

Marty L. Leonard · Andrew G. Horn

Need and nestmates affect begging in tree swallows

Received: 20 June 1997 / Accepted after revision: 19 January 1998

Abstract We conducted an experiment on nestling tree swallows (*Tachycineta bicolor*) to examine predictions from signalling models for the evolution of conspicuous begging behaviour. Specifically, we examined the relationship between (1) nestling begging intensity and hunger, (2) begging intensity and parental provisioning and (3) begging intensity and nestmate condition. Forty broods of 9-day-old nestlings were removed from their nests for 1 h and assigned to one of the following three treatments: (1) all nestlings in the brood deprived of food ($n = 13$), (2) all nestlings in the brood fed ($n = 11$) or (3) half the nestlings in the brood deprived and half fed ($n = 16$). Videotapes before and after the treatments showed that begging intensity increased in broods in which all of the nestlings had been deprived and decreased in broods in which all of the nestlings had been fed. Deprived nestlings in the half-and-half treatment did not change their begging intensity in response to treatment, while fed nestlings in this treatment group showed a decrease in begging intensity. Parent tree swallows increased their feeding rate to deprived broods and decreased their rate to fed broods. Within broods, parents decreased their feeding rate to fed nestlings, but showed no significant change in feeding to deprived nestlings. Our results suggest that begging intensity is influenced by hunger and that parents appear to respond to variation in begging intensity. The begging of nestmates also appears to influence begging independently of need. These results are consistent with predictions derived from signalling models of begging.

Key words Begging · Signalling · Sibling interactions · *Tachycineta bicolor*

Introduction

The conspicuous begging of young mammals and birds has been a focus for theories of parent-offspring conflict (Trivers 1974) and signalling behaviour (Godfray 1991, 1995a). Parent-offspring conflict theory proposes that offspring increase their fitness by extracting more resources from their parents than is optimal in terms of parental fitness. Offspring should thus be selected to beg in a conspicuous way in order to manipulate parents and outcompete nestmates for resources (Trivers 1974). Signalling models of begging suggest that begging indicates cryptic aspects of offspring need (i.e. features that parents could not otherwise assess) and that parents use the signal to distribute resources at the parental optimum (Godfray 1991, 1995a). The costs associated with producing a conspicuous signal prevent offspring from exaggerating their nutritional needs and thus maintain the reliability of the signal (Godfray 1991, 1995a).

Signalling models, in particular, have generated several testable predictions (Godfray 1995a). For instance, levels of offspring solicitation are expected to increase with increasing hunger levels and parents are expected to respond to increased begging by increasing their feeding rate. Offspring begging may also be influenced by the begging of broodmates, independently of need.

Empirical tests of these predictions, mostly from work on nestling birds, have provided some support for signalling models. For instance, begging intensity increases with food deprivation (Henderson 1975; Smith and Montgomerie 1991; Kilner 1995; Price and Ydenberg 1995) and decreases with food supplements (Litovich and Power 1992; Redondo and Castro 1992; Price and Ydenberg 1995) in a variety of species, which supports the prediction that begging conveys information about offspring hunger levels. Begging intensity may also be influenced by factors such as condition which reflects long-term need (Hussell 1988; Price et al. 1996).

Parents have also been reported to respond to increased begging by increasing their provisioning rates

M.L. Leonard (✉) · A.G. Horn
Department of Biology, Dalhousie University,
Halifax, Nova Scotia, Canada, B3H 4J1
e-mail: MLeonard@is.dal.ca, Fax: +1-902-494-3736

(e.g. Stamps et al. 1989; Smith and Montgomerie 1991; Price and Ydenberg 1995). This response, however, is complicated by the fact that parents may also allocate food based on factors other than cryptic signals of need (e.g. size). Furthermore they may not completely control the distribution of food if competition among offspring influences the probability of being fed (Kilner and Johnstone 1997).

Interactions among nestmates may also influence begging intensity independently of need. Indeed, nestlings of at least two passerine species appear to increase their begging in response to the begging of hungrier nestmates (Smith and Montgomerie 1991; Price and Ydenberg 1995; Price 1996). In some species, however, begging intensity appears not to be affected by the begging of nestmates (Kacelnik et al. 1995; Cotton et al. 1996). Thus the influence of nestmates on the begging intensity of individuals is not consistent across the species that have been tested to date.

