor*, begging calls consistently reflect hunger levels across the 20 d nestling period. We recorded begging calls at 5, 10 and 15 d posthatch, during an hour of food deprivation, and related call features to time without food (i.e. hunger) at each age. The overall correlation between call structure and hunger, as measured by canonical correlation, was consistent across ages. The particular features that correlated with hunger varied, however. Call rate and length increased with hunger at all ages, but call amplitude and frequency range increased with hunger at days 10 and 15 only. The results of our study suggest that begging calls consistently convey information about offspring hunger throughout the nestling period, with the number of call features encoding hunger increasing with nestling age. This change may enhance the ability of parents to assess offspring hunger levels by adding redundancy to the signal.

Introduction

Young animals undergo rapid and dramatic changes in their anatomy, physiology and behaviour during growth and development. Altricial songbirds, for example, progress from naked, blind, heterotherms to fully feathered, visually orienting, homeotherms within 2–3 wk of hatching (Starck & Ricklefs 1998). Dramatic changes in behaviour also occur during this time. For instance, vocal signals change from simple, short whistles to complex, stereotyped calls in the same 2–3 wk period (Khayutin 1985). Many of these behavioural changes are well understood as steps in the development of adult behaviour. However, relatively little is known about whether the changes affect the function of the behaviour during this period of development (West et al. 2003).

A particularly widespread and functionally important juvenile behaviour is begging, the display used by young animals to solicit resources from parents (Wright & Leonard 2002). In nestling birds, where the behaviour has been well studied, young give loud begging calls, and posture and gape vigorously when parents come to the nest with food. The intensity of the display varies with hunger and physical condition and so can provide parents with reliable

information on offspring need for food (Budden & Wright 2001). Indeed, the display has been an important model for studying various aspects of animal communication, particularly the evolution of reliable signalling (Johnstone & Godfray 2002).

Most empirical studies of begging, however, have been conducted over a relatively narrow range of ages during the nestling period. The display, particularly the vocal component, changes dramatically during this time (e.g. Clemmons & Howitz 1990; Redondo & Exposito 1990; Jurisevic 1999) and so, too, might the relationship between the display and offspring state. One of the few studies examining this relationship at different ages found that call rate varied with hunger levels in both younger and older reed warbler (*Acrocephalus scirpaceus*) nestlings, but the strength of the relationship increased with age (Kilner et al. 1999). Because such studies are rare, however, we know relatively little about how signal reliability varies with age. Clearly, if changes in the relationship between the signal and its function are common, then signalling between parents and young may be more dynamic than current models of biological signalling assume (Johnstone & Godfray 2002).

The purpose of our study was to determine whether the relationship between begging and hunger varied with age in nestling tree swallows. Specifically, we examined how components of the begging call changed with age and whether these changes consistently reflected hunger levels across the nestling period.

Tree swallows have altricial nestlings that are fed by both parents throughout a 20-d nestling period. Previous experiments have shown that 7 d old nestlings increase the rate and length of their begging calls over a period of food deprivation and that the largest nestlings in a brood increase the amplitude of their calls (Leonard & Horn 2001). The relationship between calling and food deprivation has not been tested at other ages, however. We focus on the acoustic component of the display because it is easily measured and in comparison with visual components such as posturing, it has more obviously evolved to serve a signalling function.

Methods

We conducted this study in the Gaspereau Valley of Nova Scotia, Canada between 1 May and 15 July 2003 on a population of box-nesting tree swallows (see Leonard & Horn 1996 for details). First egg dates and hatching dates were determined by checking nest boxes every 2 d, until 2 d before the predicted hatching date, after which nests were checked daily until hatching was complete.

When first-hatched nestlings were 4 or 5 d old (hereafter: day 5; hatch = day 1), we removed all the nestlings from each of 32 broods (mean brood size: 4.9 ± 0.10 nestlings/brood at our study site), weighed them and took the nestling from the middle of the weight hierarchy to the lab. The nestling was placed in an artificial nest cup inside a tree swallow nestbox. One side of the nestbox was opened, so we could see and video record the nestling. A heating pad beneath the nest maintained the temperature in the box at 39°C, which is about the mean temperature inside a tree swallow nestbox in natural broods at 6–7 d of age (38°C, n = 16 broods).

