Brood size and begging intensity in nestling birds

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Theoretical models suggest that sibling competition should select for conspicuous begging signals. If so, begging intensity might be expected to increase with the number of competitiors. The purpose of our study was to examine the relationship between begging intensity and brood size using nestling tree swallows (*Tachycineta bicolor*) as our model. Over 2 years, we videotaped begging behavior in unmanipulated broods of different sizes. We found that begging intensity increased with brood size. The average weight of nestlings in each brood did not vary with brood size, but feeding rate per nestling decreased with brood size, suggesting that nestlings in larger broods begged more intensively, possibly because they were hungrier. We also conducted an experiment to examine the effect of nest mates on begging in different-sized broods. We found that nestlings with similar weights, previous competitive environments, and food deprivation begged more intensively in large broods than in small broods. Overall, our study indicates that begging intensity increases with brood size in tree swallows. This relationship may result from interactions among brood mates rather than from lower feeding rates to individual nestlings in larger broods. *Key words:* begging, brood size, nestlings, parent–offspring conflict, provisioning, *Tachycineta bicolor,* tree swallows. *[Behav Ecol 11:196–201 (2000)]*

The evolution of conspicuous begging has been a topic of considerable interest to evolutionary biologists and the focus of many theoretical models (e.g., Godfray, 1991, 1995a; Harper, 1986; Parker and MacNair, 1979). What is perplexing is why a signal apparently for communicating need to parents should be so conspicuous. Parent–offspring conflict models suggest that conspicuous begging is a result of selection on offspring to exaggerate their needs and thus manipulate parents into providing more resources than parents have been selected to give (e.g., Godfray, 1995a). Alternatively, signaling models suggest that begging reliably conveys cryptic aspects of offspring need (Godfray, 1991, 1995a,b). The signal is extreme because the costs associated with its production are needed to maintain its reliability given underlying parent–offspring conflict.

Theory also suggests that competition among litter or brood mates for limited parental resources will select for intense begging (e.g., Harper, 1986; MacNair and Parker, 1979). In fact, a recent model indicates that sibling competition may be the driving force in the evolution of the begging signals commonly observed in young animals (Rodríguez-Gironés et al., 1996). Birds, particularly passerines, have served as the model system for testing many of the ideas on the evolution of begging. The current literature on these species provides some support for the idea that competition influences begging. For example, the begging behavior of individual nestlings appears to increase with an increase in the begging intensity of nest mates (e.g., Price and Ydenberg, 1995; Leonard and Horn, 1998; Smith and Montgomerie, 1991), suggesting that competition influences begging. However, this result is not consistent across all species (Cotton et al., 1996; Kacelnik et al., 1995).

The relationship between competition and begging may be established more directly by examining how begging intensity varies with brood size. Indeed, theory predicts that if competition selects for increased begging, then begging intensity should increase with brood size (Harper, 1986; MacNair and

Parker, 1979). Few studies have tested this prediction and those that have provide equivocal support (Fujioka, 1985; Henderson, 1975; Price, 1996; Stamps et al., 1989).

The main purpose of our study was to test the prediction that begging intensity increases with brood size, using nestling tree swallows (*Tachycineta bicolor*) as our model. We expand on the previous work by examining the relationship between begging and brood size in an unmanipulated field situation over a range of natural brood sizes. This descriptive study allowed us to first determine if the predicted pattern existed in our model system.

We were also interested in examining the features of brood size that might contribute to a relationship between begging intensity and brood size. That is, begging might increase with brood size if nestlings in larger broods receive less food and/or are in poorer condition than nestlings in smaller broods (e.g., Wright and Cuthill, 1990). Both hunger and condition have been shown to influence begging intensity (e.g., Cotton et al., 1996; Kilner, 1995; Kölliker et al., 1998; Lotem, 1998; Price and Ydenberg, 1995; Price et al., 1996). Similarly, begging intensity may increase with brood size if nestlings in large broods respond to the competitive environment (i.e., number of nest mates) by increasing their begging intensity. This behavioral response could occur independently of any influence of food deprivation or condition on begging if nestlings are stimulated to beg more intensively by the begging of nest mates (e.g., Price, 1996).