The purpose of our study was to test the effects of hunger and nestmates on begging by nestling tree swallows (*Tachycineta bicolor*) and to examine the response of parents to changes in begging intensity. The results of an earlier observational study suggest that begging intensity in this species varies with hunger, but not with begging by nestmates, and that parents respond, albeit weakly, to changes in begging intensity (Leonard and Horn 1996). The study was correlational, however, and relied on statistically controlling for variables that could be more convincingly controlled experimentally.

Therefore, in the present study we manipulated hunger levels by depriving or feeding entire broods. We also manipulated nestmate begging by applying these treatments within nests, so that some experimental nests contained both hungry and fed nestlings. If hunger influences begging, then begging intensity should increase after nestlings are deprived of food and decrease after nestlings are given food supplements. If nestmates influence begging, then the response of nestlings in half-brood treatments should differ from their counterparts in whole-brood treatments. Finally, if parents respond to variation in begging intensity, they should vary their feeding rates in response to changes in begging across treatments.

Materials and methods

Methods

This study was conducted at four study sites in King's County, Nova Scotia, Canada between 1 May and 15 July 1996. The study sites and general methods are described in Leonard and Horn (1996). The following treatments were applied to broods when the nestlings were 9 days old: (1) whole brood hungry: all nestlings in the brood deprived of food ($n = 13$ broods), (2) whole brood fed: all nestlings in the brood fed ($n = 11$ broods) and (3) half and half: half the brood deprived of food and half the brood fed ($n = 16$ broods). In the half-and-half treatment, the assignment of the "extra" nestling in broods with an odd number of nestlings was

alternated between broods. Treatments were balanced for brood size (whole brood hungry: 4.39 ± 0.27 ; whole brood fed: 4.82 ± 0.26 ; half and half: 4.75 ± 0.23 ; ranges for all treatments: 3–6 nestlings/brood) and study site. Otherwise we assigned broods to treatment as they hatched while rotating through the three treatments.

Forty-eight hours before a trial began we opened the hinged side of each tree swallow nestbox and placed a plexiglas plate in the opening. We then covered that side of the nestbox 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. We also marked each nestling on the head with an individually distinctive pattern of white paint.

Two days later, we mounted a Panasonic PV-900-K VHS videocamera on a tripod and covered it with the plastic bag and wooden frame. We placed the camera 15 cm from the open side of the nest, aligned it horizontally, and adjusted it so that the base of the nesthole appeared in the top right corner of the field of view. The nest was then videotaped for a 1.5-h pre-treatment period. Earlier work on this population showed that feeding rates at nests with and without cameras were not significantly different (Leonard and Horn 1996).

After the pre-treatment period, we removed the resident nestlings from their homebox for 1 h. During this time we either sham-fed the entire brood (whole brood hungry treatment), fed the entire brood (whole brood fed treatment), or fed half the nestlings and sham-fed the other half (half-and-half treatment). We fed nestlings by opening their bills and placing pieces of moistened dog chow in their gape with our index finger. A 1.05×0.5 mm piece of food (approximately 3.2 g) was divided and half given immediately following removal from the homebox and the other half 5 min before the end of the 1-h removal period. Previous experience with this species suggested that 3.2 g of food would satiate the average nestling at this age. Because we standardized the amount of food each nestling received and divided the amount over the hour, it is likely that not all nestlings were satiated. We assumed, however, that fed nestlings were less hungry than deprived nestlings. We sham-fed nestlings by opening their bills the same number of times and placing the pad of our index finger in their gape. An hour of deprivation is equivalent to approximately four to five missed feeds/nestling. The nestlings were then returned to their homebox and filmed for a 1-h post-treatment period. Pre- and post-treatment periods differed in length because the pre-treatment period was also used as part of another study examining the relationship between brood size and begging behaviour (M.L. Leonard and A.G. Horn, unpublished work).

To reduce disturbance to the parents during the 1-h removal period, we replaced the resident nestlings with four nestlings of similar age from nearby broods that were not used in the experiment. Parents and offspring do not recognize each other at this age (Leonard et al. 1997) and nest watches confirmed that parents fed replacement nestlings at the same rate as they fed their own nestlings.

