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## Provisioning rules in tree swallows

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**Abstract** Conflict between parents and offspring may result in offspring exaggerating their needs and parents devaluing their begging signals. To determine whether this occurs, it is first necessary to establish the link between need, begging and parental response. The purpose of our study was to examine these relationships in tree swallows (*Tachycineta bicolor*). Parents preferentially fed nestlings that begged sooner, reached higher and were closer to the front of the nestbox (Fig. 1). Begging intensity of both individuals and entire broods increased with relatively long periods between feeding visits. Within broods, parents responded to increased begging intensity by increasing their feeding rate, although this effect was relatively weak. Large and small nestlings did not differ in their begging behavior and all nestlings, regardless of size, were fed at similar rates. Despite the overall equity in feeding, male parents preferentially fed larger nestlings while female parents fed smaller nestlings. Nestlings did not increase their begging intensity in response to begging by nestmates. Our results suggest that begging is related to need in this species and that parents respond to variation in begging intensity.

**Key words** Begging · Signals · Sibling interactions · Manipulation

## Introduction

Begging by offspring to their parents is a widespread and seemingly simple signal. The adaptive advantages for offspring to advertise their need and for parents to respond seem obvious. Yet this relationship may not

be straightforward because parents and offspring are not genetically identical and therefore may disagree about how resources should be allocated (Trivers 1974). Parents are expected to distribute resources so as to increase the quality and quantity of young produced over their lifetime. Individual offspring, on the other hand, are expected to demand more than their share of resources from their parents. Because of this potential conflict offspring might try to gain extra provisioning by exaggerating their needs, while parents might respond by devaluing their begging (MacNair and Parker 1979; Harper 1986; Godfray 1991).

Despite these general predictions, most empirical evidence on begging behavior in nestling birds suggests that begging is a reliable indicator of need. For instance, begging intensity has been shown to increase with food deprivation in glaucous-winged gulls (*Larus glaucescens*; Henderson 1975), great tits (*Parus major*; Bengtsson and Ryden 1983) and American robins (*Turdus migratorius*; Smith and Montgomerie 1991) and decrease with food supplements in great tits (Bengtsson and Ryden 1983) and magpies (*Pica pica*; Redondo and Castro 1992).

This evidence shows that begging correlates well with hunger and therefore should be a reliable signal of an offspring's physiological state. However, this does not exclude the possibility that nestlings might still exaggerate their needs under some circumstances. Indeed, factors other than hunger appear to influence begging behavior. For instance, nestling zebra finches (*Poephila guttata*) and American robins beg more in response to begging nestmates (Mueller and Smith 1978; Smith and Montgomerie 1991, respectively), suggesting that nestlings might exaggerate their needs in the presence of competition. Budgerigar (*Melopsittacus undulatus*) nestlings increase their begging rates the more often they are fed (Stamps et al. 1985), indicating that begging is not only related to need. The relative importance of the factors influencing begging must be understood before determining

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whether offspring exaggerate their needs to extract extra resources from their parents.

The potential for offspring to manipulate parents will also depend on how parents respond to changes in begging intensity. If increased intensity results in increased feeding then offspring might benefit from exaggerating their needs (Godfray 1991). Most empirical evidence shows a positive relationship between begging intensity and parental feeding rate (e.g. Henderson 1975; Mueller and Smith 1978; Bengtsson and Ryden 1983; Gottlander 1987; Hussell 1988; Stamps et al. 1989; Smith and Montgomerie 1991). However some studies have shown that parents also use features such as offspring size (Stamps et al. 1985) or position in the nest (McRae et al. 1993; Kacelnik et al. 1995; Kilner 1995). Observations on the response of parents to variation in begging are needed to determine whether parents could be manipulated by their offspring.

