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# Begging in the absence of parents by nestling tree swallows

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Begging by nestling passerine birds has become a model system for studies in animal communication. Although most begging occurs when parents arrive at the nest to feed (here called ''primary begging''), it also occurs between feeding visits and immediately after parents leave the nest. Begging in these contexts (here called ''secondary begging'') may have relatively little influence on the probability of receiving food, but could increase the overall cost of the signal and thus influence nestling begging strategies. The purpose of our study was to determine how often tree swallow (*Tachycineta bicolor*) nestlings beg in contexts other than to parents with food and to examine what factors influence the frequency of this begging. Secondary begging ranged from 7% of measured begging responses at day 2 to 30% by day 8 and was more frequent when the interval between parental feeding visits was relatively long and when the time to respond to the arrival of parents with food was short. Increases in both age and intervisit interval were associated with decreases in nestling response times, suggesting that secondary begging may be related to the speed with which nestlings respond to stimuli. We discuss possible functions of secondary begging and raise the possibility that it may, in fact, be an error. *Key words:* begging, parent-offspring interactions, signaling, tree swallows. *[Behav Ecol 12:501–505 (2001)]*

Begging by nestling passerine birds has become a model for studies in animal communication, particularly those examining the honest signaling of need (Kilner and Johnstone, 1997). Theoretical studies of begging have been particularly useful in showing how honest signals can be evolutionarily stable (Godfray, 1991, 1995), while empirical studies have quantified the costs and benefits associated with reliable signaling. This communication system has, thus, provided some important insights into the evolution of animal signals.

Nestling birds ''beg'' by gaping, posturing and calling loudly to parents with food. This display appears to influence the distribution of food within broods (e.g., Kilner 1995; Price et al., 1996) and also regulates the feeding rate to broods as a whole (e.g., Leonard and Horn, 1998; Ottosson et al., 1997). Most begging occurs when parents arrive at the nest with food. However, it may also occur in contexts where the probability of receiving food is low, such as between feeding visits (e.g., Price and Ydenberg, 1995; Price et al., 1996) and following the departure of parents from the nest (Clemmons, 1995). Such begging may be important for understanding the evolution of the signal because it presumably does not yield the substantial payoff of begging to a parent with food, yet it potentially incurs the same energetic and predation costs (Bachman and Chappell, 1998; Haskell, 1994; Leech and Leonard, 1996, 1997; McCarty, 1996). Begging outside the context of feeding could, therefore, increase the overall cost of the signal and thus influence when and how it is used.

Most research on the costs and benefits of this display have focused on begging associated with the delivery of food (Kilner and Johnstone, 1997). Begging outside this context has not been extensively studied (but see Roulin et al., 2000), however, despite its potential to influence the cost of the signal. The purpose of our study, therefore, was to determine the extent to which nestling tree swallows (*Tachycineta bicolor*) beg in contexts other than the delivery of food by parents. Specifically, we examine the stimuli that elicit begging to determine what proportion of begging responses include begging to parents with food (here called ''primary begging'') and what proportion include begging in contexts other than feeding (here called ''secondary begging''). We also examine the factors influencing the frequency of secondary begging by determining the relationship between secondary begging and intervisit interval (i.e., a measure of hunger), nestling age, and the speed of response to stimuli. We examine the effect of age because the stimuli that elicit begging are expected to vary with age (e.g., Clemmons, 1995) and therefore potentially influence the frequency of secondary begging. We also examine the speed with which nestlings respond because the rapid begging responses of older nestlings (Leonard et al., 1997) might also affect the probability of secondary begging. At the end of the paper we discuss the possible functions of this behavior.

## METHODS

This study was conducted at four sites in the Gaspereau Valley, Nova Scotia, Canada between 1 May and 31 July 1997. The study sites are described in detail in Leonard and Horn (1996). Tree swallows at these sites nested in wooden nest-boxes. First egg dates and hatching dates were determined by checking boxes every second day until 2 days before the predicted hatching date, after which they were checked daily. Nestlings in this study were not individually marked, so although we could determine the response of individuals on each feeding visit, we could not track their behavior across different visits.

