

# Begging and the risk of predation in nestling birds

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Theoretical models of the evolution of begging in nestling passerines assume that begging is costly, either energetically or in terms of predation. However, few empirical measures of these costs exist. We examined whether nestling begging calls could attract predators to nests by comparing predation rates at artificial nests with and without playbacks of tree swallow begging calls. Nests were baited with quail eggs and placed in pairs on the ground or in modified nest-boxes. Nests with playbacks of begging calls were depredated before control nests significantly more often in both the ground and nest-box trials, suggesting that predators may use begging calls to locate nests. These results suggest that the risk of nest predation may be increased because of calling by nestlings and provide further support for the assumption that conspicuous begging is costly in terms of predation. *Key words:* begging, costs of begging, nestling birds, predation. [*Behav Ecol* 8:644–646 (1997)]

**B**egging signals used by offspring to solicit food from their parents tend to be highly conspicuous (Godfray, 1991; Redondo and Castro, 1992; Trivers, 1974). This seems surprising because parents and offspring are near each other when begging occurs, eliminating any obvious need for such a signal. Several theoretical models have been proposed to explain how conspicuous begging may have evolved (reviewed in Godfray, 1995a). Most of these models are based on the theory of parent-offspring conflict which suggests that offspring fitness would be increased by extracting more resources from parents than is optimal in terms of parental fitness (Trivers, 1974). According to the theory, offspring should be selected to exaggerate their begging in order to manipulate parents and outcompete nestmates for resources (Trivers, 1974). Models of parent-offspring conflict, have shown that this conflict can lead to the evolution of conspicuous begging (e.g., Godfray, 1991, 1995b; Harper, 1986; Macnair and Parker, 1979). Recently, models based on the more general theory of honest signaling have also shown that conspicuous begging is a likely outcome of the need for parents to ensure the reliability of the signal (Godfray, 1991, 1995a,b; Grafen, 1990; Zahavi, 1975, 1977).

Although these models differ in many ways, they all rely on the assumption that begging is a costly signal. In parent-offspring conflict models, these costs prevent the continuous escalation of the begging signal (Godfray, 1995a; Godfray and Parker, 1992), whereas in honest signaling models, the costs prevent offspring from exaggerating their nutritional needs (Godfray 1991, 1995a,b; Grafen, 1990). Despite the importance of this assumption to these models, few studies have directly measured the costs associated with begging.

Nestling birds of altricial species provide excellent models for examining the costs associated with begging. During begging, nestlings stretch their necks and bodies, gape, and flap their wings. These vigorous movements suggest that begging may be energetically costly. Nestlings also give repeated begging calls, which could attract acoustically orienting predators. Thus begging is assumed to have both energetic and predation costs. Despite the intuitive appeal of these assumptions, direct measurements are essential to determine whether the costs associated with begging are sufficient to prevent further escalation of the begging signal. Although measurements of

the energetic cost of begging have been made (Leech and Leonard, 1996; McCarty 1996), only one study has provided a direct test of the predation costs associated with begging. Haskell (1994) showed that taped begging calls of western bluebirds (*Sialia mexicana*) can attract predators to artificial nests placed on the ground, but not in trees. He also found that, for nests on the ground, predation risk increased with increasing begging intensity.

The purpose of our study was to determine whether nestling begging calls attract predators to nests. We played tapes of tree swallow (*Tachycineta bicolor*) begging calls from artificial nests placed on the ground and from inside nest boxes. The ground trials were conducted as a basic test of whether begging calls attract predators to nests, and the box trials were conducted to examine whether calls played from inside a raised cavity also attract predators. In this study we were concerned with whether predators could use begging calls to locate nests. We reasoned that the risk of predation to a species with calling nestlings would be increased if the calling attracts predators to nests. Our intent in this study was not to measure the predation cost of begging to tree swallows specifically, but rather to ask a more general question about whether begging calls could lure predators to nests. We have expanded on the work of Haskell (1994) by using several study sites, rather than a single site in which a few individual predators may be responsible for most of the predation.

## METHODS

This experiment was performed between 25 May and 26 July 1995 at 18 sites located in King's County, Nova Scotia, Canada. On average, the sites were 2775 m apart (range 450 m–20 km) and were in typical tree swallow habitat. We used many sites to ensure that our results could be generalized to more than one area and more than one predator. We also wanted to decrease the risk of predators cueing in on researchers putting out nests, which is likely to occur if sites are reused frequently (Major, 1990).