We suspended a lapel microphone (Genexxa 33-3003; InterTAN, Barrie, Canada) 10 cm above the centre of the nest cup and attached it to a stereo digital audio tape recorder (Sony DM-100; Sony of Canada Ltd., Willowdale, Canada). We also placed a 2-W speaker-amplifier (Koss hdm 111BK, response ± 3 dB from 100 Hz to 15 kHz; Logitech Electronics Inc., Barrie, Canada), attached to a compact disk (Sony D-E351) player, on a platform at the opening of the nestbox. Finally, a Panasonic PV-900-K VHS videocamera (Panasonic Canada, Inc., Mississauga, Canada) was placed at the open side of the box.

Twenty minutes after the nestling was placed in the box and every 10 min thereafter for a total of 1 h without food (i.e. six test periods), we stimulated it 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. The calls were recorded in previous years at six different nests, between days 3 and 5. Each nestling received calls from one of these six nests at every age. The playback tapes were assigned to nests by rotation, so that each playback tape was used at 8–9 nests. None of the responses analysed below differed across replicate tapes (all comparisons p > 0.45).

We video and audio taped the begging responses of the nestling to each set of contact calls. We kept the sound recording level constant and calibrated our amplitude measurements by using the same recording settings to record test tones of known amplitude.

The entire procedure was repeated on the same nestlings when they were 9 or 10 d old (hereafter: day 10) and 14 or 15 d old (hereafter: day 15). The protocol at day 10 was identical to that described above for the youngest age. We did modify the

protocol at day 15, however, because nestlings are more easily disturbed at this age, require more time to recover from disturbance and may not show the same degree of hunger for an hour of food deprivation as younger nestlings. Specifically, we: (1) conducted the trials in the field rather than the lab, (2) did not videotape the trials and (3) stimulated begging every 10 min for 2 h rather than 1 h, although we only analysed the first six test periods after begging began, as with the younger nestlings. We also did not heat the nestboxes for the oldest nestlings, because they are able to thermoregulate (Marsh 1980). As in the lab trials, nestlings in the field were removed from their home nests and placed singly in nestboxes and nest cups that were identical to those used in the lab. The playback and recording protocol was otherwise the same as for earlier ages.

Following all trials, nestlings were fed and then returned to their home box. Over 90% of nests at our site fledged their entire brood and we could attribute no mortality to this experiment.

Call Analyses

In each of the six test periods, we counted individual calls using a Unigon Model 4500 spectrum analyzer (Unison Industries Inc., Mount Vernon, NY, USA), and digitized each call (up to maximum of 25), at 44 kHz and 16 bits using Canary 1.2 software (Charif et al. 1995). Call rate was considered to be the total number of calls given to each set of parental contact calls, converted to calls per minute. We also measured: call length (ms), call amplitude (i.e. sound pressure level in dB, reference 0.02 mPa), peak frequency (the frequency with the highest amplitude, in kHz) and frequency range (highest minus lowest frequency, in kHz) for each call. We took all time and amplitude measurements from the spectrum produced by Canary (Hamming window, 699 Hz bandwidth and 50% overlap; Charif et al. 1995).

Statistical Analyses

We used multivariate analysis of variance (MANOVA), with nestling, age and test period (i.e. time without food and our measure of hunger) as the independent variables and call features as the dependent variables. We used the MANOVA to find the linear combination of call features (e.g. call rate, length and amplitude) that best explained the variation in hunger, age and their interaction, separately. We then tested whether these essentially new variables based on the combined call features differed significantly across the independent variables (Quinn & Keough 2002).