Parent-offspring conflict theory predicts that both begging intensity and parental response should change over the dependent period, with offspring intensifying their begging as parents reduce feedings prior to independence (Trivers 1974). Few studies, however, have examined how these factors vary with nestling age (see Stamps et al. 1989 for an exception). The purpose of our study was to examine the relationship between nestling need, begging intensity and parental feeding in tree swallows (*Tachycineta bicolor*) during early, middle and late nestling stages. We asked:

1. What features, if any, of nestling begging behavior influence which nestling is fed?
2. Do these features vary with hunger level?
3. Do parents use variation in these features to set their overall feeding rate?
4. Do interactions among nestlings influence begging behavior?
5. Is food evenly distributed among nestlings?

Tree swallows are ideal for examining these questions. They typically have one brood each season with an average clutch size of 5.4 eggs (Robertson et al. 1992). They readily nest in boxes which permits videotaping of extended sequences of begging behavior. In addition, their eggs hatch over 1–3 days resulting in significant differences in size among nestlings (Zach 1982). Because size is often correlated with competitive ability, a size hierarchy allows for examination of the effect of nestling competition on begging behavior.

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## Materials and methods

This study was conducted at five study sites in King's County, Nova Scotia, Canada between 1 May and 30 July 1994. Four of the five sites were apple orchards in which nestboxes were placed approximately 20 m apart in grids. The fifth site was an open field by a river. In this site the nestboxes were placed every 10 m around the

perimeter of the field. Each nestbox measured approximately 30 × 15 × 15 cm (internal dimensions), with the hole center about 20 cm above the floor. In 1994, 25–30 boxes were at each site, and 75 of 138 nestboxes were occupied by tree swallows.

Adults were trapped using nestbox traps (Stutchbury and Robertson 1986) and individually marked with acrylic paint and colored leg bands. Females were aged as second year or after second year by their back color (Robertson et al. 1992) and data from both age classes are included. Males were not aged. In addition, 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 (see below). All pairs used were monogamous as far as we knew. First egg dates and hatching dates were determined by checking nestboxes every 2nd day until 2 days before the predicted hatching date, after which they were checked daily. At hatch, nestlings were individually marked on their tarsus with felt-tipped pen.

We videotaped inside 16 nestboxes with broods of either four ( $n = 7$ ) or five ( $n = 9$ ) nestlings during three stages of the nestling period: stage 1, 4–6 days old (hatch = day 1); stage 2, 9–11 days old; stage 3, 14–16 days old. Twenty-four hours before taping we opened the hinged side of each nestbox 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 nestbox. This kept the box dark and let parents habituate to the frame which later covered the videocamera. Each nestling was then marked on the head with a distinctive pattern of white paint. The next day, a Panasonic PV-900-K VHS videocamera 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 nesthole appeared in the top right corner of the field of view. Each nest was videotaped for 2 h between 0600 and 1000 hours ADST. Parents usually resumed feeding within a few minutes of our departure from the box.

To test whether videotaping affected feeding rates, we conducted 30 min feeding watches at 11 of the 16 nestboxes, 24 h before filming. Observers sat approximately 30 m from the nestbox and recorded the number of feeding trips by parents. Observers did not approach the box before the watch. We found no significant difference between feeding rates derived from these watches and those derived from videotapes (watches:  $12.4 \pm 1.37$ ; videotapes:  $15.3 \pm 1.52$  feeds/h, paired  $t = 1.41$ ,  $P = 0.19$ ).

As part of an intensive study on nestling growth rates nestlings were weighed and measured daily, from hatch to day 15. No nestlings died during this study.

## Statistical and video analyses

Each time a parent visited the nest we recorded its sex and which nestling was fed. As the parent entered the nestbox, some or all of the nestlings begged by stretching their heads up, opening their mouths wide and calling. A parent was considered to have offered a nestling food if it placed the food item in the nestling's mouth.

The transition between entering the hole and feeding a nestling was marked by the change from a deceleration of the parent's head upon entry to an acceleration of the head toward the nestling that was fed. We measured begging behavior immediately before this transition, to ensure that begging was not affected by the parent's decision of which nestling to feed (e.g. nestlings that are certain of being fed might reach higher).