## Experimental procedure

To examine the risks associated with begging, we compared the frequency of predation at experimental nests with playbacks of begging calls to that at control nests with blank tapes. To make the experimental tapes, we recorded six 10-day-old tree swallow broods, each with five nestlings, during 30-min

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recording periods. The recordings were then placed on three, 1-min continuous tape loops with two broods on each tape. Each experimental tape consisted of 30 s of continuous begging calls followed by 30 s of silence. These calling rates mimic the maximum rates observed in our population of tree swallows (Leonard ML, unpublished data). Playback volume was set at 70 db at source, which is the natural volume of a 10-day-old brood of five begging tree swallow nestlings measured approximately 10 cm from the nest opening (Leech SM, unpublished data). The three control tapes were blank 1-min continuous tape loops.

We conducted 49 trials with nests placed on the ground and 39 trials with nests placed on platforms below nest-boxes. In the ground trials, we baited an artificial nest of dried grass with one common quail (*Coturnix coturnix*) egg and placed it on top of a 20 × 10 × 6 cm box which was covered with soil and leaves. We placed a tape recorder in the box and connected it to a speaker that broadcast sounds from a small hole cut in the side of the box. To determine which nest was taken first, we placed the egg on a trigger attached to a battery-operated clock set to 12:00. The triggers were constructed so that when the egg was removed from the nest, the circuit opened and the clock stopped.

In the nest-box trials, we placed a platform approximately 5 cm below the bottom of a tree swallow nest-box, which was mounted on a 1.3-m high metal pole. We placed an artificial nest with a quail egg on the platform, attached the egg to a clock as described above, and placed the clock inside the nest box. We placed the nest outside the box to increase the probability that a predator attracted to the nest-box would be detected. The tapes were broadcast from a speaker inside the nest-box. This experimental setup mimics the situation for a cavity nesting species more closely because calls were played from inside a raised cavity.

Sites for trials were chosen at random, without replacement until all of the 18 sites had been used once. At this point, we reused sites in the original order until the study was completed. Sites were used an average of 2.7 times (range = 1–5) for the ground trials and 2.2 times (range = 1–3) for nest-box trials. The mean time between trials at the same site was 8.7 days (range = 4–19 days). Predation occurred during at least one trial at all but two of the 18 sites for the ground trials and at all sites for the nest-box trials.

We conducted three trials per day at each of three sites. Within the sites, we placed paired nests at least 50 m apart to reduce the risk that predators could use cues such as scent trails to find the other nest in the pair. We also placed paired nests in a similar microhabitat to avoid differences in visual and auditory detectability. The order in which control and experimental nests were placed within each site was alternated between trials.

We set up the playback equipment 12 h before trials were scheduled to begin to minimize disturbance on the day of the trial. To reduce scent trails, we wore plastic gloves and plastic bags tied around our legs while setting up and checking nests (Major, 1990). Trials began at either 0500 h or 1700 h, at which point we placed the quail egg in each nest and started the playback tape. Tapes played an average of 3.5 h until the batteries were drained. Thus, playbacks were performed from 0500 h until approximately 0830 h, and again from 1700 h until approximately 2030 h. This schedule is similar to the peak feeding periods (and thus begging periods) for many nestling passerines. Twelve h after the beginning of the trial, and at each 12-h interval thereafter, the nests were checked for predation. If predation had occurred at either or both nests in a pair, the time to predation was noted and the nests were removed. If predation had not occurred, the batteries

**Table 1**  
Frequency (%) of predation at one or both paired nests during ground and nest-box trials

Type	No. of trials	Trials with predation	One nest	Both nests
Ground	49	23 (46.9)	8 (34.7)	15 (65.3)
Nest-box	39	23 (58.9)	11 (47.8)	12 (52.2)

were changed, the clock reset to 12:00, and the trial continued. Nests remained in place for a maximum of 2 days.

We considered predation to have occurred if the egg was missing or broken. If the contents of the nest were missing and the nest was torn apart, we assumed that the predator was a mammal. In contrast, if the egg was missing, but the nest itself was undisturbed, we assumed that the predator was avian (Haskell, 1994; Leonard and Picman, 1987).

Unlike earlier studies, we examined the costs of predation across numerous sites so that our results were not based on predation by a single predator at one site. Because of the time constraints of this design, we ended a trial if predation occurred rather than leave nests exposed for a standard amount of time (e.g., 2 days). Therefore, our measure of response was to determine which nest was depredated first within the 2-day period. We determined this by recording which nest was taken when predation occurred at one of the two nests and by using the clocks to determine which nest was depredated first in the event that both nests had been depredated in one time interval. Sometimes predation occurred at both nests within a trial and a clock malfunctioned ( $n = 4$  for ground trials;  $n = 5$  for nest-box trials), so we were unable to determine which nest was depredated first. These trials were not included in our analyses.

