

## Nestling Begging Call Structure and Bout Variation Honestly Signal Need but Not Condition in Spanish Sparrows

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**Paulo A. M. Marques, Luís Vicente, and Rafael Márquez (2009)** Nestling begging call structure and bout variation honestly signal need but not condition in Spanish Sparrows. *Zoological Studies* 48(5): 587-595. Nestling begging behavior in the context of parent-offspring communication has long been seen as a signal by which nestlings solicit care. Begging is a multi-component signal in which both acoustic and visual components are usually important; however, the present knowledge about the specific behavioral features that convey the information is still poor. The aim of this study was to examine how information on nestling's need is encoded in the begging calls given by nestling Spanish Sparrows (*Passer hispaniolensis*). Nestlings were individually submitted to a food-deprivation period and stimulated to beg at regular intervals within that period, and their acoustic reactions were studied. Spanish Sparrow nestlings increased their response to simulated parental visits in reaction to increasing food-deprivation periods. Results also confirmed that information on nestling need might be encoded in variables of calling behavior. The variables important to convey such information are the initial call rate (20 s rate), duration of the begging bout, call amplitude, and call high frequency. As food-deprivation periods increased, nestlings begged more frequently, extended the calling bout, increased the call amplitude, and used higher frequencies. During the deprivation period, nestlings did not change their call latency, call duration, or relative peak time. The study also found that despite expectations, lower-condition nestlings did not beg more frequently during the experiment than their higher-condition siblings. Overall, results support the view of begging as a reliable signal, namely that begging should reflect a nestling's need, and that only some call features might encode information about need.  
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Nestling begging and the communication between nestlings and parents are an important model in the study of the evolution of animal communication (Owings and Morton 1998, Budden and Wright 2001, Wright and Leonard 2002, Leonard and Horn 2005). Nestling begging behavior has long been seen as a signal by which nestlings solicit care from parents. Begging was studied in the context of parent offspring conflict where it is expected that parents and offspring

disagree on the extent and amount of care (Trivers 1974). The nature of the signal, honest or manipulative, is at the center of the discussion of the evolution of apparently excessive behavior (Harper 1986, Johnstone 1999).

Honest signaling models of offspring solicitation predict that if begging is to be used by parents as an honest signal, it should be costly and reflect nestling need (Kilner and Johnstone 1997, Burford et al. 1998, Leonard and Horn

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1998). However, these predictions could also fit the predictions of scramble competition models for the evolution of costly begging, where offspring control allocation (Parker et al. 2002, Royle et al. 2002). The relation between begging and need is well documented, and past research showed that the intensity of individual begging displays is higher both in nestlings in a poor physical condition (Hussell 1988, Lotem 1998) and in experimentally starved nestlings (Welham and Bertram 1993, Kilner 1997, Kölliker et al. 1998, Leonard and Horn 1998, Sacchi et al. 2002).

Begging is a multi-component signal in which both acoustic and visual components are usually important (e.g., Leonard et al. 2003) in increasing the information content and preventing the exploitation of parents by manipulative offspring (Kilner 2002). Although it is known that begging encodes information about a nestling's need (Cotton et al. 1996, Wright et al. 2002, Neuenschwander et al. 2003), knowledge about particular factors that convey that information is still poor (Horn and Leonard 2002). Most studies that address the relation between condition (or need) and begging use a combined index to classify nestling's begging behaviors that includes information on both acoustic and visual components of begging (Cotton et al. 1996, Wright et al. 2002, Neuenschwander et al. 2003). Although efficient, such an approach prevents the assessment of each signal component's contribution to conveying the signal. This information is of special importance since the acoustic and visual signal components may be constrained by different selective pressures, like acoustic interference or light conditions (Horn and Leonard 2002, Heeb et al. 2003), and thus each evolves to cope with those pressures. Also, different begging features might convey specific information about a particular factor that may influence nestling survival and thus its reproductive value (Sacchi et al. 2002). Specific begging components may independently convey specific information; for example, on physiological need, thermal need, or immunocompetence. Recently, the visual component of begging has received some attention, with studies on the function of gape color (Götmark and Ahlström 1997, Kilner 1997, Hunt et al. 2003, Saino et al. 2003). However, the acoustic component of begging has not been studied as intensively, and the roles of its elements in the signaling process are poorly known (but see Leonard and Horn 2001a, Aubin and Jouventin 2002, Sacchi et al. 2002). In this