We addressed the factors influencing begging in broods of different sizes by first examining whether feeding rate per nestling and the average weight of nestlings in a brood (i.e., mean brood weight) vary across unmanipulated broods of different sizes. In tree swallows begging intensity is known to increase with food deprivation (Leonard and Horn, 1996, 1998) and, across broods, with decreasing nestling weight (Hussell, 1988; Leonard and Horn, 1996, 1998). Thus, an increase in begging intensity in larger broods might occur if nestlings in these broods received less food and therefore were generally hungrier and/or weighed less than nestlings in small broods. We also conducted an experiment to test for an effect of behavioral competition on begging by comparing the begging intensity of nestlings with similar weights, previous competitive environments, and food deprivation, when placed into large or small broods.

METHODS

This study was conducted in King's County, Nova Scotia, Canada, between 1 May and 15 July 1996 and 1997. This population of tree swallows nests in boxes spaced 10–20 m apart, and the average brood size is 4.9 ± 0.10 (SE) nestlings/brood. The study sites and general methods are described in detail in Leonard and Horn (1996).

Descriptive study

We videotaped the begging behavior of 10-day-old tree swallow nestlings in broods ranging in size from 2–7 nestlings (2, $n = 1$; 3, $n = 10$; 4, $n = 7$; 5, $n = 26$; 6, $n = 11$; 7, $n = 2$). Thirty-five of the 57 broods were videotaped in 1996 and 22 in 1997.

Twenty-four hours before videotaping we opened the hinged side of each tree swallow nest-box and placed a Plexiglas plate in the opening. We then covered that side of the nest-box with a dark plastic bag supported on a small wooden frame. This procedure kept the box dark and allowed the parents to habituate to the frame that later covered the videocamera. At this time we also weighed and individually marked each nestling on the head with white paint, so that we did not need to disturb them on the day of videotaping.

The following day we mounted a Panasonic PV-900-K VHS videocamera on a tripod, placed it 15 cm from the open side of the nest, and adjusted it so that the base of the nest hole appeared in the top right corner of the field of view. We then covered the camera with the plastic bag and wooden frame and videotaped for 1.5 h. Videotaping took place between 0730 and 1800 h. Although parental feeding rates do not appear to vary across the day in tree swallows (McCarty, 1995), we did balance taping of different-sized broods for time of day.

Earlier work on this population showed that feeding rates at nests with and without cameras were not significantly different (Leonard and Horn, 1996), suggesting that parent tree swallows adjusted to the presence of the camera.

Video and statistical analyses
Each time a parent visited the nest with food, we recorded the identity of the parent and the nestling that was fed. Parent tree swallows deliver food to nestlings in a bolus, making it difficult to determine either the quantity or quality of food. Thus, our measure of food provisioning is based on feeding rate only. We assume that feeding rate reflects hunger levels to some extent. That is, broods with relatively low feedings rates per nestling during our observation period should generally be hungrier than broods with high feeding rates per nestling.

As the parent entered the nest-box, some or all of the nestlings begged by raising their heads, stretching their necks, opening their mouths wide (i.e., gaping), and calling. At each feeding visit, we measured the maximum begging intensity of each nestling in the interval between the arrival of the parent and the feeding. Maximum begging intensities were scored for each nestling based on the following scale: 1, head down, gaping, sitting; 2, head up, gaping, sitting; 3, same as 2, plus neck stretched upward; 4, same as 3, but body lifted off legs rather than sitting; 5, same as 4, plus waving wings. This scale yields raw scores that are discontinuous, but ordinal, since they represent points along a continuum of begging intensity (see Lotem, 1998). The distribution of the raw scores and their correlation with continuous, but less easily measured, variables such as nestling height (Leonard ML, Horn AG, unpublished data) and nestling energy expenditure (Leech and Leonard, 1996) suggest that they represent a linear increase

in begging intensity. By averaging the scores across nestlings for each visit by a parent and then averaging across all visits for that observation period, we convert the scale into a continuous variable that is normally distributed and provides one datum per nest.

Nestlings in this population of tree swallows hatch over a period of 1–3 days (Leonard and Horn, 1996). Hatching spread, and thus variation in nestling size, could potentially increase with brood size. This could result in differential responses by large and small nestlings in broods of different sizes. In our population the difference in weight between the largest and smallest nestlings in a brood showed a weak tendency to increase with brood size ($r^2 = .02$, df = 1, 72, $p = .09$, power = 0.38). Furthermore, we found no difference in the begging intensity of largest and smallest nestlings across broods of different sizes ($F = 1.97$, df = 1, 43, $p = .17$, power = 0.94). This result is also consistent with an earlier study on this population that found no difference in the begging behavior of largest and smallest nestlings (all $p > .66$; Leonard and Horn, 1996). Therefore, because the relationship between hatching spread and brood size is relatively weak and because differences in begging intensity by large and small nestlings are also weak, we do not include hatching spread as a variable in our analyses, nor do we examine responses by nestlings of different sizes.

