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The role of posturing and calling in the begging display of nestling birds

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Abstract Nestling birds produce a multicomponent begging display that has visual (e.g. posturing) and vocal (e.g. call rate) elements. Most work on the function of the display has focused on each component separately. However, understanding the evolution of complex displays such as begging requires knowledge of how the components function collectively. The purpose of our study was to determine how postural intensity and calling rate together influence parental feeding decisions in tree swallows, *Tachycineta bicolor*. We compared how begging components responded to a manipulation in which pairs of nestlings were either free to approach the parent when it arrived to feed (unconfined treatment) or confined to the back of their nestbox by a Plexiglass partition (confined treatment). We found no significant differences in postural intensity between treatments, but calling rate was significantly higher in the confined treatment. In both treatments, postural intensity, but not calling rate, correlated with hunger. Both components positively and independently correlated with the likelihood of a nestling being fed, although the correlation with postural intensity was stronger. Previous work suggested that both posture and call rate advertised hunger in nestling tree swallows. Here, call rate was not associated with hunger, but rather was affected by nestling position. These results suggest that calling may serve an additional role in helping nestlings in disadvantaged positions attract parental attention. The results also suggest that calling may have a complex relationship with hunger, position and nestmates.

Keywords Begging · Multicomponent signalling · Signalling · Visual display · Vocal display

Introduction

Animals often communicate using complex displays that have components in more than one sensory modality. The evolution of these multicomponent displays is favoured by two main factors. First, complex displays may increase the efficacy of communication (Rowe 1999). For instance, compound signals are detected and recognised more quickly and easily than signals produced in a single modality (Rowe 1999). Similarly, they are learned and remembered more accurately than single signals (Rowe 1999). Second, complex displays may provide receivers with more reliable information about the quality or condition of the signaller (Johnstone 1996). For example, each component of the display may carry information about different aspects of the signaller's quality and so together the components provide more overall information about quality than any single element would on its own (Johnstone 1996). Alternatively, the individual components of the display might provide the receiver with identical, and therefore redundant, information about signaller quality. Here, redundancy could help to overcome perceptual errors by the receiver and allow it to gain more complete information (Kilner 2002).

Begging is a multicomponent display used by young animals to solicit resources from their parents. In nestling birds, where the behavior has been best studied, the display consists of a visual component that includes posturing and gaping, and a vocal component that includes loud calling. The intensity of both components generally increases with hunger, poor physical condition and the begging of nestmates (Budden and Wright 2001). Parents typically feed young that beg at higher intensities and who are closer to them (Budden and Wright 2001). With few exceptions (most notably Glassey and Forbes 2002; Kilner et al. 1999), studies examining the function of the begging display have considered each component in isolation. However, understanding the evolution of complex displays, such as begging, requires an understanding of how components function collectively (Rowe 1999).

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The purpose of our study was to examine how the visual and vocal components of the begging display of nestling tree swallows, *Tachycineta bicolor*, together might function to influence parental feeding decisions. In both observational and experimental studies on this species, we showed that nestling postural intensity increased with food deprivation and that parents fed the nestling that was posturing most intensively and closest to the opening of the nestbox (Leonard and Horn 1996, 1998). In separate studies, we also found that the call rate of individual nestlings in the lab increased over a period of food deprivation (Leonard and Horn 2001a), and that in the field parents directed feedings toward nestlings calling at higher rates (Leonard and Horn 2001b). Together, the results of the previous studies suggest that both the visual and vocal components of the begging display advertise nestling hunger and thus serve redundant roles in the functioning of the display. Understanding the combined contribution of the different elements requires that the two components be examined simultaneously.