Statistical and video analyses

Each time a parent visited the nest with food, an observer, blind to the treatment, recorded the parent's sex and the identity of the nestling that was fed. Male and female parents did not differ in their response to the treatments, so we combined the feeding trips for both parents. Parent tree swallows deliver food to nestlings in the form of a bolus, so it is difficult to determine either its quantity or quality. Therefore, our measure of feeding rate is based on feeding frequency only.

As the parent entered the nestbox, some or all of the nestlings begged by raising their heads, stretching their necks, opening their mouths wide (gaping) and calling. We measured two features of begging behaviour: (1) the maximum begging intensity of each nestling in the interval between the arrival of the parent and the feeding, and (2) the proportion of nestlings begging on each feeding

trip. Maximum begging intensities were scored for each nestling based on the following scale: (1) head up, gaping, sitting, (2) same as 1, plus neck stretched upward, (3) same as 2, but body lifted off legs rather than sitting, (4) same as 3, plus wings moving.

In all analyses, nests, rather than individual feedings or nestlings, were our unit of replication. Specifically, in whole brood treatments (i.e. all nestlings deprived or fed) we averaged maximum begging intensity and proportion of nestlings begging. This yielded two data points/measure for each period (pre- or post-treatment), treatment (fed or hungry), and nest. In the half-and-half treatment, we calculated separate means for hungry and fed nestlings within the nest. Maximum begging scores yielded normal distributions when averaged across feeding trips for each nest, so we did not transform the data. We, did however, arcsine transform the data on the proportion of nestlings begging.

We did separate analyses for deprived and fed nestlings. In both cases, we used a two-way repeated measures ANOVA, with nests as blocks, pre-/post-treatment period as a within-subject (i.e. within nest) effect, and whole/half brood as a between-subject (i.e. between nest) effect. This analysis is equivalent to doing paired *t*-tests comparing pre- and post-treatment periods for each group of nestlings, but it reduces the number of tests done on the data and therefore the likelihood of falsely rejecting the null hypothesis. The analysis also allows us to directly compare the responses of whole and half broods to the treatments. A significant interaction between the main effects (pre-treatment/post-treatment and whole/half brood) would show that nestlings responded differently, depending on whether they were in a whole brood or a half brood.

Results

Effects of hunger and nestmate begging

The maximum begging intensity overall for nestlings deprived of food did not change significantly between pre- and post-treatment periods ($F = 0.01, P = 0.89, df = 1, 26$; Fig. 1). However, a significant interaction ($F = 4.76, P = 0.03, df = 1, 26$) suggested that the begging intensity of deprived nestlings depended on whether the whole brood had been deprived of food (i.e. whole brood hungry treatment) or half of the brood had been deprived (i.e. half-and-half treatment). That is, maximum begging intensity increased between pre- and post-treatment periods for nestlings in whole broods

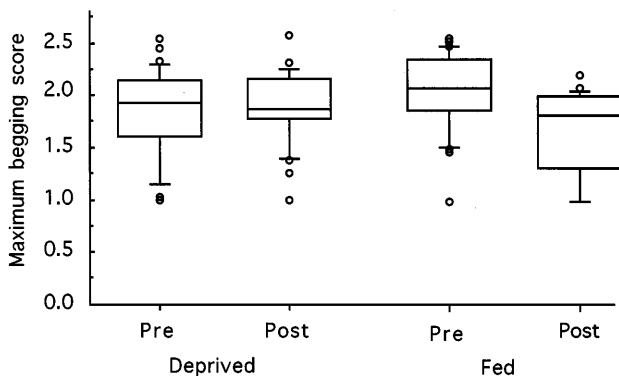


Fig. 1 Box plots (horizontal lines show the 10th, 25th, 50th, 75th and 90th percentiles and all data outside this range are plotted) of mean maximum begging scores during pre- and post-treatment periods for deprived and fed nestlings