All two-way interactions were included in the model; however, the test period by age interaction was of most interest because it specifically tested whether the relationship between the combined call features created by the MANOVA and hunger (presumed to increase with test period) varied with age. MANOVA test statistics were calculated using the GLM procedure in SAS 8.e (SAS Institute Inc., Cary, NC, USA 1999), with each effect tested against its interaction with nestling, so that nestlings, rather than test periods, were our units of analysis. We based F-tests on Roy's greatest root, which is the least conservative of the available multivariate measures of F-ratios, but is appropriate when differences are expected to lie mainly along one dimension, as for age or hunger (Johnson & Field 1993).

The MANOVA showed a significant interaction between test period and age (see Results), suggesting that the relationship between calling and hunger was not consistent across ages. To explore this result further, we repeated the MANOVA for each age separately and then correlated the best-fitting combination of call variables with test period for each age, to produce a canonical correlation that allowed us to determine whether the strength of the relationship (and whether it was positive or negative) differed with age. The standard errors of these correlations overlapped broadly, indicating that they did not differ statistically, so we did not formally test for differences among them.

We also examined whether different call features correlated with hunger at different ages by calculating the correlation between each call variable and test period at each age. We first calculated the correlations for each nestling separately and then averaged across nestlings in each age category to calculate a mean correlation coefficient, with 95% confidence intervals, for each variable at each age (following Hunter & Schmidt 1990; transformation to Fisher's z' yielded similar results). Correlations whose confidence intervals do not encompass zero are significantly different from zero at $p < 0.05$.

All analyses assume normality and homogeneity of variance, which we examined using plots of each independent variable and residual. We log transformed call rate and length to meet these assumptions. The analyses also assume that the relationship between call features and test period is linear. We checked this assumption by graphing both linear and second order polynomial fits

between each call variable and test period. The two fits were virtually indistinguishable, so we made the simpler assumption of linearity. Unless mentioned otherwise, all means are presented ± SE.

Results

Overall, begging calls showed significant age and test period (i.e. hunger) effects (age: $F_{5,17} = 2.92$, $p = 0.04$; test period: $F_{5,27} = 5.67$, $p = 0.001$; Fig. 1). There was also a significant age by test period interaction ($F_{5,120} = 7.94$, $p < 0.0001$), suggesting that the relationship between the best-fit