To examine variation in begging responses with age, we videotaped 12 broods of five nestlings when they were 2, 4, 6, and 8 days old (hatch = day 1). Because some videotapes were lost to technical problems, the final sample size for each age was: day 2, $n = 10$ broods; day 4, $n = 11$; day 6, $n = 12$; day 8, $n = 11$. The mean age of nest leaving in this population is 20 days post-hatch (Michaud and Leonard, 2000), so our study covers most of the first half of the nestling period.

Twenty-four h before taping began, we opened the hinged side of each nest-box and placed a plexiglas plate in the opening. We then covered that side of the nest-box with a dark plastic bag. This procedure kept the box dark and allowed the

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parents to habituate to the bag that later covered the videocamera. The next day we mounted a Panasonic PV-900-K VHS videocamera on a tripod and covered it with the plastic bag. We placed the camera 15 cm from the plexiglas plate, aligned it horizontally and adjusted it so that the base of the nest-hole appeared in the top right corner of the field of view. The nest was then videotaped for 2 h. Videotaping took place between 0730 and 1800 h AST. Although parental feeding rates do not appear to vary across the day in tree swallows (McCarty, 1995), we did tape individual nests at the same time of day across different ages. Parents usually resumed feeding within a few min of our departure from the box and earlier work on this population showed that feeding rates at nests with and without cameras were not significantly different (Leonard and Horn, 1996).

### Video and statistical analyses

A visit to the nest by a parent was considered to begin when it landed and/or called at the nest-box opening and to end when it departed through that opening. We measured the elapsed time between the arrival of a parent at the box and the first begging response of each nestling to determine response times. We considered a begging response to occur when nestlings raised their heads, stretched their necks and opened their mouths wide (i.e., gaped). Each time a nestling begged we recorded the event that immediately preceded begging. Stimuli that elicited begging included: (1) the sound made by the parents as they landed on or departed from the opening of the nest-box, (2) the sound made by parents as they landed on the rim of the nest, (3) contact calls (see below) given by the parent at any time during the visit, (4) movement of parents, nest mates, or the nest-box and (5) unknown. Note that in cases (1) and (2) sounds may have been accompanied by movement and/or changes in light conditions as parents passed through the nest-box opening or landed on the nest rim. We cannot assess which feature(s) stimulated begging, so we report them as responses to the sound produced, because this was detectable to the observer. Contact calls are typically given by parents when they arrive at the nest with food and sometimes when they are perched, facing outward, in the nest opening immediately before or as they depart from the box (Leonard et al., 1997). Contact calls given upon arrival stimulate begging while those given on departure may function to coordinate parental feeding trips (Leonard et al., 1997). We refer to contact calls given when parents arrive at the nest with food as ''arrival'' calls and those given when they leave as ''departure'' calls.

We considered begging to stimuli associated with the arrival of a parent with food as a primary begging response. This included begging to: (1) arrival calls and (2) the sound of a parent landing on the nest opening or rim before feeding (i.e., landing).

We considered begging to stimuli associated with the departure of a parent or stimuli produced in the absence of parents as a secondary begging response. This included begging to: (1) departure calls given as the parent flew from the nest, (2) the sound of a parent immediately after it pushed off from the nest-box opening at departure (i.e., departures), (3) movement of nestlings or nest-box in the absence of a parent (i.e., movement) and (4) unknown stimuli in the absence of a parent.

To determine the relative responses of nestlings to each stimulus, we recorded the number of begging responses on parental visits and during intervisit intervals for each brood in every 2-h taping period and then calculated the proportion of responses that each stimulus elicited. A response by more than one nestling to the same stimulus on a given visit/interval or a repeated response to that stimulus by the same nestling was treated as a single response.

**Table 1**

**Proportion of begging responses by tree swallow broods at different ages to particular stimuli**

| Age (days) | Primary begging | | Calls and movement | Secondary begging |
|---|---|---|---|---|
| | Arrival calls | Landings | | |
| 2 | 0.86 ± 0.04 | 0.06 ± 0.06 | 0.02 ± 0.01 | 0.07 ± 0.02 |
| 4 | 0.84 ± 0.04 | 0.09 ± 0.03 | 0.02 ± 0.01 | 0.04 ± 0.02 |
| 6 | 0.54 ± 0.08 | 0.19 ± 0.04 | 0.02 ± 0.08 | 0.31 ± 0.09 |
| 8 | 0.25 ± 0.05 | 0.47 ± 0.05 | 0.04 ± 0.02 | 0.30 ± 0.08 |
| Overall | 0.62 ± 0.05 | 0.20 ± 0.05 | 0.03 ± 0.01 | 0.18 ± 0.05 |

Values are mean (± SE). Begging responses are to arrival calls and landings by parents at the nest-box opening or nest rim (primary begging responses), to calls and movements after feeding (but before the departure of the parent), or all other secondary begging responses combined.

