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# PARENTAL CALLS AND NESTLING BEHAVIOR IN TREE SWALLOWS

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ABSTRACT.—Parents in many passerines are reported to produce a vocalization at the nest that stimulates nestling begging. Although this phenomenon has been well documented, relatively few studies have systematically examined the use of this call. The purpose of our study was to examine the role of Tree Swallow (*Tachycineta bicolor*) contact calls in the stimulation of nestling begging. Both male and female Tree Swallows called proportionally more at early nestling stages when nestlings generally were less responsive to the arrival of their parent. Parents called more often before feeding than after, and females called on proportionally more visits in which they brought food than on brooding visits in which they did not bring food. Parents also called significantly more often after the first call if no nestlings begged than if one or more nestlings begged. Nestlings begged in response to contact calls given by parents at the nest and during experimental playbacks of contact calls. Our results suggest that one function of the Tree Swallow contact call is to stimulate begging. *Received 19 December 1996, accepted 5 May 1997.*

INTERACTIONS BETWEEN PARENTS AND OFFSPRING of many animal species are mediated by vocalizations. Offspring call to solicit food (Muller and Smith 1978, Miller and Conover 1983), heat (Evans 1992), and protection from predators (Ritchison 1983), whereas parents call to provide offspring with information about food (Whittemore and Fraser 1974, Nuechterlein 1988), predation risk (Nuechterlein 1988), and their location (Weary and Fraser 1995).

Passerines give a variety of calls when approaching and leaving their nests (Armstrong 1973; Bengtsson and Rydén 1981; Sieber 1985; Clemmons 1995 a,b). Some of these calls are common in early nestling stages and are reported to stimulate begging (Bengtsson and Rydén 1981, Robertson et al. 1992, Clemmons 1995b). Although this phenomenon has been relatively well documented, few studies have systematically examined the influence of these calls on nestling behavior (but see Clemmons 1995a,b).

Calling near the nest may increase the risk of nest predation (Yasukawa 1989). Thus, it is surprising that parents call to stimulate begging rather than wait for nestlings to beg spontaneously. However, feeding visits may be more efficient if nestlings are gaping when parents arrive with food than if the parents wait for spontaneous begging (Bengtsson and Rydén 1981, Clemmons 1995b). Parents also may stimulate nestlings to beg in order to gain information about the condition of the brood and/or the relative condition of individual offspring (Bengtsson and Rydén 1981).

The purpose of our study was to examine the function of nest-site calls in parent-offspring interactions in Tree Swallows (*Tachycineta bicolor*). Specifically, we were interested in whether parental calls at the nest stimulate nestlings to beg. Tree Swallows are obligate, secondary cavity nesters, and males and females produce several types of calls in the vicinity of the nest site (Robertson et al. 1992). Adult Tree Swallows emit a "contact" call that is associated with food delivery to the nest (Robertson et al. 1992). We examined the function of the contact call during parental visits to the nest and in an experiment in which we played recorded calls to nestlings to determine whether they respond to calls independently of the presence of their parents.

## METHODS

This study was conducted at four sites in the Gaspareau Valley of Nova Scotia, Canada between 1 May and 15 July in 1994 and 1995. Three of the sites were apple orchards in which nest boxes were placed approximately 10 to 20 m apart in grids. The fourth site, which also was the location of the experimental study, was an open field by a river. In the latter site nest boxes were placed every 10 m around the perimeter of the field. Tree Swallows in our population

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nested in wooden nest boxes with internal dimensions of 30 × 15 × 15 cm.

In early May, adults were captured using nest-box traps (Stutchbury and Robertson 1986) and individually marked with acrylic paint and colored leg bands. Females were marked on both sides of the head with a small dot of white acrylic paint, so we could identify the parent's sex during video tape transcriptions. First-egg dates and hatching dates were determined by checking nest boxes every second day until two days before the predicted hatching date, after which they were checked daily.

