

Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*)

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Begging in avian nestlings is a highly conspicuous behavior with important implications for the study of parent-offspring conflict. In some species, nestlings also call for long bouts in the absence of parents, and it has been proposed that this behavior is used by nestlings as a means of negotiating access to food. We studied this phenomenon in the spotless starling (*Sturnus unicolor*). We found that parent-absent calls were acoustically distinct from parent-absent calls. Observations showed that the probability of parent-absent begging increased with nestling age and brood size, whereas it decreased with increasing body condition. This result was confirmed by an experiment that showed that nestlings produced higher parent-absent begging rates when food deprived than when satiated. Finally, we carried out a playback experiment to test the reaction of nestlings to parent-absent begging by fellow nestlings. Principle components analyses yielded 2 independent components of begging: 1) a general begging component and 2) a second factor that measures the relative contribution of communicative begging over competitive begging. Nestlings exposed to playback decreased their general begging levels and simultaneously increased the relative contribution of communicative over competitive begging. This behavior may favor needy nestlings to obtain impending feedings while keeping high levels of food solicitation from parents and is consistent with a cooperative strategy among nestlings. Future research should consider the actual response of parents to these signals. *Key words*: begging in the absence of parents, food deprivation, sibling competition, sibling negotiation, spotless starling, *Sturnus unicolor*. [*Behav Ecol*]

Begging by nestlings is a complex behavior that comprises multiple signals, such as gaping, posturing, calling, etc., and which is typically directed at parents when these approach the nest (Kilner 2002). Because there is a conflict between parents and offspring about the amount of investment to be spent, much effort has been devoted to study the evolutionary stability of begging (e.g., Godfray 1991; Rodríguez Gironés et al. 1996; Johnstone 1999) and the possible costs that are expected to enforce the honesty of these signals (Kilner 2001; Rodríguez Gironés et al. 2001).

In addition to direct solicitation of food when parents are at the nest, nestlings of some species also produce calls in the absence of their parents. In most species, this behavior occurs in the form of sudden bursts of calling and is most likely due to nestlings' discrimination errors caused by external stimuli that are similar to those elicited by the arrival of a parent (Budden and Wright 2001; Leonard and Horn 2001; Leonard et al. 2005; Dor et al. 2007). However, in other species, nestlings beg continuously in the absence of their parents in long bouts that do not appear to be associated with any particular stimulus (e.g., the spotless starling [this study] or in several species of the *Picidae* and *Strigidae*. Glutz von Blotzheim 1966–1997; Roulin et al. 2000). In the rest of the paper, we will use the term of “parent-absent begging” to refer to these prolonged vocalizing periods emitted in the absence of parents and “parent-present begging” to describe vocalizing periods emitted in their presence.

In the barn owl, *Tyto alba*, this phenomenon has been considerably studied. Evidence shows that prolonged parent-

absent begging can be used by fellow nest mates as information to modulate their own begging intensity when parents arrive (Roulin et al. 2000). The “sibling negotiation hypothesis” (Roulin 2000; Johnstone and Roulin 2003) suggests that nestlings use parent-absent begging to assess each other's willingness to contest the next indivisible prey to be delivered (Roulin et al. 2000; Roulin 2001). Chicks would benefit by parent-absent begging because of a reduction in the cost of active competition for food when parents arrive at the nest (Roulin 2000; Johnstone and Roulin 2003). The effort invested in parent-absent begging would determine which nestling will beg more in the presence of parents and will eventually get fed (Roulin et al. 2000; Roulin 2004).

In the spotless starling, parent-absent begging is commonplace and nests are often detected by observers because of the continuous begging that emerges from the tree cavities (Bulmer E, Celis P, Gil D, unpublished data). To study this behavior, we firstly compared the acoustic characteristics of nestling calls in both parental absence and presence. Secondly, we carried out a correlational study to determine the relationship between parent-absent begging and covariates of offspring need. Based on these observational data, we conducted a first experiment to test whether parent-absent begging was influenced by nestling need. Finally, we conducted a second experiment to test a prediction derived from the sibling negotiation hypothesis, namely that nestlings should refrain from competing when a fellow nestling has a high level of parent-absent begging.

So far, studies dealing with parent-absent begging have only considered vocal signals, ignoring the multifaceted behavior of begging, that is, calling, stretching, pushing, jockeying (Kacelnik et al. 1995; Kilner 2002). This is unfortunate because there are reasons to expect the presence of both competitive and cooperative aspects in begging displays (Johnstone 2004)

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Received 6 October 2006; revised 1 October 2007; accepted 29 October 2007.