To determine the roles of the visual and vocal components of the begging display, we conducted a manipulation designed to provoke a change in the begging display, and then examined how each component changed in response to the manipulation. Specifically, we restricted the ability of pairs of nestlings to approach the front of the nestbox (i.e. the side with the nest opening), and thus to occupy positions close to the parent. We anticipated that nestlings might compensate for this restriction by attempting to make themselves more obvious to parents. This could be achieved by increasing call rate, postural intensity or both. If the latter, it would suggest that, in addition to advertising hunger, calling and posturing may also be used to attract parental attention when nestlings are in positions further from the parent. Furthermore, if both elements responded in the same way, (e.g. both increased in intensity) it would provide support for the hypothesis that the visual and vocal components of the begging display have redundant roles in the functioning of the display. We also used the experiment to examine simultaneously how both elements of the display varied with nestling hunger and how parents responded to variation in the two components.

Methods

This study was conducted in the Gaspereau Valley of Nova Scotia, Canada between May and July 2000 and 2001 (study sites described in Leonard and Horn 1996). Tree swallows at these sites breed in wooden nestboxes and have average brood sizes of 4.9 nestlings. Hatching dates were determined by checking boxes daily around the anticipated hatching date. Nestlings were defined as 1 day old on the day that they hatched, and the age of the first-hatched nestling was considered the age of the brood. Adults were captured and banded with aluminium Canadian Wildlife Service bands.

When broods were 7 days old, we weighed and colour-banded all the nestlings in each of 31 broods and placed a small white dot on the heads of the two nestlings (i.e. target nestlings) closest in weight (mean \pm SE difference in weight: 0.15 \pm 0.02 g; $n=31$). We

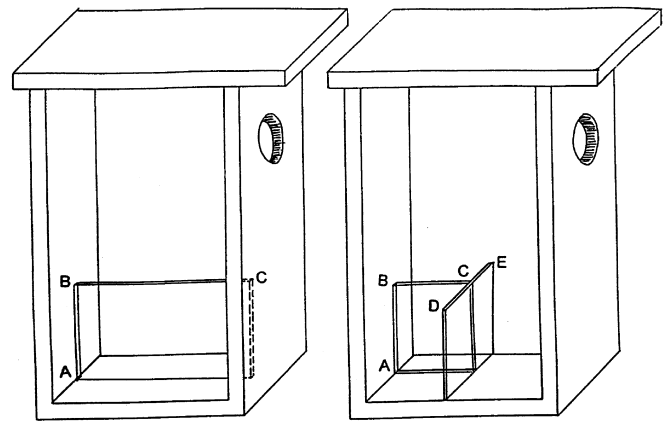


Fig. 1 Diagram of experimental set-up for nestling tree swallows, *Tachycineta bicolor*. *Left* Unconfined treatment – a clear Plexiglas plate divides the nestbox in half length-wise separating the two target nestlings, but permitting movement toward the nest opening at the top of the front side of the box. $A-B=7.5$ cm, $B-C=13.5$ cm. *Right* Confined treatment – a clear Plexiglas plate divides the rear of the box in half length-wise separating the two target nestlings and also separating the front of the box from the rear, so that nestlings cannot approach the nest opening. $A-B=7.5$ cm, $B-C=6.5$ cm and $D-E=13.5$ cm. Diagram omits nesting material for easier viewing

then opened a hinged side of the nestbox, placed a Plexiglas plate in the opening and 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 removed the entire brood from the nestbox. We standardised hunger levels for the target nestlings by stimulating them to beg using playback of parental contact calls and feeding them Hartz egg biscuit for birds until begging to the playback stopped. We then placed the entire brood in a heated container near the nestbox, so that the nestlings remained warm while out of the nest. Following this procedure, we created one of two experimental conditions that would affect the ability of nestlings to change their position within the nestbox. We either (1) divided the nest in half length-wise by placing a Plexiglas divider, extending the length of the box, into the nesting material (the 'unconfined' treatment, $n=14$ broods; Fig. 1), or (2) divided the rear of the nestbox in half length-wise and confined nestlings to this area by placing a T-shaped Plexiglas divider in the nesting material in the back half of the box (the 'confined' treatment, $n=17$ broods; Fig. 1). Nestlings in the unconfined treatment would be free to move toward the opening of the nestbox and, therefore, to approach the parent when it came to the nest to feed. Nestlings in the confined treatment would be restricted to the back of the box away from the nest opening. In both treatments nestlings could see and hear each other, but could not physically interact.