We pooled information for broods of two ($n = 1$) and three ($n = 10$) and broods of six ($n = 11$) and seven ($n = 2$) because we had so few nests in the extreme categories. Variation in begging scores and other variables were initially analyzed with a two-way ANOVA using linear contrasts, including year and the variable of interest as main effects. We found no significant interactions with year, so we present data for both years combined. Assumptions of normality and homogeneity of variance were upheld (Shapiro-Wilk and Brown-Forsythe tests, respectively).

We conducted power analyses (Cohen, 1977) on nonsignificant results in which $.25 > p > .05$. These analyses allowed us to determine the effect size that each nonsignificant test was powerful enough to detect, given the sample size and variation of the data, our criterion for significance ($p < .05$), and our desired power (i.e., probability of rejecting the null hypothesis), which we set at 0.80 following Cohen (1977).

Experimental study

In 1997 we experimentally tested whether begging intensity varied with brood size while standardizing food deprivation, weight, and previous competitive environment of the nestlings. Nestlings in seven broods of five nestlings each were weighed and individually marked on the head with white paint when they were 9 days old. The next day, we videotaped each of these broods for a 1-h control period (see above for videotaping protocol).

Following the control period, we chose the two nestlings in each brood with the smallest difference in their 9-day weight as focal nestlings. We made the assumption that the mass hierarchy remained constant in the 24-h period between weighing the nestlings and conducting the experiment. Both nestlings were then removed from each nest and kept in a small container lined with paper towels for 0.5 h to standardize periods of food deprivation. A 0.5 h period of deprivation is equivalent to approximately two to three missed feedings per nestling (Leonard and Horn, 1996). Each nestling was then randomly assigned to either a large brood treatment or a small brood treatment. Focal nestlings assigned to large brood treatments were placed in a nest containing either six ($n = 6$) or seven ($n = 1$) nestlings; focal nestlings assigned to small brood treatments were placed in broods of two ($n = 1$) or

Table 1

Mean (± SE) weight, begging intensity scores in the control period, and number of feedings in the experimental period for focal nestlings in small and large broods

Nestling characteristics	Small brood focal	Large brood focal	Paired t	p
Weight (g)	19.3 ± 0.30	19.5 ± 0.40	−1.40	.20
Control begging intensity	2.60 ± 0.10	2.80 ± 0.20	−0.60	.56
Number of feedings/h	5.7 ± 1.35	3.8 ± 1.04	1.40	.20

Means were compared using a paired t test; $n = 7$ for all comparisons.

three ($n = 6$). In both cases we removed the resident nestling closest in weight to the focal nestling. Parents and young do not appear to recognize each other at this age (Leonard et al., 1997), so we assumed that parents would respond to focal nestlings in the same way as resident nestlings. The three broods (i.e., home brood, large brood, and small brood) used in each trial differed in age by no more than 1 day (mean ± SE difference in age between small broods and home broods: 0.60 ± 0.20 days, range: 0–1; large broods and home broods: 0.40 ± 0.20 days, range 0–1). By matching home and experimental broods for age, we intended to control for the size of focal nestlings (see Table 1 for average body mass) and their counterparts in large or small broods. The mean (± SE) difference in weight between a focal nestling and the nestling that it replaced was 0.80 ± 0.30 g (range 0.10–1.60 g) for small broods and 0.60 ± 0.20 g (0.10–1.60 g) for large broods. Following this exchange, large and small broods were videotaped for a 1-h experimental period. All nestlings were returned to their home nests at the end of each trial.

Video and statistical analyses
Videotapes were analyzed and maximum begging intensity scores assigned to nestlings as described above. We used paired t tests to compare large and small brood focals and unpaired t tests to compare begging by host nest mates in large and small broods. We tested directional hypotheses (e.g., begging intensity in large broods is greater than in small broods), so p values are one-tailed for t tests reported in the results. Variables were normally distributed and showed equal variances among groups (Shapiro-Wilk and Brown-Forsythe tests, respectively).