85 and these might not be identified when considering a single behavioral category. In this study, we have taken a global approach, analyzing parent-absent begging from a multiple-component perspective.

METHODS

90 The study was carried out between June and July 2004 in a population of spotless starlings breeding in nest-boxes in an open oak woodland in Soto del Real (Madrid, Spain). Spotless starlings are altricial, medium-sized passerines, with a modal clutch size of 4 eggs in this population (Bulmer E, Celis P, Gil D, unpublished data). Hatching is slightly asynchronous (1–2 days). Paternal care varies widely: whereas some pairs exhibit biparental care throughout the nestling period, in other cases females are left alone to rear the brood (Moreno et al. 1999). Food brought to the nest by parents is divisible, consisting of a mixture of worms and other insects. Parents may feed 1–3 nestlings per visit (Bulmer E, Celis P, Gil D, unpublished data), and the overall visiting rate is 10.41 visits/h (standard deviation [SD] = 5.17) when nestlings are 105 14 days of age. Fledging occurs at approximately 23 days. Spotless starling siblings compete in the nest through gaping, calling loudly, and pushing for positions close to the nest's entrance when the parents arrive. In parental absence, they also perform some of these behaviors, although less energetically.

Sound recording of nestling calls in parental absence and presence

110 We recorded nestling parent-absent calls by approaching nest-boxes where begging was heard with an omnidirectional microphone (Audio-Technica AT804) mounted onto a pole and placing the microphone in the entrance. Nestling vocalizations in parental presence were recorded by leaving the same microphone hidden inside the nest-box and waiting for parents to enter the nest-box and feed. All recordings were made when nestlings were 10–12 days of age with a Sony Walkman Professional WM-D6C tape recorder. Recordings were digitalized using a Sound Blaster Live Series sound card (Creative Technology, Singapore) at 44 kHz (16 bit), edited using Adobe Audition (San Jose, CA), and analyzed with Avisoft Pro (Berlin, Germany). In each vocalization, we measured duration, maximum and minimum frequencies, and 125 number of frequency modulations.

Correlative study

130 In a sample of 30 nest-boxes, we observed undisturbed levels of parent-absent begging by quietly approaching nest-boxes and recording the number of nestling calls produced in 30 s, after a period of 1 min. All observations were performed in 3 consecutive days to minimize seasonal effects, and each box was only observed once. Breeding in these nest-boxes was closely followed for another study (Celis P, unpublished data), so we knew the precise age (3–15 days) and the size of the brood (2–5) at the time it was observed. Weight was recorded with an electronic balance (Ohaus) to the nearest 0.1 g when nestlings were 6 days old. Mean brood weight at 6 days was used as an estimate of nestling condition because this measure was available for all nests and was highly correlated with mean 140 weight at later ages, for example, 14 days (Pearson's $r = 0.495$, $N = 90$, $P < 0.001$).

Begging behavior observations inside the nest

We observed nestling behavior by videotaping the inside of nest-boxes with mini surveillance CCD video cameras linked

by radio to a video recorder. Pilot observations were carried 145 out to determine the behavioral patterns that could be observed in parental absence. These included both vocal and physical behaviors. We included in our analysis all categories of observed behavior that were noted in nestlings, irrespective of their presumed function. For instance, preening was included because it was found to disturb adjacent nestlings in the nest and could be involved in nestling competition. Due to the limited size of the nest cup, preening results in the rearrangement of the nestlings' limbs and beaks and may consequently lead to changes in their general position with 150 respect to one another in the nest. Vocal behavior was recorded by the video camera's microphone.

The following categories of nestling behavior or nestling position were observed and recorded from the video recordings noting occurrence/absence on a 1-min basis for each of the nestlings in the nest: 1) *pushing*: any pushing of fellow sibs in the nest; 2) *gaping*: sustained gaping action (which was mostly observed in the parent's presence and different to yawning or panting); 3) *calling rate*: short vocalizations carried out by the chicks; 4) *top climbing*: behavior whereby chicks 155 would climb on top of each other; and 5) *preening*: any feather-cleaning behavior exhibited by the chicks.