In 1994 we video-taped inside 11 nest boxes with broods of either four ($n$ = 3) or five ($n$ = 8) nestlings at early (4 to 6 days; hatching = day 1) and late (14 to 16 days) nestling stages. Tree Swallows in this population fledge at approximately 18 days (range 15 to 22 days; Leonard unpubl. data). Twenty-four h before taping we opened the hinged side of each nest box and placed a plexiglass plate in the opening. We then placed a dark plastic bag supported on a small wooden frame around that side of the nest box. This kept the box dark and let parents habituate to the frame that later covered the video camera. Each nestling was then marked on the head with a distinctive pattern of white paint. The next day, a Panasonic PV-900-K VHS video camera was mounted on a tripod and covered by the plastic bag and frame. The camera was a standard distance from the nest (15 cm from objective to edge of nest), aligned horizontally, and adjusted so that the base of the nest hole appeared in the top right corner of the field of view. Each nest was video-taped for 2 h between 0600 and 1000 ADST. Parents resumed feeding within a few minutes of our departure from the box (see Leonard and Horn 1996).

*Video and statistical analyses.*—Each time a parent visited the nest we determined its sex, how often it called, and whether it fed a nestling. We also recorded the location of each call and whether it was given before or after a feeding. Call location was divided into three categories: (1) outside the box, which also included calling as the parent entered; (2) standing in the box adjacent to the nestlings; and (3) perched in the nest-box opening facing outside the box. We timed the duration of each visit and recorded whether the female brooded. A trip or visit to the nest was considered to begin when a parent landed or called outside the box and to end when it departed through the nest-box opening. Often we could not see when parents arrived at the nest, because they remained outside the box initially. However, we used the sound produced by parents as they landed to determine arrivals in the absence of calling.

We examined the response of each nestling to the arrival of a parent at the nest box (with or without calls) and to the calls of the parent. Nestlings were considered to have responded if they raised their head and gaped. We considered a nestling to have gaped if it opened its mouth for longer than 2 s. We pooled the data for broods of four and five nestlings because parental feeding rate, nestling mass, and begging behavior do not differ significantly between broods of these sizes (Leonard and Horn 1996). Unless stated otherwise, we examined the effect of calling for early stage nestlings only. This is because calling occurs most frequently at this stage, thus providing a more robust sample size. Trips in which females brooded were omitted from analyses examining the factors that influence visit duration.

We observed 658 trips to the 11 nests over both nesting stages. In 620 of these trips parents carried food, and in the remaining 38 trips they came to the nest without food. Thirty-four of these trips were by nine females to brood young in early nestling stages.

We used repeated-measures ANOVA with nests as blocks, so nests rather than individual trips were our unit of replication. All data were plotted to visually confirm that they were normally distributed, and proportions were arcsine transformed (although untransformed means are reported).

*Playback experiment.*—A playback experiment was conducted in 1995 to examine the response of nestlings to contact calls independently of the presence of their parents. Parental calls were recorded at 16 nest boxes when the nestlings were three to five days old. A Realistic lapel microphone was placed inside each nest box, and the calls given by parents on regular visits to the nest were recorded using a Marantz PMD222 cassette recorder. No distinctions were made between the calls of male and female parents.

Two calls from each nest were digitized at 8 bits and a 22-kHz sampling rate using SoundEdit (Farallon, Berkeley) software. Using the same software we highpass-filtered the calls at 2 kHz to reduce background noise. We then created a 5-s sequence for each nest consisting of two 0.1-s calls separated by an interval of 1 s, and then followed by approximately 3.8 s of silence. This sequence was repeated 12 times to produce a one-min tape loop (experimental tape). This tape was free of nestling begging calls. We also made two control tapes, one of synthesized white noise (control 1), which was highpass-filtered at 2 kHz, and the other a blank tape (control 2). The white noise tape had the same time sequence as the experimental call tape (i.e. two, 0.1-s bursts of noise at 1-s intervals followed by 3.8 s of silence). The blank tape was played continuously for 1 min. Experimental and control presentations were separated by at least 2 min of silence to allow the nestlings to return to a resting position (i.e. head down). In total, each trial lasted 7 min from the beginning of the first playback. The order in which the tapes were presented was randomized for the first trial, after which we cycled through the combinations (e.g. control 1, control 2, experimental followed by experimental, control 1, control 2, and so on).