## RESULTS

### Ground trials

Predation occurred in almost half of the ground trials across all sites (Table 1). Overall, experimental nests were depredated before control nests in 16 of the 19 trials in which the time to predation was recorded (binomial test,  $p = .002$ ). This was not a result of several predation events at a few sites because experimental nests were depredated first at 15 of the 16 sites at which predation occurred (control nests were depredated first at 3 sites, 2 of which also had a trial with experimental nests depredated first). Seventy-five percent of the experimental nests were depredated during (55%) or within 2 h (42%) of the playback period.

We recorded the condition of the nests after predation for 20 ground trials. Of the 40 ground nests (20 trials × 2 nests), 31 nests were depredated. Fifteen of these nests were torn apart and 16 were undisturbed ( $\chi^2 = 0.04$ ,  $p > .90$ ). We found remnants of the egg shell around 1 of the 15 nests that were torn apart.

### Nest-box trials

Predation occurred in more than half the nest-box trials across all of the sites (Table 1). Overall, experimental nests were depredated before control nests in 13 of the 18 trials in which the time to predation was recorded (binomial test,  $p = .04$ ). Again, this pattern was consistent across sites, with each of the 13 trials in which experimental nests were depredated first occurring at different sites. Ninety percent of the experimental nests were depredated during (44%) or within 2 h (56%) of the playback period.

We recorded the condition of the nests following predation for 17 nest-box trials. Of the 34 nests (17 trials  $\times$  2 nests) at nest-boxes, 25 were depredated. Significantly more of these nests were found intact ( $n = 22$ ) than torn apart ( $n = 3$ ;  $\chi^2 = 14.4$ ,  $p < .005$ ). No traces of egg shell were found around any of the nests depredated in nest-box trials.

The number of experimental and control nests depredated overall for ground and nest box trials did not differ significantly ( $\chi^2 = 0.40$ ,  $p = .50$ ) nor did the number of experimental versus control nests depredated first ( $\chi^2 = 1.5$ ,  $p = .22$ ), suggesting that the pattern of predation was similar at ground nests and nest-boxes. However, the power of these tests is low (0.05 and 0.06, respectively) because of our sample size and predation rate.

## DISCUSSION

In this study, experimental nests associated with begging calls were depredated before control nests without calls, suggesting that begging by nestling birds could attract predators. In many of our trials both nests were depredated, although experimental nests were generally taken first. This pattern suggests that predators used the begging calls to locate the experimental nest and found the control nest (despite our precautions) by following scent trails or disturbed vegetation. Nonetheless, the results suggest that begging calls could attract predators to both ground and cavity nests. Once the predator is drawn to the nest, the probability that it will depredate the nest will presumably be affected by factors such as the accessibility of the nest or nestlings, the effectiveness of parents in deterring predators, and so on. In general, however, our results suggest that the likelihood of predation is increased by nestling begging calls.

In a similar study, Haskell (1994) showed that the begging calls of the cavity-nesting western bluebird attracted predators to nests on the ground, but not in trees. The results of our study strengthen Haskell's (1994) conclusions because our trials were performed over several sites rather than a single site, thus making the results applicable to more than a few individual predators at a single location.

Like Haskell's study, our results may overestimate the costs of begging for ground nesting birds. The begging calls of cavity-nesting species such as tree swallows may have an acoustic structure that makes them easier to locate than the begging calls of ground-nesting species (Redondo and Arias de Reyna, 1988). If so, our trials might inflate the predation risk for those species. Similarly, the relatively high calling rate used in this study may have increased detection of experimental nests in both ground and box trials. This effect was, however, counteracted by the fact that tapes were only played in the morning and evening, rather than throughout the day as in Haskell's study.

We do not have direct information on the types of predators that depredated nests in our trials, but the state of the nests suggests that both mammals and birds were involved (Haskell, 1994; Leonard and Picman, 1987). Nests on the ground appeared to be depredated equally by both mammalian and avian predators. Nests at boxes, however, were depredated mostly by birds. Although we did not directly witness predation during this study, a variety of mammalian and avian predators, including red squirrels (*Tamiasciurus hudsonicus*), raccoons (*Procyon lotor*), American crows (*Corvus brachyrhynchos*), common grackles (*Quiscalus quiscula*), and blue jays (*Cyanocitta cristata*), were observed at the field sites.

The results of the present study and of the earlier study by Haskell (1994) indicate that begging may carry a significant predation cost for nestling birds. Furthermore, the energetic cost of begging, although low, also appears to be significant

(Leech and Leonard, 1996; but see McCarty, 1996). Together these results support the assumptions of many theoretical models that conspicuous begging is accompanied by significant costs. As suggested by the models, the costs associated with begging may prevent the exaggeration of this signal and ensure its honesty.

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