Food deprivation experiment

170 In June/July 2004, broods ($N = 9$) were selected and used for the experiment when chicks were on average 14–15 days old. We chose 1 medium-sized nestling per brood as experimental chick and observed its behavior in relation to the treatment. Prior to videotaping, all chicks were removed from the nest, weighed, and marked individually on the head with a Tipex pen to allow individual identification. There were no indications from video observations that these marks affected parental or nestling behavior in any way. After marking, whereas the other chicks were put back into the nest, the experimental chick was removed to a warm box where it underwent one of the following 2 treatments: 1) left undisturbed and food 175 deprived for 1 h or 2) fed a baby porridge mixture (about 3 mL) every 15 min for the span of an hour period. After treatment, experimental chicks were brought back to their original nests to rejoin their siblings and video recording was begun. The whole procedure was repeated on the same nestling the following day but with the opposite treatment; therefore, each nestling was used as its own control. The order of treatments was randomly assigned to each nest.

Nestling video recording observations of the experimental chick were carried out using the abovementioned behavioral 190 categories. As we were able to observe nestling behavior both in presence and absence of their parents, we placed nestling observations under 2 main categories: 1) *parent present*, which represented occasions when the parent actually entered the nest and (2) *parent absent*, occasions when the parent was not 195 in the nest-box, and therefore, the nestlings were exempt from any direct stimuli (we excluded observations recorded during the 30 s before and after a parental visit). In addition, the proportion of the total number of parental visits where the experimental chick was fed was also noted. 200

Playback experiment

This experiment was carried out in June and July 2005. The sample consisted of 16 broods, with an average brood size of 3.29 nestlings (2–6 nestlings). At the age of 10–11 days, broods received the 2 experimental treatments on different 205 days, in random order. Treatments consisted of 40 min of silence or begging call playback that was presented to the brood on successive days. Parent-absent begging was recorded

throughout the 40-min playback period and an additional
 210 period of 40 min. These 40-min periods were split for the
 analyses in two 20-min periods (early vs. late) to control for
 the expected changes in hunger with time. In a preliminary
 pilot study, we found that our experimental setup (playback
 system and camera) disturbed some of the adult birds, thus
 215 affecting their parental behavior and reducing feeding rate in
 some cases. Therefore, we decided to forgo observations of
 adult behavior in this experiment and standardized nestling
 observations by excluding adult visits altogether. To this end,
 one of us sat in the vicinity of the nest throughout the tests,
 220 thus avoiding parents from approaching and feeding nestlings
 during this time. No parental alarm calls were heard in the
 vicinity of the nest.

For the playback stimuli, we used recordings of calls of 10-
 day-old nestlings taken in 2004 at the nest entrance with an
 225 omnidirectional microphone (Audio Technica AT804) and
 digitalized (see section above). Playback stimuli were one of
 4 different recordings from 4 different broods, at an average
 calling rate of 57 calls/min (SD = 25) and standardized in
 amplitude. Mean natural rate in the population is 49.37 calls/
 230 min (SD = 9.97). A digital Archos AV420 recorder and a home-
 made amplifier connected to a miniature 1-W speaker were
 used to play back the nestlings' calls inside the nest. The
 speaker was mounted behind a double wall of the nest-box,
 set a week before the experiment took place to habituate the
 235 nestlings to its presence.

The experiment complies with the ASAB/ABS Guidelines
 for the Treatment of Animals in Behavioral Research and was
 approved by the Spanish Ministry of Education and Science
 (BOS2002-00105).

240 Statistics

We used multiple regressions to analyze the effect of brood
 size, nestling age, and condition on the rate of parent-absent
 calling. In this analysis, observations were carried out at the
 brood level, measuring total calling rate heard in the nest.
 245 Behavior observations in the nest were analyzed by principle
 components analysis in order to simplify patterns, reduce the
 probability of type I errors, and identify independent compo-
 nents of behavior (Frey and Pimentel 1978; Tabachnick and
 Fidell 1996). We built models in SAS using a general linear
 250 model (GLM) procedure to analyze the results of the experi-
 ments. The deprivation experiment was analyzed by means of
 a repeated-measures GLM model, and only the behavior of
 the experimental nestling was studied. The playback experi-
 ment was analyzed by a mixed linear model with repeated
 255 measures. In this case, the observation unit was the nestling
 and analyses took account of this by including nest identity
 as random factor. All residuals from the models were checked
 for normality.