call features and hunger was not consistent across the three ages. This pattern was not the result of differences in the strength of the relationship between the combined call features and test period, because when each age was tested separately, the canonical correlation coefficients between call features and test period were similar across ages (day 5: $r = 0.74 \pm 0.11$; day 10: $r = 0.83 \pm 0.07$; day 15: $r = 0.84 \pm 0.07$). It appeared, however, that different call features correlated with test period at different ages. Call rate and length showed significant increases with test period at all ages (Figs 1 and 2), but call amplitude and frequency range increased significantly only at days 10 and
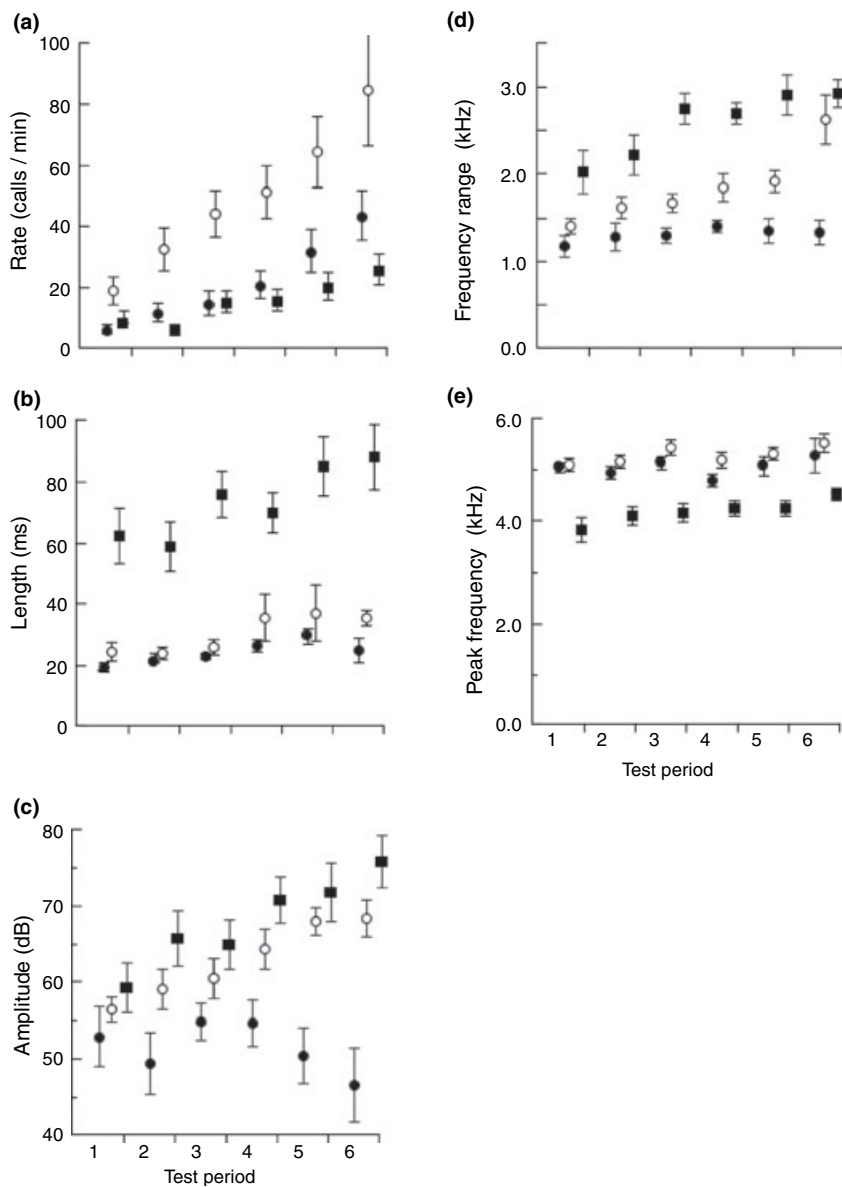

Fig. 1: Mean (± SE) (a) call rate, (b) call length, (c) amplitude, (d) frequency range and (e) peak frequency for tree swallow nestlings across six test periods without food (i.e. our measure of hunger) at days 5 (●), 10 (○) and 15 (■) post-hatch.
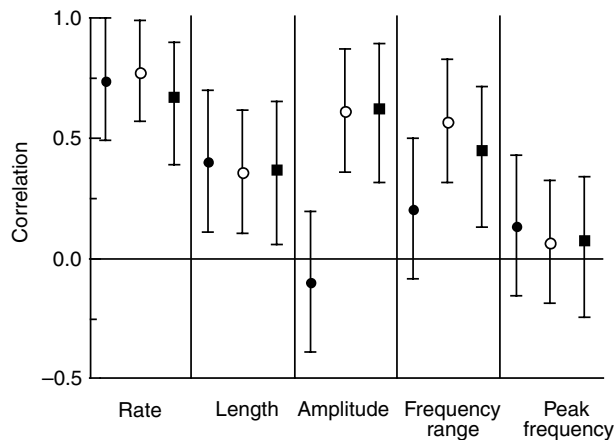
Fig. 2: Mean correlation coefficients (± 95% confidence intervals) between test period and call rate (calls/min), call length (ms), amplitude (dB), frequency range (kHz) and peak frequency (kHz) for nestling tree swallows at days 5 (●), 10 (○) and 15 (■) post-hatch.

15 (Figs 1 and 2). Peak frequency did not vary with test period at any age (Figs 1 and 2). Thus, while the strength of the correlation between the best-fitting combination of call features with test period remained constant, the variables that made up that combination, and, equivalently, the strength of their individual correlations with test period, did change with age.