To examine how secondary begging varied with time since a parental feeding visit and potentially hunger, we divided visits at day 8 (see rationale for using this age below) into those preceded by either a long or short time interval and compared the proportion of visits with secondary begging in each of those categories. The average interval of time between feeding visits at this age is about 3 min (2.88 ± 0.13 min), so we considered intervals of 3 min or less as short intervals and intervals of more than 3 min as long intervals.

We used parametric statistics when assumptions were met. Otherwise we used nonparametric equivalents. To avoid pseudoreplication we averaged the responses of nestlings across visits within nests, so our degrees of freedom are in terms of broods. We excluded visits in which a second parent arrived at the nest before the first parent had departed and visits in which parents did not arrive with food. Proportions were arcsine transformed, although untransformed means are presented. We report all means ± 1 SE and set our significance level at $p = .05$.

## RESULTS

### Stimuli eliciting begging

Across ages, 82% of begging responses were to the arrival of parents with food and therefore considered primary begging (Table 1). The proportion of responses with begging to arrival calls and to parents landing on the nest-box or nest rim varied with age (Repeated Measures ANOVA, calls: $F = 34.02$, df = 3, 27, $p = .0001$; landing: $F = 21.46$, df = 3, 27, $p = .0001$; Table 1). Responses to arrival calls decreased from an average of 86% of responses at day 2 to 25% at day 8 while responses to landings increased from 6% on day 2 to 47% on day 8 (Table 1). The proportion of responses that were classified as secondary begging also varied with age ($F = 4.24$, df = 3, 31, $p = .01$), increasing from 7% at day 2 to 30% at day 8 (Table 1).

A small proportion of responses were to calls and movement following feedings, but before the departure of the parent (Table 1). Begging in the presence of the parent, regardless of whether it has food, could influence the probability of feeding on future visits, although it is unlikely to have the impact of primary begging responses. Because these responses do not meet our definition of either primary or secondary begging we exclude them from further analyses.

**Table 2**

**Proportion of secondary begging responses by tree swallow broods at different ages to particular stimuli**

| Age (days) | Departure calls | Departures | Movement | Unknown |
|---|---|---|---|---|
| 2 | 0.46 ± 0.17 | 0.40 ± 0.18 | 0.11 ± 0.09 | 0.03 ± 0.03 |
| 4 | 0.50 ± 0.22 | 0.28 ± 0.16 | 0.11 ± 0.11 | 0.11 ± 0.11 |
| 6 | 0.25 ± 0.08 | 0.28 ± 0.09 | 0.36 ± 0.10 | 0.11 ± 0.04 |
| 8 | 0.33 ± 0.11 | 0.37 ± 0.06 | 0.20 ± 0.07 | 0.09 ± 0.03 |
| Overall | 0.39 ± 0.06 | 0.33 ± 0.12 | 0.20 ± 0.08 | 0.09 ± 0.05 |

Values are mean (± SE). Secondary begging responses are to departure calls, the sound of a parent leaving the box (i.e., departures), movement of nestlings or nest-box between feeding visits (i.e., movement), or unknown stimuli between feeding visits (i.e., unknown).

### Secondary begging responses

Across all ages, 39% of secondary begging responses were preceded by departure calls, 33% by departures, and 29% by movement and unknown stimuli in the absence of the parents (Table 2). The proportion of responses attributable to each stimulus did not vary significantly with age (Friedman's test, all $p > .59$).

With the exception of the analyses reported in Table 3, we focus the remaining analyses on 8-day-old nestlings because the frequency of secondary responses at this age is relatively high (Table 1). We also restrict our analyses to secondary begging that occurs in relation to a feeding visit (i.e., in response to departure calls and departures), rather than an intervisit interval because this allows us to compare secondary begging to primary begging on the same visit.

Because secondary begging occurs later in a visit (e.g., as parents leave) than primary begging (e.g., as parents arrive with food), it is possible that it is simply begging by nestlings that are slow to respond to the parent with food. This was not the case, however, because 80% (± 0.5) of secondary responses were performed by nestlings that had already begged in response to the parent's arrival.