Table 1

Means (SD) of different measurements of begging calls produced in parental absence and presence

Measurement	Parent absent	Parent present	Statistic
Call length (ms)	158.8 (36.4)	419 (43.9)	$F_{1,119} = 38.8^{***}$
Maximum frequency (Hz)	6147 (366)	8726 (390)	$F_{1,144} = 118.3^{***}$
Minimum frequency (Hz)	3300 (304)	3269 (326)	$F_{1,144} = 0.02^{NS}$
Frequency range (Hz)	2875 (508)	5453 (524)	$F_{1,141} = 131.8^{***}$
Frequency modulations	2.3 (0.4)	3.1 (0.5)	$F_{1,95} = 9.94^{**}$
Frequency modulations/s	11.7 (1.5)	9.7 (1.7)	$F_{1,93} = 3.18^{NS}$

Statistics come from repeated-measures analyses of variance, where individual calls are nested within
 nest of origin. Sample size is 146 calls coming from 10 different nests. Significance values are * $P < 0.05$,
 ** $P < 0.01$, *** $P < 0.001$. NS, not significant.

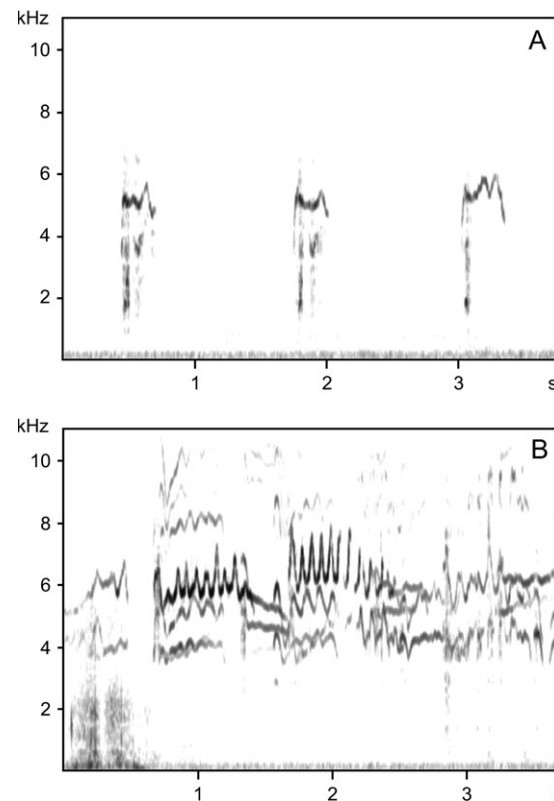


Figure 1

Spectrogram of parent-absent (A) and parent-present calls (B). Note
 that the former are shorter, lower pitched, and less modulated than
 the latter.

RESULTS

Sound analyses of nestling calls

260 Parent-absent calls were acoustically distinct from parent-
 present calls (Figure 1). The former were shorter, had a
 lower maximum frequency, a narrower frequency range, and
 fewer frequency modulations per call than parent-present
 265 calls (Table 1).

Covariates of parent-absent begging in undisturbed nests

270 We measured parent-absent begging in a sample of 30 unma-
 nipulated nests that varied in age and brood size. We explored
 whether age and brood size influenced calling rate in addition
 to weight, a measure that we expect to be negatively correlated
 with nestling need corrected for age. Multiple regression