The experiment appeared to produce similar conditions for large and small focal nestlings. That is, focal nestlings placed in large and small broods did not differ significantly in their weights or begging intensity in the control period (Table 1).
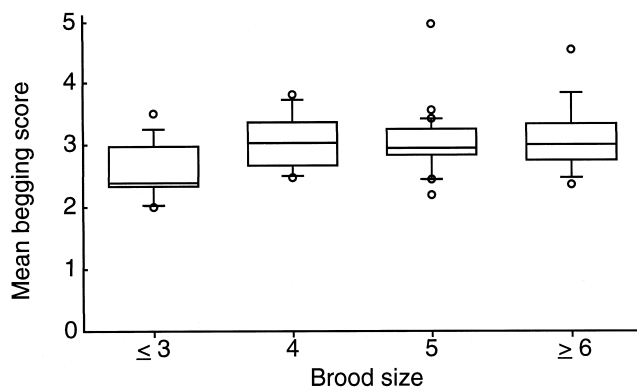
Nestlings also had the same period of food deprivation before they were placed in the host nests, and their feeding rates during the experimental period did not differ significantly (Table 1). The detectable effect size of these tests was small for weight (0.3 g), but not for feeding rate (4 feeds/h). Thus we are relatively confident that the focal nestlings had similar weights and begging intensities before being transferred, but we are less confident that they were fed at similar rates during the experimental period.

RESULTS

Descriptive study

Begging intensity varied significantly with brood size, with intensity increasing with brood size ($F = 4.49$, df = 1, 53, $p = .046$; Figure 1). It appeared, however, that this effect was due mostly to an increase in begging intensity between brood sizes of fewer than three nestlings and the remaining brood sizes. Indeed, these were the only comparisons that were significant in post hoc tests (Fisher's least significant difference test, $p < .05$). Mean brood weight did not vary significantly with brood size ($F = 0.69$, df = 1, 71, $p = .41$). However, feeding rate per nestling decreased with brood size ($F = 8.00$, df = 1, 56, $p = .007$; Figure 2). This suggests that nestlings in larger broods might be hungrier than nestlings in smaller broods, which could potentially contribute to the relationship between begging intensity and brood size.

Experimental study

The begging intensity scores of focals in large broods were significantly higher than focals in small broods (paired t test: $t = 2.94$, df = 6, $p = .01$; Figure 3). This difference is associated with significantly higher begging scores by host nestlings in large broods as compared to those in small broods
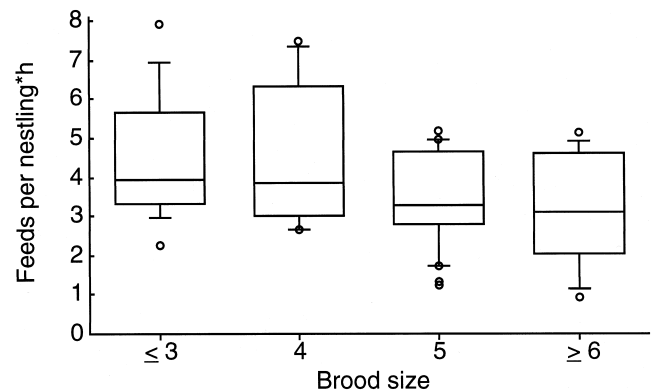

Figure 1
Mean maximum begging intensity scores in relation to brood size. Horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles; all data outside this range are plotted.

Figure 2
Mean feedings/nestling/hour in relation to brood size. Horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles; all data outside this range are plotted.
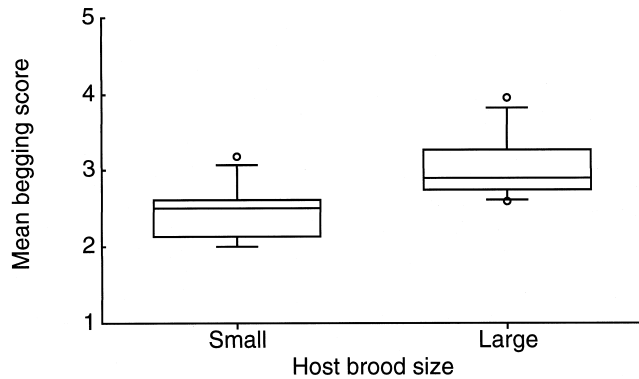
Figure 3
Mean maximum begging intensity scores of focals in small and large broods. Horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles; all data outside this range are plotted.