Playbacks were presented to 16 broods of nestlings when they were 5 to 8 days old ($\bar{x}$ = 6.2 days; i.e. the

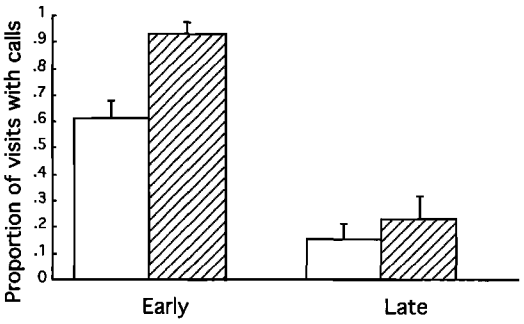


FIG. 1. Proportion of nest visits ($\bar{x} \pm$ SE) with calls by male (dark bars, $n = 11$) and female (light bars, $n = 11$) Tree Swallow parents at early (4 to 6 days) and late (14 to 16 days) nestling stages.

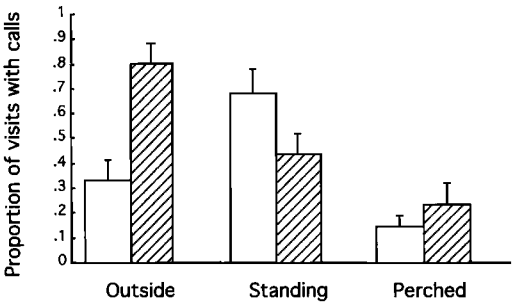


FIG. 2. Proportion of nest visits ($\bar{x} \pm$ SE) with calls given outside the nest box, standing beside the nestlings inside the box, and perched in the nest opening by male (dark bars, $n = 11$) and female (light bars, $n = 11$) Tree Swallow parents at the early (4 to 6 days) nestling stage.

early stage) and again to 13 of the same 16 broods when they were 14 to 17 days old ($\bar{x} = 15.3$ days; i.e. the late stage). Before each trial, three randomly chosen nestlings were removed from their home box and placed in a test box lined with Tree Swallow nesting material. The test box was at least 20 m from the home box and was equipped with the same video setup used in the descriptive study, but was otherwise similar to the home boxes. We tested nestlings away from their home box because the alarm calls of their parents could interfere with the trials. We waited at least 2 min for early stage nestlings and 10 min for late-stage nestling after they were moved into the test box and until they had their heads down before beginning the playback.

The tapes were played through a Realistic 40-1259B speaker amplifier held approximately 20 cm from the opening of the test box and connected to a Marantz PMD222 cassette recorder. The speaker was held adjacent to the entrance of the nest, rather than directly opposite, to prevent a shadow from falling across the opening. Volume was adjusted to natural levels and kept constant throughout the trials. Nestlings were returned to their home box after completion of the trials.

Nestling responses to the control and experimental tapes were recorded as the proportion of intervals following the playback of a call (maximum of 12) in which at least one nestling: (1) raised its head, (2) gaped, or (3) called.

## RESULTS

*General description.*—When parents arrived without calling, older nestlings were more likely to beg than were younger nestlings (older, 0.60 ± SE of 0.04; younger, 0.20 ± 0.04, paired $t = 8.70$, df = 9, $P = 0.0001$), suggesting that older nestlings were more responsive to the arrival of their parents. The average length of a feeding trip (excluding trips with brooding) was significantly longer at early nestling stages than at late nestling stages (early, 43.3 ± 6.3 s; late, 11.4 ± 1.2 s; paired $t = 5.50$, df = 10, $P = 0.0003$), indicating that feeding trips may be more efficient when nestlings are older and when they beg in response to the arrival of their parents.

The proportion of nest visits during which the parents called was higher at early than at late nestling stages for both sexes (stage effect, $F = 62.44$, df = 1 and 8, $P = 0.0001$; Fig. 1), and males called on significantly more trips than females at both stages (sex effect, $F = 7.65$, df = 1 and 8, $P = 0.02$; Fig. 1). At early stages, parents gave proportionally more calls outside the box and standing beside nestlings than perched at the nest opening (location effect, $F = 13.12$, df = 2 and 18, $P = 0.000$; Fig. 2). Males and females also differed in where they called, with males calling outside the box on proportionally more trips than females and females calling while standing beside the nestlings on proportionally more trips than males (location × sex, $F = 8.25$, df = 2 and 18, $P = 0.007$; Fig. 2). In late nestling stages, males and females called significantly more outside the nest box than standing inside the box or perched in the opening (location effect, $F = 14.88$, df = 2 and 6, $P = 0.005$).