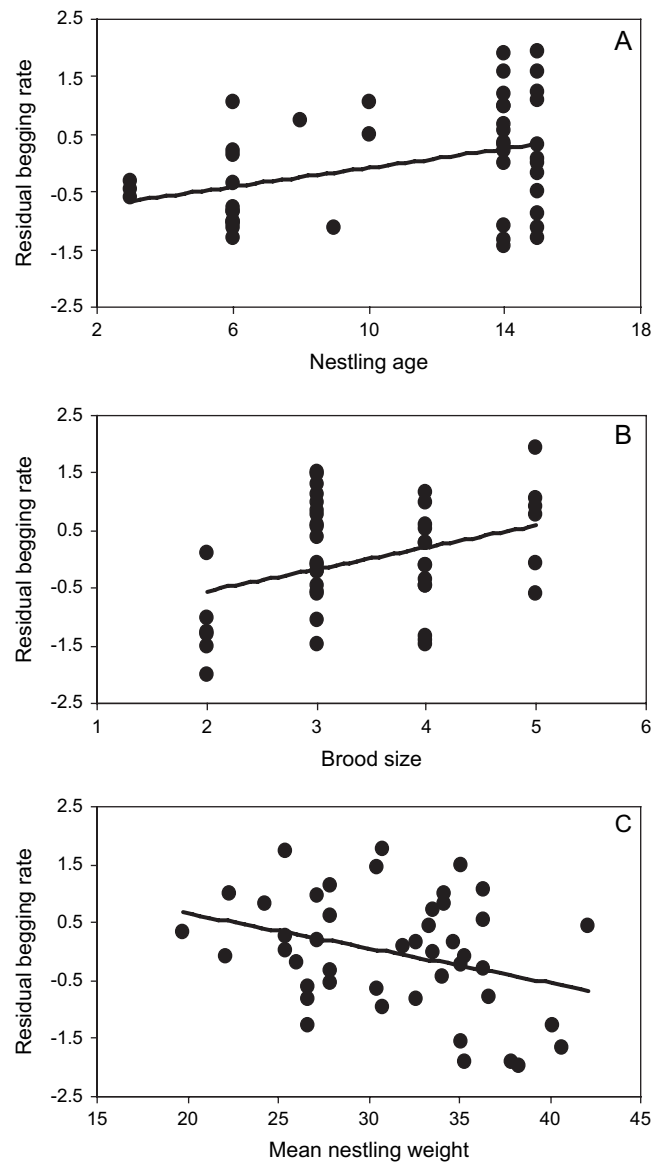


Figure 2
Partial regression plots showing the relationship between the probability of parent-absent begging and (A) nestling age, (B) brood size, and (C) average nestling weight at day 6. In each graph, we plot the residuals of begging levels obtained from a simplified regression that was carried out with the 2 remaining covariates (Neter et al. 1996).

showed that parent-absent begging was simultaneously affected by brood size, nestling age, and average nestling weight at 6 days of age ($F_{3,41} = 4.61$, $P < 0.01$, $r^2 = 0.25$). The probability of parent-absent begging increased with nestling age ($t_{3,41} = 2.57$, $P < 0.05$; slope [standard error, SE] = 2.03 [0.79], Figure 2A) and brood size ($t_{3,41} = 2.39$, $P < 0.05$; slope [SE] = 9.05 [3.80], Figure 2B) and decreased with increasing average nestling weight ($t_{3,41} = -2.22$, $P < 0.05$; slope [SE] = -1.44 [0.65], Figure 2C).

Food deprivation experiment

A principal component analysis was used to reduce the number of variables recorded in the observations of nestling behavior to a few uncorrelated factors. We extracted the first 2 components, which accounted, respectively, for 48% and 21%

Table 2

Loadings of the original variables observed in the food deprivation experiment on the 2 components extracted by principle components analysis

Behavioral category	PC1	PC2
Pushing	0.761	0.052
Preening	0.158	0.938
Gaping	0.859	-0.222
Calling rate	0.865	-0.183
Climbing on top	0.543	0.297

For a description of the variable names, see Methods section.

of the variance (total variance explained = 69%). Loadings of the first component (PC1) showed that it measured an overall begging intensity (consisting of both vocalizing [calling and gaping] and nestling competitive behaviors [pushing and climbing on top]), whereas the second component (PC2)

was loaded singly by preening behavior (Table 2). Nestlings begged more intensively (higher PC1 scores) when deprived of food than when satiated, both in presence and in the absence of parents (Wilcoxon signed-rank test: presence: $Z = -2.31$, $N = 9$, $P = 0.02$; absence: $Z = -2.07$, $N = 9$, $P = 0.038$; Figure 3). The preening component (PC2) was not affected by the food deprivation treatment in either situation (Wilcoxon signed-rank test: presence: $Z = -0.29$, $N = 9$, $P = 0.76$; absence: $Z = -0.41$, $N = 9$, $P = 0.67$; Figure 3).

Parents fed more frequently food-deprived than satiated nestlings (mean proportion [SE] of visits in which experimental nestlings were fed during the hour after the manipulation—deprived: 0.54 [0.23], satiated: 0.12 [0.14]; Wilcoxon signed-rank test: $Z = -2.52$, $N = 8$, $P < 0.05$).