Figure 4
Mean maximum begging intensity scores of focal nestlings in relation to the mean maximum begging intensity scores of nest mates in large (crosses) and small (circles) broods. The line indicates equal begging by focals and nest mates.

(large: 3.24 ± 0.20, small: 2.70 ± 0.20; unpaired $t = 2.20$, df $= 6$, $p = .025$) and a correlation between the begging intensity of the focals and their host nest mates ($r = .81$, df $= 1$, 14, $p = .0001$; Figure 4). Thus, focal nestlings may have matched the begging scores of their host nest mates, which might explain why focals placed in larger broods begged more intensively than focals in small broods.

An alternative explanation, however, is that focals placed in large broods begged more intensively because they received less food during the experimental period and therefore were hungrier than focals in small broods. Although the difference in feeding rate to large and small brood focals during this time was not significant (Table 1), the detectable effect size of this comparison was too large for a sensitive test (4 feeds/ h; see Methods). Thus, focals in large broods may simply have been hungrier than focals in small broods and therefore begged more intensively.

Given this possibility and the relationship between feeding rate and brood size identified in the descriptive study, we examined the relative influence of feeding rate and host begging intensity on focal begging. We controlled statistically for each of these possible effects by first regressing focal begging intensity against focal feeding rate and host begging intensity. We then examined whether the residuals of each regression showed a difference in begging intensity between focals placed in large and small broods.

When we controlled for feeding rate, the difference in begging intensity between large and small brood focals remained (paired $t = 1.92$, df $= 6$, $p = .05$). However, this was not the case when we controlled for host begging intensity (paired $t = 1.00$, df $= 6$, $p = .18$; detectable difference in begging score was 0.4 units). This suggests that the effects of nest mates on begging rather than feeding rate may explain the observed difference in begging intensity between large and small brood focals.

DISCUSSION

The results of our descriptive study found that the begging intensity of nestling tree swallows increased with brood size. We could identify at least two factors that might explain a relationship between begging intensity and brood size in this population. First, feeding rate per nestling decreased with increasing brood size, suggesting that nestlings in larger broods may be hungrier than nestlings in smaller broods (see below). Previous descriptive and experimental studies on this population of tree swallows found an increase in begging intensity associated with periods of food deprivation (Leonard and
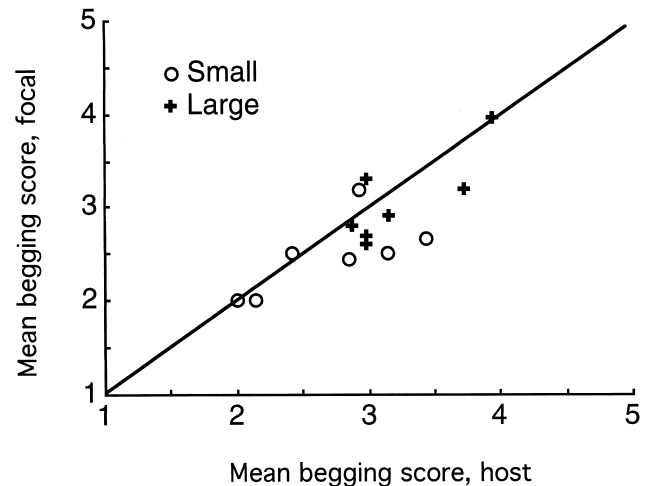
Horn, 1996, 1998). Second, in our experiment, focal nestlings, matched for weight and previous competitive environment, begged more intensively in large broods than in small broods, and they also appeared to match the begging intensity of their host nest mates. Differences in begging intensity between focals persisted when we statistically controlled for feeding rate to large and small focals, but not when we controlled for the begging intensity of host nestlings. These experimental results suggest that nestling tree swallows may also increase their begging intensity in response to the number and/or begging intensity of nest mates. The only other study that controlled for hunger when examing the relationship between begging and brood size found that the duration of begging bouts by yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) increased when brood size was increased from three to four nestlings (Price, 1996).