### Secondary begging and nestling response time

The mean time to the first begging response by tree swallow broods varied across ages (Two-way Repeated Measures ANOVA, $F = 17.7$, df = 3, 21, $p = .0001$) with response times decreasing with age (Table 3). If secondary begging responses are associated with generally faster responses, then this pattern of decreasing response times might explain the increase in secondary begging with age (Table 1). Indeed, the time to the first begging response was significantly shorter on parental visits in which a secondary begging response occurred immediately after the visit (e.g., as parents departed) than on visits without secondary begging ($F = 14.8$, df = 1, 21, $p = .0009$; Table 3). This difference, however, decreased with age (interaction: $F = 4.54$, df = 3, 21, $p = .013$; Table 3).

### Secondary begging and intervisit interval

The proportion of visits with secondary begging was significantly higher when the interval between parental visits was long than when it was short (long, 0.45 ± 0.08; short, 0.31 ± 0.04; paired $t$ test, $t = 2.23$, df = 8, $p = .05$), suggesting that hungrier nestlings were more likely to have secondary begging. Nestlings also tended to respond more quickly on visits preceded by longer intervals (response time for long intervals: 0.79 ± 0.29 s, short: 1.56 ± 0.50 s; paired $t = 2.05$, df = 10, $p = .06$), suggesting that the relationship between hunger and secondary begging may be related to the speed with which nestlings respond.

**Table 3**

**Time to first begging response by tree swallow broods for visits with and without secondary begging at different ages**

| | Response time | |
|---|---|---|
| Age (days) | With secondary begging | Without secondary begging |
| 2 | 5.0 ± 0.8 | 12.8 ± 2.2 |
| 4 | 3.3 ± 0.7 | 6.4 ± 1.4 |
| 6 | 1.9 ± 0.6 | 3.1 ± 0.7 |
| 8 | 0.7 ± 0.2 | 1.6 ± 0.5 |
| Overall | 2.7 ± 0.6 | 5.9 ± 1.2 |

Response times are given in s; values are mean (± SE).

## DISCUSSION

### Secondary begging

The results of this study indicate that nestling tree swallows beg in contexts other than the arrival of parents with food. Indeed, by 8 days post-hatch 30% of begging responses are in these contexts. We suggested at the beginning of the article that begging that occurs outside the context of feeding has few direct benefits relative to receiving food. There are, however, at least three possible benefits to begging in these contexts. First, secondary begging might influence parental feeding decisions. For instance, a parent hearing a begging call as it flew from the nest might allocate the next feeding to the nestling that called or decrease the time to the next feeding visit. We, unfortunately, do not have the data to test the first hypothesis because the nestlings in this study were not marked. It does seem unlikely, however, that an adult could effectively hear begging calls given inside the box when flying away from the nest. We did find that the mean time to return across ages did not differ between visits in which nestlings begged after parents departed and those in which they did not (begging: 6.49 ± 0.50 min, no begging: 5.43 ± 0.48 min; paired $t = 1.25$, df = 8, $p = .25$), suggesting that begging in this context does not influence feeding rates. Similarly, if parents remained on the nest-box following departures, they could potentially assess nestling begging calls and adjust their feeding rates accordingly. However, parents rarely perched on the nest-box following departure (less than 1% of feeding visits by day 8; Leonard ML, unpublished data), and so would have little opportunity to assess begging following departure. In summary, although it is possible that secondary begging could influence parental feeding decisions, it is likely to have considerably less impact than begging to a parent with food.

Secondary begging might also be used to solicit brooding, a particularly important resource for young ectothermic nestlings. The increase in secondary begging with age is, however, contrary to the expected pattern if nestlings solicit heat by begging in these contexts. Tree swallow nestlings are endothermic by 8 to 10 days post-hatch (Marsh, 1980) and thus unlikely to require brooding. Furthermore, recent work suggests that cues used to solicit brooding by nestling red-winged blackbirds (*Agelaius phoeniceus,* Glassey B and Forbes S, submitted manuscript) and tree swallows (Leonard and Horn, 2001) are encoded in primary begging responses. Together this information suggests that secondary begging is unlikely to influence the delivery of heat.