*Do contact calls stimulate nestling begging?*—Parents called before feeding more often than after feeding (proportion of trips with calls before, 0.90 ± 0.03; after, 0.10 ± 0.03; paired $t = 11.10$, df = 10, $P = 0.0001$), as would be expected if calling stimulates begging. Parents

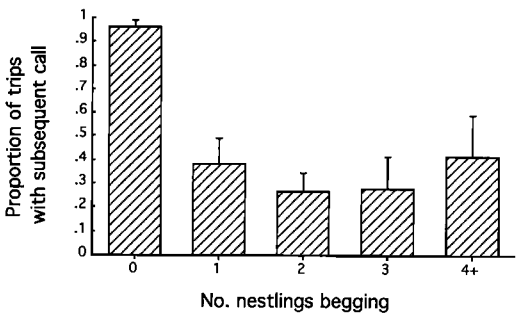


FIG. 3. Proportion of trips in which Tree Swallow parents called again ($\bar{x} \pm$ SE) following the first call in relation to the number of nestlings begging after that first call ($n$ = 11 nests).

also gave subsequent calls more often if no nestlings begged following the first call before feeding than if one or more nestlings begged ($F$ = 10.90, df = 4 and 12, $P$ = 0.0006; Fig. 3). Parents also should be more likely to call when they arrive with food than when they arrive without food. We examined this prediction using females because at early stages females will come to the nest without food. Females called on proportionally more nest visits when they arrived with food than when they arrived without food (with food, 0.80 ± 0.04; without food, 0.20 ± 0.10; unpaired $t$ = 4.50, df = 15, $P$ = 0.0004). Finally, if calling is used to stimulate begging, then nestlings should beg in response to calls. As predicted, fewer nestlings begged following an arrival without a call than following an arrival with a call. That is, the increase in the proportion of nestlings that begged after their parents arrived without calls was significantly lower than the increase after parents called outside the nest following arrival (difference before and after arrival, 0.10 ± 0.04, before and after first call, 0.30 ± 0.10; paired $t$ = −2.20, df = 9, $P$ = 0.05).

*Playback experiment.*—Nestlings did not respond to the control tapes, but they did respond to parental calls in 75% (12/16) of trials during early stages and 84.6% (11/13) of trials during late stages. Nestlings responded by raising their heads, gaping, and calling (Table 1). The mean proportion of intervals in which at least one nestling raised its head did not differ significantly with age. However, nestlings gaped during more intervals at early stages and called in more intervals at late stages (Table 1).

TABLE 1. Proportion of playback intervals ($\bar{x} \pm$ SE) in which early (5 to 8 days) and late-stage (14 to 17 days) Tree Swallow nestlings responded to playback of parental contact calls. Responses were compared using a paired $t$-test.

| Response | Early stage | Late stage | $t$ | $P$ |
|---|---|---|---|---|
| Head raised | 0.4 ± 0.10 | 0.6 ± 0.10 | −0.8 | 0.45 |
| Gape | 0.3 ± 0.10 | 0.1 ± 0.02 | 2.4 | 0.03 |
| Call | 0.0 ± 0.00 | 0.4 ± 0.10 | −3.9 | 0.002 |

## DISCUSSION

Tree Swallow parents called more often at early stages when nestlings were less responsive to stimuli associated with the arrival of the parent. Similarly, calling occurred more often before feedings than after and also was associated with the delivery of food to the nest. Nestlings also begged in response to the calls. Together, these results suggest that one function of Tree Swallow contact calls is to stimulate nestling begging.

Several species of passerines are reported to use vocalizations to encourage nestlings to beg (see Bengtsson and Rydén 1981, Clemmons 1995b). For example, Black-capped Chickadees (*Parus atricapillus*) give a "squawk" vocalization early in the nestling stage that appears to stimulate begging (Clemmons 1995a, b). They also squawk most often when no nestlings are begging following their arrival (Clemmons 1995b). These results are consistent with the results of our study, suggesting that this pattern is relatively common in passerines.