We measured three features of the begging behavior of each nestling: (1) the order in which nestlings gaped (first to gape = 1), (2) the height (cm) that nestlings reached above the nest rim and (3) the horizontal distance (cm) from the corner of the bill to the front of the box (i.e. the side with the nest opening). Nestlings that did not beg were not scored. Each of these variables reflected different aspects of begging. We took height as our main measure of the intensity of begging, because it varied considerably between and even within parental visits. We also used the number of begging nestlings as a measure of the intensity of the brood. Distance

reflected the position of nestlings relative to the nest opening. Because nestlings do not climb over one another during a parental visit, distance was less likely to reflect short-term changes in begging intensity. Gape order was used to measure the relative sequence in which nestlings begged. These three measures were only weakly intercorrelated (correlations performed for each nest on data corrected for stage:  $r < 0.54$  for every nest).

Nestlings that tied in gape order were assigned the same rank (e.g., nestlings tied for second place were both scored "2") and those that begged after food had been offered to another were not included in the analyses. Height and distance were measured by placing a transparent sheet with a grid of 1 cm squares over the video screen during transcription. The video display showed images at their actual size. Parents delivered food in the form of a bolus, so we could not estimate either the quality or quantity of food delivered. Therefore we report the frequency of feedings only.

Nestlings hatched over 2 ( $n = 11$  nests) or 3 ( $n = 4$  nests) days (at one nest hatching time was not determined). This resulted in hatching spreads of 1–3 days, and relatively large differences in size among nestlings. To examine the effect of body size on begging behavior and feeding, we randomly chose two nestlings from each nest that hatched at least a day apart. The earlier hatching nestling was assigned to the large size class and the later hatching nestling to the small size class. The difference in body weight between the two classes of nestlings was significant and maintained throughout the nestling period (mean across all nestling stages: large:  $18.6 \pm 0.79$  g; small:  $17.0 \pm 0.84$  g;  $F = 13.31$ ,  $P = 0.003$ ,  $df = 1, 14$ ), though it decreased across stages (differences between means for each stage: 2.4, 1.8, and 0.9; stage  $\times$  size class interaction  $F = 8.68$ ,  $P = 0.001$ ,  $df = 2, 28$ ). Analyses of begging by individual nestlings in relation to need were performed separately for large and small nestlings. The results were not significantly different for the two classes, so we report the results for large nestlings only.

All data were plotted to visually confirm that they were normally distributed and variances were homogeneous. The gape orders of individual nestlings were discontinuously distributed, although their means were normally distributed. Nonparametric tests involving gape order gave results equivalent to the ANOVAs reported here.

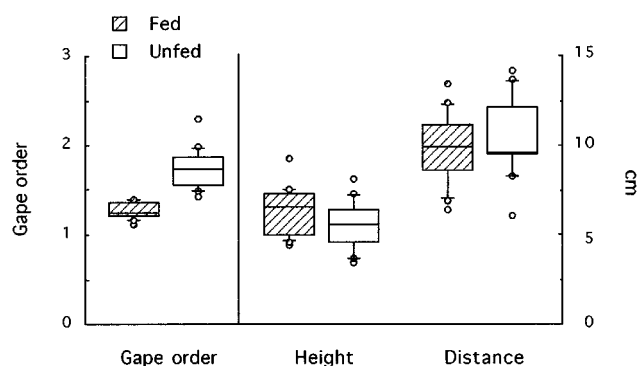
An important consideration in all analyses was that nests (rather than individual feedings or nestlings) were our unit of replication. Unless stated otherwise, we used repeated measures ANOVAs with nests as blocks and stage as a within-subject effect. When we were testing for a relationship between two continuous variables, we calculated a standardized regression coefficient for each nest and used a one sample  $t$ -test to test whether the coefficients were significantly different from zero (coefficients are standardized to meet the assumption of normality for the  $t$ -test). By using this method we avoided pooling raw data from different nests and performing 16 separate  $t$ -tests (Petrinovich and Widaman 1984). Similarly, the coefficients could be entered in ANOVAs to test for changes in regressions, for example with stage.