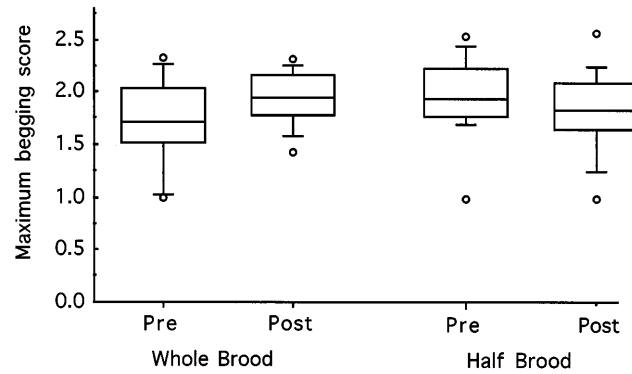


Fig. 2 Box plots (horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles and all data outside this range are plotted) of mean maximum begging scores during pre- and post-treatment periods for deprived nestlings in whole- and half-brood treatments

deprived of food, but did not change significantly for deprived nestlings in half and half treatments (Fig. 2). The proportion of deprived nestlings begging increased between pre- and post-treatment periods ($F = 8.56, P = 0.007, df = 1, 27$; Fig. 3), regardless of whether the entire brood was deprived or only half of the brood was deprived (interaction $F = 1.35, P = 0.26, df = 1, 27$).

Overall, for nestlings that were fed, both maximum begging intensity and proportion begging changed significantly between pre- and post-treatment periods (maximum begging intensity: $F = 14.63, P = 0.0009, df = 1, 22$; Fig. 1; proportion begging: $F = 17.46, P = 0.0003, df = 1, 24$; Fig. 3). Maximum begging intensity and the proportion of nestlings begging decreased between periods for fed nestling regardless of whether they were in broods in which every nestling was fed or in broods in which only half the brood was fed (interaction: maximum begging intensity: $F = 1.09, P = 0.31, df = 1, 22$; proportion begging: $F = 1.36, P = 0.25, df = 1, 24$).

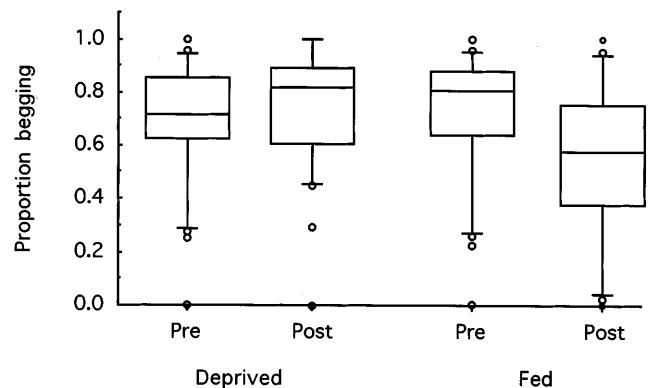


Fig. 3 Box plots (horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles and all data outside this range are plotted) of the mean proportion of deprived and fed nestlings during pre- and post-treatment periods

Parental provisioning

Feeding rates by parents to deprived nestlings changed significantly between pre- and post-treatment periods ($F = 4.24$, $P = 0.04$, $df = 1$, 27; Fig. 4). A near significant interaction ($F = 3.41$, $P = 0.07$, $df = 1$, 27) suggested that feeding rates to deprived nestlings depended on whether the entire brood was deprived of food or half the brood was deprived. That is, parents significantly increased their feeding rates between periods to broods in which all of the nestlings were deprived of food, but did not alter their feeding rates to deprived nestlings in half and half treatments (Fig. 5).

Feeding rates by parents to fed nestlings in whole and half brood treatments also changed significantly between pre- and post-treatment periods ($F = 29.5$, $P = 0.0001$, $df = 1$, 25; Fig. 4). Feeding rates decreased to nestlings in broods in which all the nestlings were fed and they also decreased to fed nestlings in the half and half treatment (interaction: $F = 0.04$, $P = 0.83$, $df = 1$, 25).