Two other studies also provide some support for the results reported in the current study, although the focus of these studies was not the relationship between begging and brood size. In another population of tree swallows, two measures of begging intensity were positively related to brood size (Hussell, 1988). Similarly, nestling starlings (*Sturnus vulgaris*) that spent time in large foster broods (of eight nestlings) also increased their begging intensity when returned to their home brood as compared to nestlings that spent time in small broods (of two nestlings; Kacelnik et al., 1995). This study did not control for differences in feeding rate to large and small broods, so the observed response may have been a result of the decreased feeding rates experienced by nestlings in larger broods or adjustments by the nestlings to the begging levels of nest mates.

Brood size and competition

In some passerine species, feeding rates per nestling decrease as brood size increases (e.g., Biermann and Sealy, 1982; Kacelnik et al., 1995; Wright and Cuthill, 1990), suggesting that nestlings in larger broods receive less food than their counterparts in smaller broods. Reduced feeding rates, in turn, presumably explain the slower growth rates (e.g., Wright and Cuthill, 1990) and lower prefledging weights (e.g., Greig-Smith, 1985) that have also been observed in larger broods.

In some tree swallow populations, feeding rates per nestling

(Leffelaar and Robertson, 1986; Rendell W, unpublished data) and growth rates (Rendell W, unpublished data) decrease with increasing brood sizes, while in others there is little variation in these features across broods of different sizes (De Steven, 1980; Wheelwright et al., 1991; Zach and Mayoh, 1982). In our population, feeding rates per nestling appear to decrease with increasing brood size, yet weight did not vary significantly across broods of different sizes. We could not quantify either the amount or the quality of food delivered on each trip. So, although nestlings in larger broods were fed less frequently, it is possible that they received more food per trip or that the food was of higher quality. If true, this might explain why weight did not vary across brood sizes despite differences in feeding rates per nestling and also suggests that hunger levels in broods of different sizes may be similar. Alternatively, differences in feeding rate may take longer than 9 days (the age at which our subjects were weighed) to yield their cumulative effect on weight.

Brood size and begging untensity

Nest mates

Our experimental results suggest that focal nestlings increased their begging intensity at least partly in response to the numbers and/or begging intensity of their brood mates. Increased begging in large broods may be a response to potential competition under variable feeding conditions (e.g., Mock and Lamey, 1991; Price, 1996). Specifically, if feeding conditions vary unpredictably, then it might be advantageous for nestlings to beg at relatively high intensities when presented with reliable indicators of potential competition, such as nest mates. Some empirical evidence suggests that this may be the case. For instance, siblicidal egrets reduce aggression to nest mates when broods are reduced, but not when food is increased (Mock and Lamey, 1991).

Another possibility is that increased begging in the presence of nest mates is needed to increase the detectability of the begging signal in a noisy environment (Dawkins and Guilford, 1997). To assess nestling begging signals, parents must detect and discriminate the signal of individual nestlings against a background of many begging young. This task may become more difficult if the young are in large broods. Under these circumstances, nestlings may be selected to signal in ways that increase detectability (e.g., Dawkins and Guilford, 1997; Wiley, 1994). This may include signaling with greater intensity (Wiley, 1983, 1994).

Feeding rate

Our descriptive results suggest that nestlings in larger broods might also beg more intensively because they receive less food, and therefore are hungrier, than nestlings in small broods. A positive relationship between begging intensity and food deprivation has been well established across a variety of avian species, including tree swallows (see above). Increased begging in larger broods may also keep parental feeding rates elevated (Hussell, 1988; Leonard and Horn, 1998), thus ensuring that individual nestlings receive an adequate amount of food overall. This may be particularly important to nestlings in larger broods. Again, earlier work with our population showed that parent tree swallows respond to increases in begging intensity with increases in feeding rate (Leonard and Horn, 1998).

In conclusion, our results support the contention that increases in brood size result in escalation of offspring solicitation signals, and hence that sibling competition may account for much of the apparent conspicuousness of these signals. In our population, the increase appears to result partly from the poorer short-term condition (i.e., greater hunger) of offspring in larger broods, but also from the direct effect of begging nest mates. Both effects are predicted by parent–offspring conflict and biological signaling models. The important direct effect of signaling by nest mates, however, raises the interesting possibility that exaggeration of solicitation signals may result from the need to increase detectability in a noisier environment, and may not require more elaborate evolutionary explanations.

REFERENCES

Biermann GC, Sealy S, 1982. Parental feeding of nestling yellow warblers in relation to brood size and food availability. Auk 99:332–341.

Cotton PA, Kacelnik A, Wright J, 1996. Chick begging as a signal: are nestlings honest? Behav Ecol 7:178–182.