We do not report effects involving nest or nestling stage except where their interaction with the main variable being tested is significant (i.e. the effect is not consistent across nestling stages or nests). Broods of four and five nestlings did not differ in begging behavior (height, distance, or mean number of begging nestlings),

**Table 1** Feeding rate (feeds/h) in relation to parent's sex and nestling stage<sup>a</sup>

Parent's sex	Stage		
	1	2	3
Male	$8.5 \pm 0.76$	$11.4 \pm 1.57$	$10.2 \pm 1.50$
Female	$10.5 \pm 1.04$	$13.8 \pm 1.34$	$11.6 \pm 1.42$

<sup>a</sup>Two-way repeated measures ANOVA on nest means: sex of parent  $F = 0.31$ ,  $P = 0.59$ ,  $df = 1, 14$ ; stage  $F = 3.86$ ,  $P = 0.03$ ,  $df = 2, 28$



**Fig. 1** Box plots (*horizontal lines* show the 10th, 25th, 50th, 75th, and 90th percentiles and all data outside this range are plotted) of begging behavior of nestlings that received food (fed; *filled bars*) and those which did not receive food (unfed; *open bars*,  $n = 16$  nests throughout). ANOVA results: gape order  $F = 53.81$ ,  $P = 0.0001$ ,  $df = 1, 15$ ; 16/16 nests fed < unfed, height (cm)  $F = 45.76$ ,  $P = 0.0001$ ,  $df = 1, 15$ ; 16/16 nests fed > unfed, distance (cm)  $F = 9.11$ ,  $P = 0.0001$ ,  $df = 1, 15$ ; 11/16 nests fed < unfed

the mean mass of nestlings or parental feeding rate (two-way ANOVAs with nestling stage, all  $F < 0.48$ ,  $P = 0.50$ ,  $df = 1, 42$ ). Therefore data on broods of different sizes are pooled for analyses. All means are reported  $\pm 1$  SE.

## Results

### Feeding and begging rates

Overall, feeding rates varied significantly with nestling stage, but not with the sex of the parent (Table 1). Feeding rates of both parents were therefore, pooled in subsequent analyses unless stated otherwise.

The number of nestlings that begged at each feeding varied significantly with nestling stage, with more nestlings begging during stages 2 and 3 than during stage 1 (stage 1:  $2.1 \pm 0.06$ , stage 2:  $3.4 \pm 0.05$ , stage 3:  $3.1 \pm 0.05$ ,  $F = 159.00$ ,  $P = 0.0001$ ,  $df = 2, 30$ ).

### Factors influencing the distribution of food

All three measures of begging behavior affected whether a nestling was fed. At all nestling stages, nestlings that gaped sooner, reached higher and were closer to the front of the box were more likely to be fed (gape order:  $F = 53.81$ ,  $P = 0.0001$ ,  $df = 1, 15$ ; 16/16 nests fed < unfed, height (cm):  $F = 45.76$ ,  $P = 0.0001$ ,  $df = 1, 15$ ; 16/16 nests fed > unfed, distance (cm):  $F = 9.11$ ,  $P = 0.0001$ ,  $df = 1, 15$ ; 11/16 nests fed < unfed; Fig. 1).

### Does begging intensity vary with need and condition?

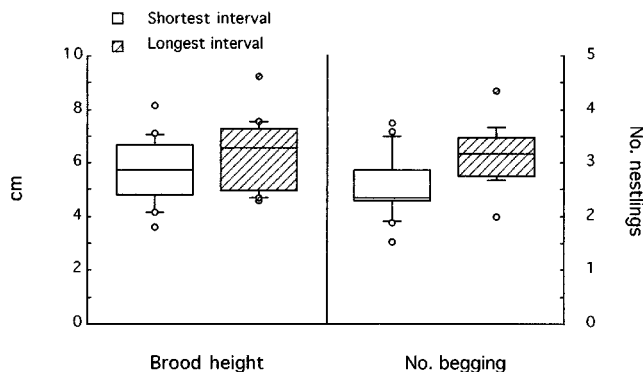
If begging intensity is related to need then each nestling should beg more intensely the longer it has been since