Given the potential risk of calling near the nest (Yasukawa 1989), it is surprising that parents call to induce begging if they could feed their young during spontaneous bouts of begging (see Bengtsson and Rydén 1981, Clemmons 1995b). Indirect evidence suggests that Tree Swallow parents increase the efficiency of feeding trips by stimulating begging. Specifically, trips are significantly shorter for older nestlings, perhaps because they are prepared to feed (i.e. they gape) upon arrival of the parent. Parents presumably would have shorter feeding trips if they stimulated nestlings to beg than if they waited for potentially infrequent bouts of spontaneous begging. This idea is difficult to test, however, because parents almost always call if no nestlings are begging. Parents also might stimulate begging to assess brood

condition and relative hunger levels (Bengtsson and Rydén 1981). In this case, they should call until at least two or more nestlings are begging. In our study, calling rates decreased once a single nestling gaped, suggesting that parents do not stimulate begging in order to assess the condition of their chicks.

The results of our playback experiment suggest that nestling Tree Swallows recognize the contact calls as distinct from that of a synthesized sound of comparable duration. Nestlings gaped, raised their heads, and called in response to the experimental tapes but not to the control tapes. However, it is difficult to assess the role of the call in stimulating begging independently of the presence of the parent because the begging response in general was relatively weak. This may have been a function of our experimental design, which entailed testing nestlings away from their home nest boxes. However, Black-capped Chickadee nestlings also showed low rates of gaping in response to playback of adult chickadee calls, including the squawk, even when playbacks were conducted *in situ* (Clemmons 1995a). Alternatively, the weak response during the experiment may indicate that nestlings require cues in addition to the calls to fully stimulate begging.

Male Tree Swallows called significantly more often than females, and most of their calls were given outside the box. Thirty percent of these calls were given when females were inside the box brooding and typically resulted in the female leaving the box (Leonard unpubl. data). This suggests that another function of the contact call is to alert the female to the male's arrival with food. In addition, both sexes occasionally called as they left the nest. We suggest that these calls coordinate the passage of the parents in and out of the nest hole.

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## LITERATURE CITED

ARMSTRONG, E. A. 1973. A study of bird song. Dover Publications, New York.

BENGTSSON, H., AND O. RYDÉN. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. Zeitschrift für Tierpsychologie 56:255–272.

CLEMMONS, J. R. 1995a. Development of a selective response to an adult vocalization in nestling Black-capped Chickadees. Behaviour 132:1–20.

CLEMMONS, J. R. 1995b. Vocalizations and other stimuli that elicit gaping in nestling Black-capped Chickadees (*Parus atricapillus*). Auk 112: 603–612.

EVANS, R. M. 1992. Embryonic and neonatal vocal elicitation of parental brooding and feeding responses in American White Pelicans. Animal Behaviour 44:667–675.

LEONARD, M. L., AND A. G. HORN. 1996. Provisioning rules in Tree Swallows. Behavioral Ecology and Sociobiology 38:341–348.

MILLER, D. E., AND M. R. CONOVER. 1983. Chick vocal patterns and non-vocal stimulation as factors instigating parental feeding behaviour in the Ring-billed Gull. Animal Behaviour 31:145–151.

MULLER, R. E., AND D. G. SMITH. 1978. Parent-offspring interactions in Zebra Finches. Auk 95: 485–495.

NUECHTERLEIN, G. L. 1988. Parent-young vocal communication in Western Grebes. Condor 90:632–636.

RITCHISON, G. 1983. The function of singing in female Black-headed Grosbeaks (*Pheucticus melanocephalus*): Family group maintenance. Auk 100: 105–116.

ROBERTSON, R. J., B. J. STUTCHBURY, AND R. R. COHEN. 1992. Tree Swallow (*Tachycineta bicolor*). *In* The birds of North America, no. 11. (A. Poole, P. Stettenheim, and F. Gill, Eds). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SIEBER, O. J. 1985. Individual recognition of parental calls by Bank Swallow chicks (*Riparia riparia*). Animal Behaviour 33:107–116.

STUTCHBURY, B. J., AND R. J. ROBERTSON. 1986. A simple trap for catching birds in nest boxes. Journal of Field Ornithology 57:64–65.

WEARY, D. M., AND D. FRASER. 1995. Calling by domestic piglets: Reliable signals of need? Animal Behaviour 50:1047–1055.

WHITTEMORE, C. T., AND D. FRASER. 1974. The nursing and suckling behaviour of pigs. II. Vocalization of the sow in relation to suckling behaviour and milk ejection. British Veterinary Journal 130: 346–356.

YASUKAWA, K. 1989. The costs and benefits of a vocal signal: The nest-associated 'Chit' of the female Red-winged Blackbird, *Agelaius phoeniceus*. Animal Behaviour 38:866–874.

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