Cohen J, 1977. Statistical power analysis for the behavioral sciences. New York: Academic Press.

De Steven D, 1980. Clutch size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*). Evolution 34:278–291.

Dawkins MS, Guilford T, 1997. Conspicuousness and diversity in animal signals. Perspect Ethol 12:55–72.

Fujioka M, 1985. Sibling competition and siblicide in asynchronously-hatching broods of the cattle egret *Bubulcus ibis*. Anim Behav 33:1218–1242.

Godfray HCJ, 1991. Signalling of need by offspring to their parents. Nature 352:328–330.

Godfray HCJ, 1995a. Evolutionary theory of parent-offspring conflict. Nature 376:133–138.

Godfray HCJ, 1995b. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. Am Nat 146:1–24.

Greig-Smith P, 1985. Weight differences, brood reduction and sibling competition among nestling stonechats *Saxicola torquata* (Aves:Turdidae). J Zool 205:453–465.

Harper AB, 1986. The evolution of begging: sibling competition and parent-offspring conflict. Am Nat 128:99–114.

Henderson BA, 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. Condor 77:488–492.

Hussell DJT, 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. Am Nat 131:175–202.

Kacelnik A, Cotton PA, Stirling L, Wright J, 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. Proc R Soc Lond 259:259–263.

Kilner R, 1995. When do canary parents respond to nestling signals of need? Proc R Soc Lond 269:343–348.

Kölliker M, Richner H, Werner I, Hebb P, 1998. Begging signals and biparental care: nestling choice between parental feeding locations. Anim Behav 55:215–222.

Leech SM, Leonard ML, 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? Proc R Soc Lond 263:983–987.

Leffelaar D, Robertson RJ, 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav Ecol Sociobiol 18:199–206.

Leonard ML, Horn AG, 1996. Provisioning rules in tree swallows. Behav Ecol Sociobiol 38:341–347.

Leonard ML, Horn AG, 1998. Need and nestmates affect begging in tree swallows. Behav Ecol Sociobiol 42:431–436.

Leonard ML, Horn AG, Brown CR, Fernandez NJ, 1997 Parent-offspring recognition in tree swallows (*Tachycineta bicolor*). Anim Behav 54:1107–1116.

Lotem A, 1998. Differences in begging behaviour between barn swallow, *Hirundo rustica,* nestlings. Anim Behav 55:809–818.

MacNair MR, Parker GA, 1979. Models of parent-offspring conflict. III. Intra-brood conflict. Anim Behav 27:1202–1209.

McCarty J, 1995. Effects of short-term changes in environmental conditions on the foraging ecology and reproductive success of tree swallows, *Tachycineta bicolor* (PhD dissertation). Ithaca, New York: Cornell University.

Mock DW, Lamey TC, 1991. The role of brood size in regulating egret sibling aggression. Am Nat 138:1015–1026.

Parker GA, MacNair MR, 1979. Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. Anim Behav 27:1210–1235.

Price K, 1996. Begging as competition for food in yellow-headed blackbirds. Auk 113:963–967.

Price K, Harvey H, Ydenberg R, 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus,* in relation to need. Anim Behav 51:421–435.

Price K, Ydenberg R, 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav Ecol Sociobiol 37:201–208.

Rodríguez-Gironés MA, Cotton PA, Kacelnik A, 1996. The evolution of begging: signalling and sibling competition. Proc Natl Acad Sci USA 93:14637–14641.

Stamps JA, Clark A, Arrowood P, Kus B, 1989. Begging behaviour in budgerigars. Ethology 81:177–192.

Wheelwright NT, Leary J, Fitzgerald C, 1991. The costs of reproduction in tree swallows (*Tachycineta bicolor*). Can J Zool 69:2540–2547.

Wiley RH, 1983. The evolution of communication: information and manipulation. In: Animal behaviour, vol. 2, Communication (Halliday TR, Slater PJB, eds). Oxford: Blackwell; 156–189.

Wiley RH, 1994. Errors, exaggeration, and deception in animal communication. In: Behavioural mechanisms in evolutionary ecology (Real LA, ed). Chicago: University of Chicago Press; 157–184.

Wright J, Cuthill I, 1990. Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris.* Behav Ecol 1:116–124.

Zach R, Mayoh KR, 1982. Weight and feather growth of nestling tree swallows. Can J Zool 60:1080–1090.