Playback experiment

As in the food deprivation experiment, a principle components analysis was used to reduce the number of behavioral variables recorded in the observations. Two components were extracted that accounted for 38.8% and 21.8% of the variance (total variance explained = 60.6%). PC1 was also here shown to represent general begging intensity, accounting for both vocalizing and nestling-competitive behaviors (Table 3). In contrast to the previous experiment, PC2 also measured an

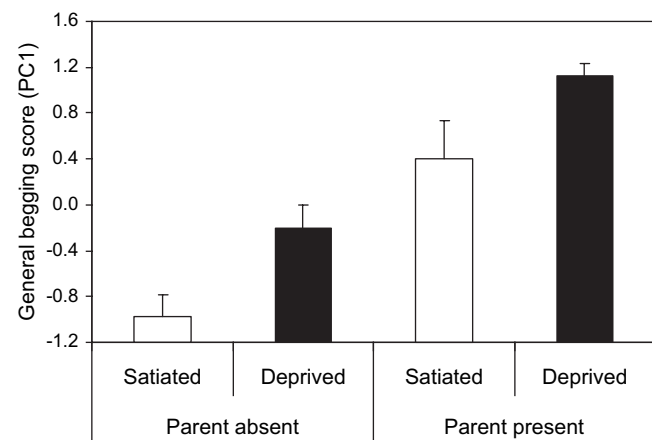


Figure 3
Overall begging intensity (PC1) of nestlings in parental absence and presence in relation to the experimental treatment in the food deprivation experiment.

Table 3
Loadings of the original variables observed in the begging call playback experiment on the 2 components extracted by principle components analysis

Behavioral category	PC1	PC2
Pushing	0.708	-0.181
Gaping	0.465	0.610
Calling rate	0.387	0.711
Preening	0.779	-0.269
Climbing on top	0.683	-0.323

For a description of the variable names, see Methods section.

independent component of begging behavior, being loaded positively by calling rate and gaping and negatively by the rest of the variables (Table 3). We interpret PC2 as a measure of the relative contribution of communicative begging over competitive begging, independently of PC1 that encompasses both kinds of behaviors.

Playback of begging calls resulted in a significant decrease in PC1 in both early and late observations ($F_{1,103} = 52.98$, $P < 0.001$; Figure 4A). As expected, if parent-absent begging is influenced by hunger, PC1 increased from early to late obser-

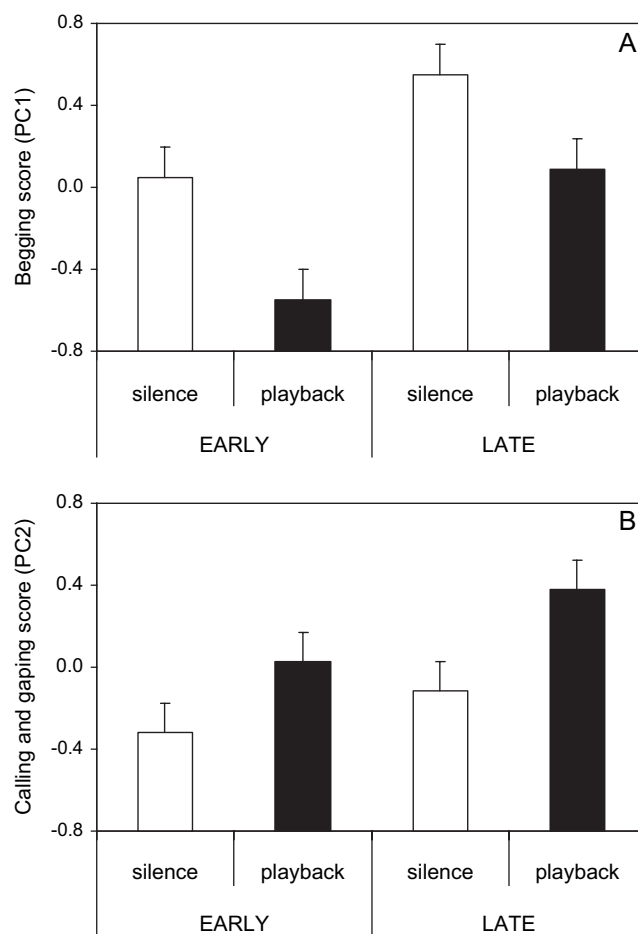


Figure 4
 Results of the playback experiment showing differences in (A) general parent-absent begging intensity (PC1) and (B) parent-absent gaping and tweeting score (PC2) in the early and late observation periods. Filled bars: playback treatment; open bars: control treatment. Points represent means and error bars 1 SE.

variations ($F_{1,103} = 13.67$, $P < 0.001$), whereas the interaction between treatment and time was not significant ($F_{1,103} = 0.98$, $P = 0.34$). In contrast to this negative effect, playback of nestling calls increased PC2 ($F_{1,103} = 6.69$, $P < 0.01$). PC2 also increased with time ($F_{1,103} = 11.51$, $P < 0.001$), showing again hunger dependency. There was, however, no interaction between treatment and time ($F_{1,103} = 0.78$, $P = 0.78$).