We then secured lapel microphones (Genexxa 33-3003) to the right and left sides of the nestbox and connected each to the corresponding channel of a stereo digital-audio tape recorder (Sony DM-100). The microphones were placed just below the surface of the nesting material, midway along the length of the nestbox on the left and right edges. We returned all but the two target nestlings to the nest and placed a Panasonic PV-900-K VHS videocamera on a tripod facing the open side of the box. We covered the camera with the plastic bag, but did not turn the camera on. We then waited 45 min to allow the parents to adjust to the experimental situation and the target nestlings to become hungry.

Following the acclimation period, we quickly removed the non-target nestlings that had been in the box and randomly placed each of the target nestlings in either the back right or left corner (regardless of treatment) of the box opposite the opening. We then randomly selected two of the remaining nestlings, fed them about

four mouthfuls of moistened Hartz's egg biscuit for birds, an amount that would keep them from begging for approximately 1 h, and placed them in the front left and right corners of the box. These nestlings did not beg during the trials, but were used to make the experimental situation more realistic for parents (i.e. brood size of four). Once the nestlings were in the box, we replaced the Plexiglas side, turned on the videocamera and tape recorder and covered the side of the box and the camera with the plastic bag. We then recorded the begging display of the two target nestlings and the response of parents to those displays for 1 h. We randomly selected the treatment for the first trial of each year and then alternated confined and unconfined treatments in remaining trials. Following each trial, we removed the equipment from the nest and fed and returned the remaining nestlings.

Video analyses

Each time a parent came to the nest with food, we recorded the identity of the nestling that was fed and scored the maximum postural begging intensity of each target in the interval between the arrival of the parent and the feeding. Postural scores were assigned based on the following scale of increasing intensity: 0 = head down, no gaping; 1 = head down, gaping, sitting on tarsi; 2 = head up, gaping, sitting on tarsi; 3 = same as 2, plus neck stretched upward; 4 = same as 3, but body lifted off tarsi; and 5 = same as 4, plus wings waving. We also placed a transparent acetate sheet with a grid of 1 cm squares over the video screen and used this to measure (1) the horizontal distance (cm) between the corner of the nestling's bill and the front wall (i.e. side with opening) of the nestbox, and (2) the horizontal distance (cm) between the corner of the parent's bill immediately before feeding a nestling and the front wall of the nestbox. We used time since feeding as a measure of nestling hunger.

Acoustic analyses

We digitised all calls at 44 kHz and 16 bits using Canary 1.2 software (Charif et al. 1995). From spectrographs of the calls (filter bandwidth 699 Hz, grid resolution 3 ms \times 22 Hz) we counted the number of calls given by each nestling from a parent's arrival to the feeding and converted this to call rate based on calls/sec. When two nestlings were calling in the same recording session, we used the amplitude of the calls on the time waveform (oscilloscopic) 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). In similar stereo recordings in the laboratory (Leonard and Horn 2001c), the calls of nestlings begging alone in one side of the nestbox never had higher amplitudes in the opposite channel. Nevertheless, in the present experiment we excluded calls from the analysis if amplitudes in the two channels were within 10% of each other (3% of calls).

Statistical analyses

For all analyses, sample sizes are the number of trials, rather than the number of nestlings or parental visits. To test for overall treatment effects, we used two-sample *t*-tests comparing confined and unconfined treatments. For correlational analyses, we calculated a correlation coefficient for each trial, using parental visits as observations. We then used a two-sample *t*-test to test whether these coefficients differed significantly between treatments. After we determined that they did not (all *P*-values $>$ 0.33), we used a one-sample *t*-test on the pooled correlations from both treatments to test whether they differed significantly from zero. If one of the variables was the time since a nestling had last been fed, we calculated a correlation for each nestling and then averaged them to provide the correlation coefficient for the trial.