Finally, nestlings may beg in the absence of parents to communicate with their nest mates. For instance, vocalizations given between parental feeding trips by nestling barn owls (*Tyto alba*) are apparently used to negotiate which nestling will beg on the next feeding visit and thus reduce sibling competition (Roulin et al., 2000). Although this is a potential function of secondary begging in tree swallows, one important difference between the systems suggests that this is not the case. Secondary begging by nestling tree swallows almost always occurs in response to a stimulus (e.g., departure calls or sounds). If the main function of this begging is to communicate with nest mates, then it seems unlikely that it would be so tightly linked to external stimuli.

In conclusion, it is possible that nestlings gain some benefits from secondary begging that are yet unidentified. However, more research is needed to determine how these benefits compare to those associated with primary begging.

### Factors influencing secondary begging

Secondary begging may be an inevitable consequence of the relatively rapid begging responses of nestling passerines. The first nestling to beg upon the arrival of the parent with food has the highest probability of being fed (e.g., Teather, 1992). Thus, a rapid response to the first sign of a parent is likely to result in a feeding. Although a swift response is advantageous in competition, it may increase the risk of responding to inappropriate stimuli (Wiley, 1983) or in inappropriate contexts.

The results of our study are consistent with the notion that secondary begging may be related to short response times. Within ages, secondary begging was associated with shorter response times, while across ages it increased as response times decreased. Secondary begging also increased with hunger (i.e., intervisit interval), an effect that may have been mediated through the decreasing response times associated with longer intervals between visits.

A recent experiment on begging in yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) found that food-deprived nestlings begged more often between parental visits than satiated nestlings and that hungry nestlings responded more quickly to parental arrivals (Price and Ydenberg, 1995). This result is consistent with the pattern observed in our study. However, contrary to our results, small nestlings in unmanipulated broods begged more often between parental visits despite being slower to respond to parents. Clearly, more work is required to establish the link between response time and secondary begging.

The frequency of secondary begging responses might also be influenced by the change in stimuli that elicit begging as nestling age. That is, young nestlings responded to vocalizations typically given before feedings. However, as the nestlings matured they became increasingly responsive to cues such as sounds/movement of the parent landing on the box. Although associated with the arrival of food, these cues also occur in other contexts (i.e., with the departure of the parent) and therefore may be less reliable indicators of the parents' arrival. This uncertainty, coupled with a decrease in response time, may result in a higher rate of secondary begging with age.

### Cost of secondary begging

A number of recent studies have focused on the costs associated with begging (e.g., Bachman and Chappell, 1998; Haskell, 1994; Leech and Leonard, 1996, 1997; McCarty, 1996), mainly to determine their impact on the evolution of honest signaling. Most studies examining the energetic cost of this display have concluded that the energy expended during primary begging is low (e.g., McCarty, 1996). We used primary and secondary begging rates and durations from the current field study and estimates of the energy expended per second of begging calculated for this population of tree swallows (Leech and Leonard, 1996) to examine the impact of secondary begging on nestling energy budgets. Our results show that secondary begging raises the daily energy expenditure for begging 27% above estimates based on primary begging only. However, further calculations indicate that primary and secondary begging together make up less than 1% of a nestling's total daily energy budget, so it is unlikely that secondary begging would have any impact on fitness.

Several recent studies, however, have shown that begging by nestling birds, including tree swallows, increases the risk of predation (Haskell, 1994; Leech and Leonard, 1997). Although we have not quantified this risk, it seems likely that an additional consequence of secondary begging is to make nests more susceptible to predation.

### Begging and error

Future studies should test whether secondary begging may, in fact, be an error that results from selection for rapid begging responses. That is, a nestling that responds quickly to most sounds or movements may increase its chances of receiving food, however, it may also be more likely to beg in contexts in which it will gain few, if any, benefits. Nestlings may, therefore, have to accept a certain level of error in order to increase their chances of receiving food. This level should reflect the balance between the benefit of a feeding and the cost of responding when the likelihood of receiving food is low. The balance between these responses is likely to vary with factors such as hunger level and condition. For example, a hungry nestling may be willing, on the short-term, to pay the relatively small energetic cost of secondary begging in return for an increased chance of a feeding. Hungry nestlings may, therefore, respond quickly to most sounds or movements and show relatively little discrimination among potential stimuli. Thus, nestling begging strategies could potentially be affected by secondary begging.

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