DISCUSSION

Prolonged parent-absent begging is a common behavior in the spotless starling. Our observations show that parent-absent begging is a lower intensity signal than parent-present begging, thus reinforcing the difference of this behavior with erroneous begging bouts that are observed in many altricial species (Budden and Wright 2001; Leonard et al. 2005; Dor et al. 2007). Prolonged parent-absent begging seems to be an uncommon phenomenon peculiar to a handful of species (Glutz von Blotzheim 1966–1997; Roulin et al. 2000; this study).

Our observational data showed that the probability of prolonged parent-absent begging increased with age and brood size, and it decreased with average nestling mass at day 6. Because sensory discrimination abilities increase with age in altricial species (Khayutin 1985), an increase of parent-absent begging with age suggests that the occurrence of this behavior is not due to nestlings' discrimination errors (Budden and Wright 2001; Leonard and Horn 2001; Dor et al. 2007). The positive correlation with brood size is expected because the probability of a nestling calling should increase with increasing numbers of nestlings in the nest. However, the negative correlation with nestling weight is consistent with parent-absent begging being influenced by need. Our food deprivation manipulation confirmed the above relationship: nestlings presented higher begging scores after the food deprivation treatment than after satiation. Our data thus agree with previous experiments showing a relationship between need and begging, both in parental absence (Roulin 2001; Maurer et al. 2003) and presence (Redondo and Castro 1992; Price and Ydenberg 1995).

We conducted a playback experiment to test whether nestlings reduced their own begging intensity when confronted with a stimulus representative of a needy nestling (high level of parent-absent begging), as predicted by the sibling negotiation hypothesis (Roulin et al. 2000). It should be noted that playbacks were carried out during a period of 40 min in order to reproduce natural situations where uninterrupted calling in absence can be heard from nests over long periods of time. Nestling behavior in response to playback revealed a complex pattern, and the principal component analysis extracted 2 different components of begging behavior. The PC1 was a general begging score, loaded positively by both communicative and competitive behavioral patterns. Preening also loaded positively in this component, supporting our observations that it could be related to sibling competition. We found that nestlings exposed to calls in absence reduced their general begging score (PC1). This result supports our prediction and is consistent with a mechanism by which less needy nestlings would forgo begging and ease the way for needy nestlings to access an impending food resource, as would be expected in a sibling negotiation scenario (Roulin et al. 2000; Johnstone and Roulin 2003). On the other hand, it can be argued that, by reducing parent-absent calling, less needy nestlings may be selfishly exploiting the calling effort of their needy siblings in the nest (Maurer et al. 2003).

The interpretation of the PC2 is more complex. We considered it to be a measure of the relative contribution of communicative begging over competitive begging, independent of general begging intensity (PC1). Some theoretical models

support this possibility, explicitly modeling begging behavior as a multicomponent behavior encompassing 2 independent factors: 1) a communicative component that influences overall food delivery to the nest and 2) a competitive component that affects the allocation of food among siblings (Johnstone 2004). Contrary to the decrease observed in PC1, the playback treatment resulted in an increase of PC2. Our interpretation of this increase in PC2 will vary depending on whether this behavior is directed at parents or fellow siblings in the nest. We find it unlikely for siblings to be the recipients of PC2 and consider it more plausible for it to be directed at parents because they have ample opportunity to hear parent-absent begging as they arrive at the nest or forage in its vicinity (Maurer et al. 2003) (i.e., parent-absent begging is audible to the human ear far away from the nest-box, but see Roulin 2000). The increase that we observed in PC2 may thus be interpreted as an enhancement of parental solicitation from the nestlings' part to increase overall food supply to the nest.

Although our results suggest that prolonged begging in parental absence in the spotless starling is a signal of need and that nestlings may use it in a cooperative way, further research is needed to observe the consequences of this behavior on parental feeding decisions.

FUNDING

Spanish Ministry for Education and Science (BOS2002-00105 and Ramon y Cajal Fellowship to D.G.); CONACYT, México (PhD grant to P.C.).