We used repeated measures ANOVAs to examine differences between fed and unfed nestlings (repeated measures) within nests,

while also testing whether these differences varied across treatments (between subjects variable). The main treatment effects for these analyses were equivalent to the two-sample *t*-tests for overall treatment effects described above, so in reporting the results for these ANOVAs we only report the effects for the repeated measure and its interaction with treatment.

We analysed whether posturing and calling had independent effects on which nestling parents fed by first converting the mean difference between fed and unfed nestlings in postural score to a correlation coefficient for each nest (Rosenthal et al. 2000). This conversion is equivalent to assigning unfed nestlings a value of -1 and fed nestlings a value of 1 and correlating those values to the nestlings' postural scores. We also used the same method to convert the mean difference in calling rate to a correlation coefficient. We then calculated the correlation between posture and calling differences within each nest, and used it to convert each of the correlations calculated in the first step to a partial correlation between: (1) posture and whether a nestling was fed, holding calling constant or (2) calling and whether a nestling was fed, holding posture constant. To test whether posture and calling had independent effects on which nestling was fed, we compared these partial correlations to zero using one-sample *t*-tests. To test whether one of the components contributed proportionally more to which nestling was fed, we compared their partial correlations using a paired *t*-test.

Sample sizes vary depending on whether data were available for particular nestlings or broods. All means are presented ± 1 SE. Male and female parents did not differ in their response to the treatments or begging components (all *P*-values $>$ 0.12), so we pooled them for analyses.

Results

Effect of treatment on nestling position and parental behavior

Our experimental design was effective in controlling nestling position. That is, nestlings in the confined treatment could not approach the front of the box, and hence access the parent as closely as nestlings in the unconfined treatment [closest approach (cm): confined=11.8 \pm 0.65, *n*=17; unconfined=5.5 \pm 0.74, *n*=13; *t*=6.43, *P* $<$ 0.0001]. Our treatments did not, however, affect important aspects of parental behavior. For example, there was no significant difference in feeding rates between the two treatments (feeds/h: confined=14.0 \pm 1.18, *n*=17; unconfined=12.6 \pm 1.35, *n*=13; *t*=0.77, *P*=0.45) nor in the distance parents went into the nestbox to feed a nestling [distance (cm): confined=9.0 \pm 0.62, *n*=17; unconfined=8.3 \pm 0.70, *n*=14; *t*=0.78, *P*=0.44].

Effect of treatment on begging components

The postural scores of individual nestlings were significantly correlated with their call rates (mean \pm SE *r* across trials=0.15 \pm 0.04; one-sample *t*-test: *n*=28, *t*=3.59, *P*=0.001). Nonetheless, the visual and vocal components of begging responded differently to the two treatments. Nestling postural score did not differ significantly between confined and unconfined treatments (*t*=0.36, *P*=0.72; Fig. 2). However, calling rates were significantly

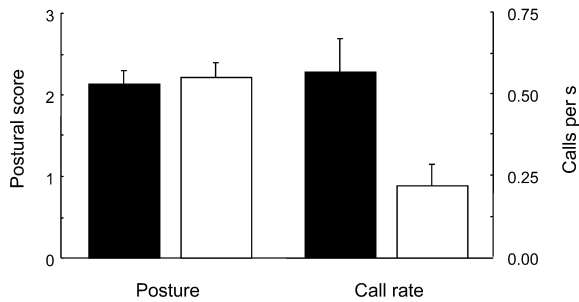


Fig. 2 Mean (\pm SE) postural score and call rate of target nestlings in the confined ($n=17$, black) and unconfined ($n=13$, white) treatments

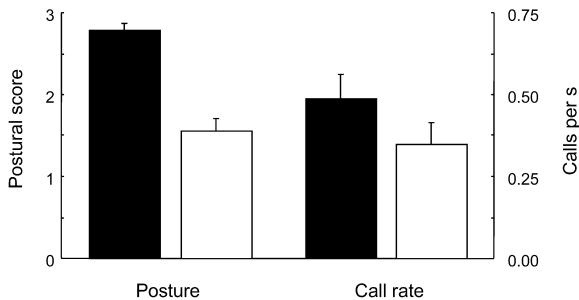


Fig. 3 Mean (\pm SE) postural score and call rate of fed (black) and unfed (white) nestlings

higher in the confined treatment than in the unconfined treatment ($t=2.65$, $P=0.013$; Fig. 2).