study, we address this subject, by studying a highly colonial Palaearctic passerine species. We use an experimental approach that simulates parental visits to initially satiated nestlings over a food-deprivation period with each nestling tested separately to avoid confounding effects due to the presence of siblings. The vocal component of begging is particularly interesting because it can attract predators to the nest and thus might account for an important share of the possible begging costs (Kilner and Johnstone 1997, Halupka 1998, Briskie et al. 1999, but see Haskell 2002).

The aim of this study was to examine how information on Spanish Sparrows (*Passer hispaniolensis*) nestling's need is encoded in its begging calls. The 1st question addressed whether Spanish Sparrow nestlings' vocal begging behavior changes with hunger, with the expectation of an increase in the response to simulated parental visits (a binary variable with values of a response and no response) with an increase in the food-deprivation period. This was done by experimentally playing back adult calls at different times in the test period to nestlings with a standardized hunger level and recording the acoustic reaction, using a methodological approach similar to that used by Leonard and Horn (2001a). The 2nd question addressed how the information on nestling need might be encoded in call variables (studied at the level of a single call) and bout variables (studied at the level of the call bout, i.e., a series of calls); it was hypothesized that these call features convey information about hunger. We expected that if begging is a signal of nestling hunger, then during food deprivation, a nestling's begging calls should change in a way that is informative about hunger. Several authors working with different species found an effect of hunger (or need) on call-bout variables (e.g., Welham and Bertram 1993, Leonard and Horn 2001a), and based on several studies, we expected increases in the bout duration and call rate, and a decrease in call latency. Few studies have examined call structural components; but based on several studies (Price et al. 1996, Leonard and Horn 2001a, Sacchi et al. 2002), we expected increases in the call duration and call amplitude, and an absence of change in the frequency characteristics.

To explore how nestling condition influences calling behavior, we carried out the experiment on both the largest and smallest (by mass) nestlings within each brood. In the study of the relation

between the condition and response level (number of responses to the 9 test periods), it was expected that the smallest nestlings (with a lower condition) would show a stronger response (Cotton et al. 1999). It was also expected that the relation between nestling condition and its response level to the playback would differ from 0 and would be negative, with larger nestlings (higher condition) presenting lower response levels. Nestlings differing in size were also expected to differ in the effect of the food-deprivation period on their signaling behavior.

## MATERIALS AND METHODS

### Species and study site

The Spanish Sparrow is a social and nomadic passerine species with highly synchronized breeding phases and which builds roughly spherical nests. Its breeding colonies can be very dense with several nests packed together (Alonso 1984, Marques 2003a). Its breeding success is variable, ranging 0%-44%, with predation being the most important cause of nest failure (Marques 2003b). In this species, males desert the nest, leaving the female to care for the brood alone (Marques 2004). Nestlings can use different cues (acoustic, visual, or tactile) to detect the presence of parents and begin begging.

The study was conducted in 2005 from Mar. to mid-June in Almodôvar, southern Portugal (37°31'N, 08°04'W). Nestlings from 16 Spanish Sparrow nests with bi-parental care were studied, and the brood size ranged 3-5 (mean,  $4.2 \pm 0.86$  (standard deviation; SD)) nestlings at the time of the experiment.