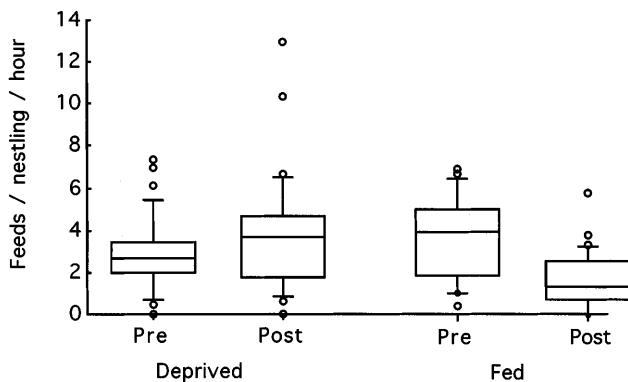


Fig. 4 Box plots (horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles and all data outside this range are plotted) of mean parental feeding rate to broods (whole treatments) and nestlings (half treatments) deprived of food and fed during pre- and post-treatment periods

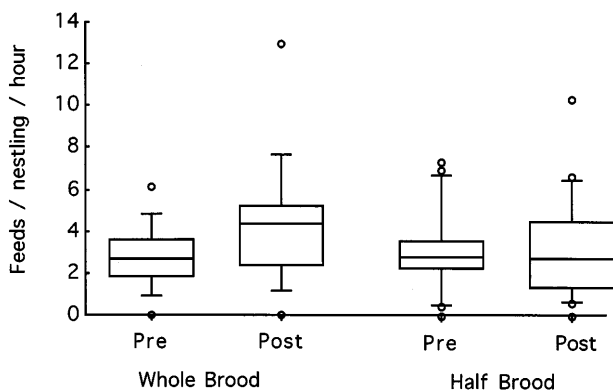


Fig. 5 Box plots (horizontal lines show the 10th, 25th, 50th, 75th, and 90th percentiles and all data outside this range are plotted) of mean parental feeding rate during pre- and post-treatment periods for deprived nestlings in whole- and half-brood treatments

Discussion

Begging and need

In our study the begging intensity of tree swallows varied in relation to their hunger levels. When nestlings in whole broods were deprived of food, a greater proportion of nestlings begged and they begged more intensely, whereas when nestlings were fed, both measures of begging decreased. These experimental results support our earlier observational results, in which begging intensity and the number of nestlings begging increased after relatively long periods without food (Leonard and Horn 1996). A positive correlation between begging intensity and hunger appears to be common among passerine birds (e.g. Redondo and Castro 1992; Kilner 1995; Price and Ydenberg 1995), suggesting that begging carries reliable information about short-term need such as hunger.

Begging and provisioning

Parent tree swallows apparently adjust their feeding rate to the begging intensity of the brood. Overall feeding rate to broods increased when nestlings were hungry and decreased when they were fed. Within broods, parents directed fewer feedings to fed nestlings, while maintaining pre-treatment rates to deprived nestlings. In all cases, the changes in feeding rate corresponded to changes in begging intensity of the nestlings, suggesting that parents were sensitive to changes in nestling begging. In our previous descriptive study we found that parents returned to the nest sooner the more intensively nestlings reached on the previous visit, but the effect was relatively weak (Leonard and Horn 1996).

Increased begging intensity has been associated with increased parental provisioning in a variety of species (e.g. Stamps et al. 1989; Smith and Montgomerie 1991; Kilner 1995; Price and Ydenberg 1995) suggesting that begging signals influence the distribution of resources. Clearly, however, factors other than begging intensity may influence parental feeding decisions. For example, in the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) parents use both begging signals and relative offspring size in allocating food (Price and Ydenberg 1995). In tree swallows, large and small nestlings do not vary in how intensively they beg nor in their likelihood of being fed (Leonard and Horn 1996), suggesting that variation in size within broods does not influence provisioning in this species.

Begging and nestmates

Hungry nestlings in the half and half treatment begged less intensely following deprivation than their counterparts in whole brood treatments, suggesting that com-

petitive interactions could heighten begging intensity for the same amount of need. Alternatively, the increased begging of individuals in hungry broods could function to increase provisioning rates on the longer term rather than provide a competitive edge in the current feeding bout. Whatever the case, an effect of nestmates on begging suggests that begging is not strictly a signal of offspring need, although a slight effect of nestmates on begging is consistent with signalling models (Godfray 1995b).

Previous studies on the influence of nestmates on begging have provided conflicting results. Two recent studies on yellow-headed blackbirds (Price and Ydenberg 1995; Price et al. 1996) and another on American robins (*Turdus migratorius*; Smith and Montgomerie 1991) found that nestmates increased their begging in response to the begging of hungrier nestmates. In contrast, starling (*Sturnus vulgaris*) nestlings under two different experimental regimes did not adjust their begging effort to that of their nestmates (Kacelnik et al. 1995; Cotton et al. 1996). These inconsistencies are difficult to evaluate, however, because experimental conditions varied from study to study. Nonetheless, they show interesting differences not only in whether nestmates match each other's begging intensity, but also in whether it is hungry or fed nestlings which vary their begging.