Begging components and hunger

Nestling postural score was significantly correlated with the time since the nestling had last been fed ($r=0.43\pm 0.04$, $n=28$, $t=10.57$, $P<0.0001$). However, the relationship between calling rate and hunger was not significant ($r=0.06\pm 0.08$, $n=28$, $t=0.86$, $P=0.40$). A relationship between calling rate and hunger might be obscured if nestmates varied their call rate in response to the calling of siblings, independently of their hunger level. This was not the case, however, as the call rates of nestmates were not significantly correlated ($r=0.10\pm 0.09$, $n=19$, $t=1.13$, $P=0.27$).

Begging components and parental choice

On a given feeding trip, nestlings that parents chose to feed had significantly higher postural scores and calling rates than nestlings that were not fed (posture: $F_{1,28}=74.24$, $P=0.0001$, interaction $F_{1,28}=1.31$, $P=0.26$; call rate: $F_{1,28}=16.87$, $P=0.0003$, interaction $F_{1,28}=0.78$, $P=0.38$; Fig. 3). This could be a result of the correlation between posturing and calling. However, each component of the begging display appeared to have an independent association with which nestling parents chose to feed.

That is, parents preferentially fed nestlings with higher postural scores, even when calling rate was held constant (partial $r=0.47\pm 0.080$, $n=21$, $t=5.87$, $P<0.0001$) and preferentially fed nestlings with higher call rates, when postural score was held constant (partial $r=0.19\pm 0.092$, $n=21$, $t=10.57$, $P=0.048$), although the correlation between postural score and which nestling was fed was significantly higher (comparison of partial correlations: $t=10.57$, $n=21$, $P=0.041$).

Discussion

We found that nestlings confined to the back of the nestbox increased their call rate, but not their postural intensity, compared to nestlings that were free to approach the parent. In both treatments, postural intensity varied with the time since a nestling had been fed, but call rate did not. Parents preferentially fed nestlings with higher postural scores or calling rates, although their preference for higher postural scores was stronger than their preference for higher calling rates.

Below we consider the role of each component in light of these results, and then address the contribution of the combined signal to the functioning of the begging display.

Posturing

Many studies have found that nestling posture correlates with hunger and parental feeding decisions (Budden and Wright 2001). Our previous results on tree swallows showed that postural intensity increased with hunger and parents preferred to feed nestlings with higher postural scores (reviewed in Horn and Leonard 2002). However, this earlier work did not examine the influence of posture independently of calling. The results of the present study suggest that posture can convey information about nestling hunger and influence parental feeding decisions independently of call rate.

Although posture appears to be a reliable indicator of nestling hunger, evidence from work on canaries, *Serinus canaria*, suggests that the reliability of this component may decrease with nestling age (Kilner 2002). Our study was conducted at only one age, so it is possible that the role of posturing may change as nestlings get older. However, we found in an earlier descriptive study that the positive relationship between nestling height (part of postural intensity) and hunger persisted across three nestling stages ranging from 4 days post-hatch to 16 days post-hatch (Leonard and Horn 1996). This suggests that posture consistently advertises hunger throughout much of the tree swallow nestling stage.

Unlike call rate, nestling posture did not differ significantly between the confined and unconfined treatments. Our failure to detect a difference was not likely caused by a ceiling effect in postural scores, because the mean scores for both treatments were well below their maxima. Perhaps any advantage that a nestling would

gain by posturing more intensely would be small, especially compared to the benefits of calling more frequently (see below). For instance, a more intense posture may not move the nestling significantly closer to the nest opening or make the nestling more obvious to parents.