it was fed. To determine the relationship between begging and need, we compared the height of a large nestling from each brood, after its shortest interval without food (mean across nests:  $2.4 \pm 0.31$  min) to its height after the longest interval without food ( $31.9 \pm 2.49$  min). At all nestling stages, nestlings reached higher after longer intervals than after shorter intervals (height after long intervals:  $6.9 \pm 0.65$  cm; short intervals:  $5.7 \pm 0.68$  cm,  $F = 12.26$ ,  $P = 0.003$ ,  $df = 1, 15$ ). Similarly, if begging is linked to need, then each nestling might also be expected to reduce its begging intensity following a feeding. After individual nestlings were fed, their height decreased significantly (height: the visit in which they were fed  $6.4 \pm 0.33$ , the following visit:  $5.7 \pm 0.30$ ;  $F = 24.67$ ,  $P = 0.0002$ ,  $df = 1, 15$ ).

These results suggest that the begging intensity of individual nestlings increases after relatively long periods without food. This relationship may also apply to the begging intensity of the brood as a whole. Both the mean height of the brood and the mean number of nestlings begging was higher when parents were gone from the nest for longer periods of time (Fig. 2). Begging intensity among broods was also influenced by the condition of nestlings. Among nests, mean brood height decreased as the mean mass of nestlings increased. That is, broods of heavier nestlings on average begged less intensively than broods of lighter nestlings (ANCOVA across nests with nestling stage as main effect:  $F = 7.74$ ,  $P = 0.01$ ,  $df = 1, 39$ ).

#### Do parents respond to variation in begging intensity?

If parents respond positively to begging intensity, then the more intense the begging of the brood at a given feeding, the sooner parents should return with food. We tested this prediction by calculating the regression between the mean height of the brood at each feeding



**Fig. 2** Box plots (as in Fig. 1) of height (cm) of the brood ( $F = 12.26$ ,  $P = 0.003$ ,  $df = 1, 15$ ) and the mean number of nestlings begging ( $F = 17.93$ ,  $P = 0.0007$ ,  $df = 1, 15$ ) when the time since the parents' last visit was relatively short ( $1.1 \pm 0.65$  min) versus when the time was relatively long ( $11.1 \pm 0.61$  min;  $n = 16$  nests throughout).

and the time to the next visit by that parent to the nest. When this was done for each nest and stage, the resulting standardized regression coefficients did not vary significantly with nestling stage ( $F = 0.25$ ,  $P = 0.78$ ,  $df = 2, 28$ ). The mean coefficients averaged across all stages were low but significant (standardized  $r = -0.10 \pm 0.04$ ,  $t = -2.50$ ,  $P = 0.03$ ,  $df = 14$ ). Thus parents returned to the nest sooner the higher nestlings reached on the previous visit. The same analyses using the number of nestlings as the measure of begging intensity showed no significant effects at any nestling stage, nor overall (standardized  $r = -0.02 \pm 0.04$ ,  $t = -0.50$ ,  $P = 0.64$ ,  $df = 14$ ).

We found no relationship between mean brood height or number of nestlings begging and parental feeding rate (ANCOVA across nests with nestling stage as a main effect: brood height  $F = 1.26$ ,  $P = 0.27$ ,  $df = 1, 42$ ; number of begging nestlings  $F = 0.73$ ,  $P = 0.40$ ,  $df = 1, 42$ ).

#### Interactions among nestlings

Interactions among nestlings may influence the distribution of food if larger nestlings outcompete smaller nestlings by begging sooner, reaching higher and monopolizing positions closer to the front of the nest. Within nests, at all nestling stages, large nestlings did not differ from small nestlings in their gape order, height or distance to the front of the nest ( $F \leq 0.20$ ,  $P > 0.66$ ,  $df = 1, 15$ ), nor did they beg at more parental visits ( $F = 0.07$ ,  $P = 0.80$ ,  $df = 1, 15$ ).

Interactions among nestlings might also influence begging intensity if nestlings stimulate each other to beg. That is, individual nestlings might base their height on the average height of the brood or on the number of nestlings begging. We have shown that the height of individual nestlings is positively related to the interval since the last feeding and the height of the brood is positively related to the interval since the last visit by the parent. Therefore the height of the individual and the height of the brood are likely intercorrelated.