Begging and signals of need in tree swallows

Studies of begging in our population of tree swallows support predictions of biological signalling models of begging (Godfray 1995b). That is, begging intensity appears to convey information about aspects of offspring need and parents appear to respond to variation in begging intensity. A further prediction, that begging is costly, is also supported by earlier work in this population which showed that begging has significant energetic and predation costs (Leech and Leonard 1996, in press). Although our results are consistent with signalling models for the evolution of begging they are also assumed or predicted by other models of begging (reviewed in Godfray 1995a). Determining which of these models best describes the patterns existing in our population will require further work.

A next step might be to examine begging signals in more detail. For example, one reason to study begging is that the signal seems more exaggerated than necessary for effective transmission between sender (the young) and receiver (the parent). Sender-receiver systems, however, must be understood in the context of signal detection theory (Wiley 1994). Receivers must weigh the probability of correctly detecting a signal against the probability of making mistakes. In this case, parents must weigh the benefits of correctly assessing the need of each nestling against the costs of the time taken to assess offspring condition. Their threshold for detecting a hungry nestling may therefore be raised, so that nestlings

have to produce a more readily detectable signal to get their message across (P.K. McGregor, personal communication). Questions about begging may prove more tractable when posed in terms of information exchange (Getty 1997).

Acknowledgements We thank David Hussell, John Reynolds, Danny Weary, Nat Wheelwright, Hal Whitehead and an anonymous reviewer for reading the manuscript and the Behavioural Ecology group at the University of Nottingham for discussion. All provided many helpful comments. We also thank Sherman Boates for access to the field sites and the Brown, Eaton, Hines, and Coldwell families for allowing us to use their land. We especially thank Susan Leech and Satya Ramen for help in the field. This work is supported by grants to M.L.L. from the Natural Sciences and Engineering Research Council of Canada.

References

- Cotton PA, Kacelnik A, Wright J (1996) Chick begging as a signal: are nestlings honest? *Behav Ecol* 7:178–182
- Getty T (1997) Deception: the correct path to enlightenment? *Trends Ecol Evol* 12:159–160
- 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
- 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
- Kilner R, Johnstone RA (1997) Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol Evol* 12:11–15
- Leech S, Leonard ML (1996) Is there an energetic cost to begging in tree swallows (*Tachycineta bicolor*)? *Proc R Soc Lond* 263:983–984
- Leech S, Leonard ML (1997) Begging and the risk of predation in nestling birds. *Behav Ecol* 8: 644–646
- Leonard ML, Horn AG (1996) Provisioning rules in tree swallows. *Behav Ecol Sociobiol* 38: 341–347
- Leonard ML, Horn AG, Brown CR, Fernandez NJ (1997) Parent-offspring recognition in tree swallows (*Tachycineta bicolor*). *Anim Behav* 54:1107–1116
- Litovich E, Power HW (1992) Parent-offspring conflict and its resolution in the European starling (Ornithological monograph 47). American Ornithologists Union, Washington
- Price K (1996) Begging as competition for food in yellow-headed blackbirds. *Auk* 113:963–967
- Price K, Ydenberg R (1995) Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behav Ecol Sociobiol* 37:201–208
- 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
- Redondo T, Castro F (1992) Signalling of nutritional need by magpie nestlings. *Ethology* 92:193–204

- Smith HG, Montgomerie R (1991) Nestling American robins compete with siblings by begging. *Behav Ecol Sociobiol* 29:307–312
- Stamps JA, Clark A, Arrowood P, Kus B (1989) Begging behaviour in budgerigars. *Ethology* 81:177–192
- Trivers RL (1974) Parent-offspring conflict. *Am Zool* 14:249–264
- Wiley RH (1994) Errors, exaggeration, and deception in animal communication. In: Real LA (ed) *Behavioral mechanisms in behavioral ecology*. University of Chicago Press, Chicago pp 157–189

Communicated by J.D. Reynolds