Mercedes Muñoz, Isabel López, and Montserrat Gil helped in the field. Clotilde Biard provided advice with statistics. Permission to work in the study area was granted by the Ayuntamiento de Soto del Real and the Consejería de Medio Ambiente de la Comunidad de Madrid.

REFERENCES

- Budden AE, Wright J. 2001. Falling on deaf ears: the adaptive significance of begging in the absence of a parent. *Behav Ecol Sociobiol.* 49:474–481.
- Dor R, Kedar H, Winkler DW, Lotem A. 2007. Begging in the absence of parents: a “quick on the trigger” strategy to minimize costly misses. *Behav Ecol.* 18:97–102.
- Frey DF, Pimentel RA. 1978. Principal component analysis and factor analysis. In: Colgan PW, editor. *Quantitative ethology*. New York: John Wiley & Sons. p. 219–246.
- Glutz von Blotzheim UN. 1966–1997. *Handbuch der Vögel Mitteleuropas*. Wiesbaden (Germany): Aula Verlag.
- Godfray HCJ. 1991. Signalling of need between parents and offspring. *Nature.* 352:328–330.
- Johnstone RA. 1999. Signaling of need, sibling competition, and the cost of honesty. *Proc Natl Acad Sci USA.* 96:12644–12649.
- Johnstone RA. 2004. Begging and sibling competition: how should offspring respond to their rivals? *Am Nat.* 163:388–406.
- Johnstone RA, Roulin A. 2003. Sibling negotiation. *Behav Ecol.* 14:780–786.
- 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 B Biol Sci.* 259:259–263.
- Khayutin SN. 1985. Sensory factors in the behavioral ontogeny of altricial birds. *Adv Study Behav.* 15:105–152.
- Kilner RM. 2001. A growth cost of begging in captive canary chicks. *Proc Natl Acad Sci USA.* 98:11394–11398.
- Kilner RM. 2002. The evolution of complex begging displays. In: Wright J, Leonard ML, editors. *The evolution of begging*. Dordrecht (The Netherlands): Kluwer. p. 87–106.
- Leonard ML, Horn AG. 2001. Begging in the absence of parents by nestling tree swallows. *Behav Ecol.* 12:501–505.
- Leonard ML, Horn AG, Mukhida A. 2005. False alarms and begging in nestling birds. *Anim Behav.* 69:701–708.
- Maurer G, Magrath RD, Leonard ML, Horn AG, Donnelly C. 2003. Begging to differ: scrubwren nestlings beg to alarm calls and vocalize when parents are absent. *Anim Behav.* 65:1045–1055.
- Moreno J, Veiga JP, Cordero PJ, Minguéz E. 1999. Effects of paternal care on reproductive success in the polygynous spotless starling *Sturnus unicolor*. *Behav Ecol Sociobiol.* 47:47–53.
- Neter J, Kutner MH, Wasserman W, Nachtsheim CJ. 1996. *Applied linear regression models*. New York: McGraw-Hill/Irwin.
- Price K, Ydenberg R. 1995. Begging and provisioning in broods of asynchronously hatched yellow headed blackbird nestlings. *Behav Ecol Sociobiol.* 37:201–208.
- Redondo T, Castro F. 1992. Signaling of nutritional need by magpie nestlings. *Ethology.* 92:193–204.
- Rodríguez Gironés MA, Cotton PA, Kacelnik A. 1996. The evolution of begging: signaling and sibling competition. *Proc Natl Acad Sci USA.* 93:14637–14641.
- Rodríguez Gironés MA, Zúñiga JM, Redondo T. 2001. Effects of begging on growth rates of nestling chicks. *Behav Ecol.* 12:269–274.
- Roulin A. 2000. The sibling negotiation hypothesis. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication*. Dordrecht (The Netherlands): Kluwer. p. 107–126.
- Roulin A. 2001. Food supply differentially affects sibling negotiation and competition in the barn owl (*Tyto alba*). *Behav Ecol Sociobiol.* 49:514–519.
- Roulin A. 2004. Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the barn owl, *Tyto alba*. *Evol Ecol Res.* 6:1083–1098.
- Roulin A, Kölliker M, Richner H. 2000. Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proc R Soc Lond B Biol Sci.* 267:459–463.
- Tabachnick BG, Fidell LS. 1996. *Using multivariate statistics*. New York: HarperCollins.