We tested for an effect of nestmates on begging intensity independently of hunger by relating the height of nestlings that had been fed within the last 2 min to the height of their nestmates. We predicted that these recently fed nestlings might increase their begging intensity to match that of their hungrier nestmates. Although not all nestlings will be equally satiated by a single feeding, we reasoned that on average this restriction would hold hunger relatively constant and low. Because nestlings are rarely fed twice in the span of two minutes, the restriction limited our sample size to 14 nests at stage 2 or 3 only (if a nest was sampled at both nestling stages, we used the mean of the standardized  $r$ 's for each stage). Given the lack of a relationship between size class and begging (above), it seemed unnecessary to restrict our sample size still

further by holding size/age constant. The height of nestlings that had just been fed was not significantly related to the mean height of the brood nor the number of begging nestmates (height:  $r = -0.07 \pm 0.070$ ,  $t = -0.95$ ,  $P = 0.36$ ,  $df = 13$ ; number:  $r = -0.10 \pm 0.061$ ,  $t = -1.68$ ,  $P = 0.12$ ,  $df = 13$ ).

### Distribution of food among nestlings

We tested whether the number of feeds was equally distributed among nestlings by performing separate goodness-of-fit  $G$ -tests for each nest on the number of feeds each nestling received at each stage. Nestlings received similar numbers of feedings ( $P > 0.26$  for each of 13 nests; cell totals at three nests were too small to test).

Some earlier studies found a difference in how male and female parents provisioned large and small nestlings (e.g. Stamps et al. 1985; Gottlander 1987), so we also compared the mean feeding rate, by nest, to large and small nestlings at different stages in a three-way ANOVA. Across all nestling stages and nests, there was no significant main effect of nestling size ( $F = 0.01$ ,  $P = 0.70$ ,  $df = 1, 49$ ), however, there was a significant interaction between parent's sex and nestling size ( $F = 8.10$ ,  $P = 0.007$ ,  $df = 1, 39$ ). Males preferentially fed large nestlings (mean feeds/h over all stages to large:  $2.5 \pm 0.22$ , small:  $1.9 \pm 0.21$ ) and females preferentially fed small nestlings (large:  $1.9 \pm 0.21$ , small:  $2.5 \pm 0.28$ ).

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## Discussion

### Factors influencing the distribution of food

In our study nestlings that gaped sooner, reached higher and were closer to the front of the box were more likely to be fed. Several earlier studies have also shown that begging behavior (e.g. Smith and Montgomerie 1991; Teather 1992; Leonard et al. 1994) and position in the nest (e.g. Ryden and Bengtsson 1980; Greig-Smith 1985; Gottlander 1987; McRae et al. 1993; Kacelnik et al. 1995; Kilner 1995) influence the probability of a nestling receiving food. These results suggest that interactions among nestlings (e.g. reaching higher or getting access to favored positions) may often determine the distribution of food rather than active selection of particular nestlings by parents. Although this "laissez-faire" pattern is most common, some exceptions seem to occur. Female budgerigars and pied flycatchers (*Ficedula hypoleuca*; under some circumstances) preferentially feed their smallest nestlings while males of both species feed large and small nestlings at similar rates (Stamps et al. 1985; Gottlander 1987, respectively).

In our study male parents preferentially fed large nestlings while females preferred small nestlings. We

found no evidence that nestlings of either size were more or less effective in their begging behavior (as in e.g. Ryden and Bengtsson 1980), possibly because the differences in size were relatively small. The lack of a difference in begging suggests that the preferences of males and females are not simply a passive acceptance of the differing abilities of these nestlings. Preliminary observations of fledglings suggest that the brood is not divided (unpublished work), so the bias is not likely the beginning of brood division. It is not clear why parents differed in this regard. Indeed, the apparent preferences had little effect because all nestlings, regardless of size, received similar numbers of feedings. What this result does suggest is that the distribution of food in tree swallows is not strictly under nestling control.