Discussion

Our main finding was that tree swallow begging calls were consistently correlated with offspring hunger levels across the nestling period, despite changes in call structure during this time. We also found that the number of call features encoding hunger increased with nestling age. We cannot entirely rule out the possibility that our methods account for the latter result, but it seems unlikely. Specifically, although younger nestlings (days 5 and 10) were recorded in the lab and the older nestlings were recorded in the field, the experimental protocol was otherwise similar. Similarly, while the protocol may have differentially affected nestlings of different ages, for example because of age related changes in responsiveness to contact calls, we have no reason to expect that such differences would interact with the effects of hunger on calls or affect call structure.

Nestling tree swallows in this study showed changes in the structure of their begging calls with age. Day 5 nestlings had calls that were shorter, lower in amplitude, higher in frequency and narrower in frequency range than day 15 nestlings. Changes in call structure with age have been shown for many passe-

rines (e.g. Clemmons & Howitz 1990; Redondo & Exposito 1990; Jurisevic 1999; Butchart et al. 2003; Hauber & Ramsey 2003), including tree swallows (Robertson et al. 1992), and presumably result partly from the maturation of the syrinx and associated structures (Jurisevic 2003), and partly from practice and learning (e.g. Brittan-Powell et al. 1997). In many species, the modified calls eventually form part of the adult vocal repertoire, with other adult vocalizations appearing after fledging (e.g. Howe-Jones 1984). The same is likely true of tree swallows (Robertson et al. 1992), although their call development has not been systematically studied.

Despite these changes in structure, nestling begging calls showed a consistently strong relationship with hunger across age. Both call rate and length increased with food deprivation at all ages, while call amplitude and frequency range increased with hunger at days 10 and 15. Thus, tree swallow begging calls appear to encode reliable information on nestling hunger levels throughout much of the nestling period.

Our results are consistent with work on reed warblers, which found that call rate increased with hunger levels in nestlings at both 3 or 4 and 6 or 7 d after hatching (Kilner et al. 1999), although the relationship was strongest in the older nestlings. They are also consistent with work on brown-headed cowbirds (*Molothrus ater*), which found that various call features of both nestlings (Dearborn & Lichtenstein 2002) and fledglings (Hauber & Ramsey 2003) varied positively with hunger levels. Collectively, these studies suggest that begging calls provide reliable information on offspring hunger levels throughout the dependent period.

Although our results do not suggest an age-related shift in the overall reliability of the display, measured as its correlation with time without food, they do show an age-related increase in the redundancy of the display. That is, more features of the calls, specifically call amplitude and frequency range, encoded information on hunger as nestlings aged. This increased redundancy in the display with age might enhance the parents' assessment of nestling hunger among older nestlings in at least two ways. First, mistaken perception of one call feature might be corrected by accurate perception of another feature. For example, if part of a nestling's call is occluded by the overlapping calls of a nestmate, its call rate, amplitude and frequency range could still convey the nestling's hunger. Second, variation in an ensemble of call features might be easier to perceive than variation in just one, because multicomponent

stimuli are generally easier to detect, discriminate and learn than univariate stimuli (Rowe 1999). Thus, even if begging calls encode a similar amount of information on hunger as nestlings age, they may nevertheless convey that information more effectively. We speculate that this increase in efficiency might be one reason why nestlings repeat each call less frequently after day 10 (Fig. 1), although other explanations, notably the cost of rapidly repeating longer calls, are possible.

Why would older nestlings have more call redundancy than younger nestlings? Greater call redundancy might be an adaptive response to the increasingly noisy and competitive environment of the nest. As nestlings age, their calls become louder, longer and more frequent, all of which may make it more difficult for parents to assess the calls of individual nestlings. Increased redundancy might serve to overcome this acoustic interference and enhance reception by parents. Alternatively, increasing call redundancy may simply be a developmental consequence of aging. As nestlings mature, their calls become more complex structurally and thus have more degrees of freedom for potentially informative variation. Either way, the consequences of the changes in calling shown here depend on how parents perceive the begging display in the changing behavioural context of natural nests.

Acknowledgements

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