Calling

The results of this study suggest that nestlings may alter their calling behavior in response to their position relative to the parent. Nestlings called more when confined to the back of the nestbox than when they were free to approach the parent. Further, a post-hoc analysis showed that nestlings in the unconfined treatment called at significantly higher rates in trials in which one or both nestlings stayed in the back of the nestbox (i.e. within 6 cm of the rear wall, as if they had been in the confined treatment), as compared to when they both moved to the front of the box during the trial (back: 0.34 ± 0.07 , $n=8$; front: 0.06 ± 0.08 , $n=5$; $t=2.33$, $P=0.04$). In tree swallows, the nestling closest to the opening when parents arrive with food has the highest probability of being fed (Leonard and Horn 1996). Nestlings at the rear of the box might increase their call rate in order to attract parental attention and improve their chances of receiving food. In many communication systems receivers are differentially attracted to the first signal they hear (Greenfield 1994), so nestlings calling at a high rate may increase their chances of being detected before a competing nestmate.

Begging call rate correlates with nestling hunger and parental provisioning in a variety of birds (Budden and Wright 2001), although most work has focused on how call rate reflects brood hunger levels and influences overall feeding rates. An unexpected result of this experiment was that the call rate of individual nestlings was not significantly associated with the time since feeding. This is in contrast to a previous laboratory experiment on this species showing that call rate increased with food deprivation (Leonard and Horn 2001a). The earlier result was robust, but the experimental situation was very different from that of the current study. In the previous study, single nestlings were taken to the lab, and then stimulated to beg every 10 min for an 80 min period of food deprivation (see Leonard and Horn 2001a for more details). In the current study, however, we added nestmates and manipulated nestling position. Both factors could influence calling behavior and potentially obscure the relationship between calling and hunger. Nestling tree swallows have higher call rates when they call with a nestmate than when they are alone (Leonard and Horn 2001c). In this study, we did not find a correlation between the call rates of nestmates, but that may have been because the effect of nestmates depends on their relative position, as discussed above. Thus, the correlation between calling and hunger might only be apparent when the effects of calling and positioning by nestmates is held constant, rather than allowed to vary as in the present

study. In summary, nestlings may increase call rate when they are in suboptimal positions in the nest. This suggests that calling may serve an additional role besides advertising hunger. The results also suggest that calling, unlike posturing, may not have a straightforward relationship with hunger.

Relationship between posturing and calling

Two recent studies have examined the role of the visual and vocal components of begging on food allocation. In red-winged blackbirds, *Agelaius phoeniceus*, postural intensity was important in determining food distribution within the nest, while the vocalisations of the brood influenced parental foraging rates (Glasse and Forbes 2002). In reed warblers, *Acrocephalus scirpaceus*, the total gape area (i.e. the visual component) of the brood and brood call rate were correlated with the duration of food deprivation and the two elements together explained more variance in nestling hunger than either could alone (Kilner et al. 1999). Here, it appears that multicomponent begging displays provide parents with more detailed information on nestling hunger.

Our previous work on tree swallows indicated that postural intensity and call rate had similar relationships with nestling hunger (Leonard and Horn 1996, 1998, 2001a). In the present study, though, posture appeared to be the main bearer of information on hunger and was used by parents independently of differences in call rate. Calling, in contrast, did not correlate with food deprivation, and although parents preferred nestlings calling at a higher rate when postural cues were held constant, overall they were more responsive to differences in posturing. Also, as argued above, calling in particular might serve to increase the efficacy of the display when nestlings are in suboptimal positions.

Thus, the results of this study suggest that under some circumstances posturing and calling may play different roles in the begging display of nestling tree swallows. Together with the strong relationship between calling and food deprivation shown previously (Leonard and Horn 2001a), the results suggest that call rate in particular may have multiple roles and may be affected by factors such as nestmates and nestling position in complex ways. Clearly, further experimentation is required to determine how calling contributes to the functioning of the begging display.

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