### Begging and need

If begging intensity is a reliable signal of need, nestlings should beg more intensely if they are hungry and less intensely if they are fed. We found some evidence for both requirements. Across all stages, both individuals and broods reached higher and more nestlings begged during relatively longer absences by the parents. Nestlings that had just been fed did not reach as high on the visit following the feeding. Furthermore, broods of lighter nestlings begged more intensively than broods of heavier nestlings, again suggesting that begging intensity was related to need. The latter result corroborates the study of Hussell (1988) on variation in begging and provisioning in another population of tree swallows. Hussell found a negative correlation between begging and nestling mass, and higher begging at a study site with low food abundance than one with higher food abundance.

Several experimental studies have also shown a link between begging intensity and hunger. For example, by swapping broods between sites with high and low food abundance, Hussell (1988) abolished the difference in begging intensity between sites, which along with other evidence suggested that in the short term begging decreases with feeding rate. In several species, nestlings increased their begging intensity in response to food deprivation (Henderson 1975; Bengtsson and Ryden 1983; Gottlander 1987; Smith and Montgomerie 1991) and decreased their begging intensity when given food supplements (Bengtsson and Ryden 1983; Redondo and Castro 1992). Although none of these studies directly address whether nestlings exaggerate their begging, they do suggest a link between begging intensity and need.

### Do parents respond to variation in begging intensity?

If begging is a signal of need, then parents should presumably respond to an increase in begging intensity by

increasing their rate of provisioning. Parent tree swallows returned to the nest sooner the higher nestlings reached on the previous visit, although the effect in general was relatively weak.

In several species, parents increased their feeding rate in response to taped begging calls of hungry nestlings (e.g. Mueller and Smith 1978, Bengtsson and Ryden 1983). Likewise, increased begging intensity within broods was associated with an increase in the number of feeding trips by parents in several species (e.g. Henderson 1975; Bengtsson and Ryden 1983; Hussell 1988; Stamps et al. 1989; Smith and Montgomerie 1991).

We detected no change with nestling stage in the relationship between begging intensity and how soon parents returned. However, the relationship is weak overall and any changes could easily be obscured. In contrast, we did find an increase in both the number of begging offspring and parental feeding rate with nestling stage, particularly between stages 1 and 2. Both results may reflect the increase in the needs of nestlings as they grow and the response of parents to those needs.

In contrast to the relationship between begging and provisioning within nests, between nest variation in provisioning was not related to begging intensity. Predictions for the direction of the relationship between begging and feeding between nests are not as straightforward as they are within nests. Feeding rate and begging rate are interdependent, so parents may feed more at nests where nestlings beg more, while at the same time nestlings may beg less at nests where parents feed them more (Hussell 1988). Additionally, because parental feeding rate may be constrained by food availability (Hussell 1988) and begging rate is modified by the condition of the young (Hussell 1988, this study), mean parental feeding rate over the long term may be similar among different broods regardless of nestling begging intensity (Hussell 1988). Testing these alternatives requires experimental manipulation of begging and food availability (Hussell 1988).

### Begging and sibling interactions

In this study nestmates did not appear to have a significant influence on begging intensity, though we recognize that an experimental test would be more convincing. Three earlier studies provided evidence for a link between the begging intensity of nestmates and that of individual nestlings, though none have been conclusive. Harper (1986) drawing on the results of several studies on cotingids, found that begging intensity was lower in species with one chick per clutch than for species with two or more. Similarly, the frequency of begging by nestling zebra finches increased after exposure to playbacks of begging calls (Mueller and Smith 1978). Smith and Montgomerie (1991) showed that

changes in the begging intensity of American robin nestlings correlated with the changes (usually increases) in the begging intensity of their food-deprived nestmates.

In conclusion, the results of this study suggest a link between nestling need, begging intensity and parental feeding in tree swallows. This, in turn, suggests that begging may be a honest signal of need in this species. Nestlings did not increase their begging in response to nestmates, although they might under other circumstances (e.g. larger broods, food limitation). Experiments are now under way to examine this latter possibility and to test whether such a conspicuous signal is really necessary to honestly advertise need.

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