### Field protocols

To study hunger signaling, we experimentally stimulated initially satiated nestlings to beg over a food-deprivation period of 110 min. Nestlings were collected between the 4th and 6th days of age and were weighed (with a digital balance to the nearest 0.1 g), and the tarsus and wing were measured (with calipers to the nearest 0.01 mm). The heaviest and lightest nestlings in the same nest were then removed from the nest and taken to the experimental site. In 3 cases, extremely small nestlings were not used to prevent using terminally ill individuals. In those cases, we used the next lightest nestling. To standardize hunger levels,

before each experimental trial, each nestling was fed to satiation by hand, providing it with 5% of its body weight or until the nestling refused to swallow. Nestlings were fed insectivorous bird food mix with water.

After satiation, a single nestling was placed in one of the 2 experimental nests. Nestlings were initially left in the nests for a resting period of 30 min. Nestlings from the same brood were tested synchronously. Nestlings in the experimental nests were deprived of food during the duration of the trial. To examine how begging call behavior varied with hunger level, nestlings were stimulated to call every 10 min during 80 min, resulting in a total of 9 test periods in each trial. Audio recordings of nestling calling behavior were obtained during the test periods. In each test period, we stimulated nestlings to call by playing parental calls. The stimuli were composed of 4 parental calls recorded during nestling growth in 2005 in a non-experimental nest from an earlier colony (calibrated at  $\pm 75$  dB at 5 cm for sound amplitude, Radioshack SPL meter (cat. no. 33-2050; Korea), on fast setting with A weighting. The playback was done through a headphone (Sony MDR 2806; Japan) placed at the nest entrance, followed by covering the nest entrance. Stimuli and acoustic reactions were recorded with a Sony WM-D6C and a Realistic electret omnidirectional microphone (cat. no. 33-1052; Japan), onto 60 min chromium dioxide tapes (TDK SA, Luxembourg). Throughout this paper, a trial refers to a complete set of playbacks to a nestling from a particular nest, and the test period refers to the emission of 1 test playback.

The 2 experimental nests, containing the largest and smallest nestlings, were 5 min out of phase with each other, and nestlings were randomly assigned to one of the nests, and the starting order was alternated between nests. After each set of trials, the nestlings were fed and returned to their home nest < 2.5 h after their removal. The experiment did not have an effect on the breeding success of sparrows, with the breeding success of experimental nests being similar to that of non-experimental nests with hatched nestlings ( $\chi^2 = 0.86$ , *d.f.* = 1, *n* = 26, *p* > 0.25, at 80% and 63%, respectively).

The experimental setup consisted of a tent to prevent abrupt temperature changes and for protection from the wind. The experiments were carried out in 2 empty experimental nests placed over a styrofoam board, approximately 1 m apart with two 50 mm styrofoam boards in between. This

ensured the elimination of scramble competition within the brood; nestlings never answered to each other calls or stimulus. The nests were used to expose nestlings to the experimental conditions and record their begging vocalizations. The nests used in this experiment had been removed from an earlier colony, and were nests which had been abandoned during the laying phase.

The internal temperature of the experimental nests, in °C, was monitored using a stainless-steel temperature probe (Vernier TMP-BTA, Beaverton, OR, USA) and with a surface temperature probe in the nests in natural conditions (Vernier STS-BTA) both connected to a Powerbook G4 (Apple Macintosh; CA, USA) sampled at a rate of 1 sample/s using the software Logger Lite 1.2 (Vernier).

### Sound analysis

Recordings were digitized with a Digi 001 16 bit, 44.1 kHz sound board, and Pro Tools software (Digidesign, Daly City, CA, USA) in an Apple Macintosh G4 computer. Files were edited with PEAK software vers. 4. (BIAS, Petaluma, CA, USA), and then sound files were bandpass-filtered to remove noise (low filter at 300 Hz and high filter at 16,000 Hz in RAVEN 1.2, Cornell Laboratory of Ornithology, Ithaca, NY, USA) and normalized (peak 96%). Temporal variables were measured using oscillograms and frequency variables in the audiospectrogram (with a Hamming window, fast Fourier transform (FFT) of 1025 samples, with 90% overlap). Four to 10 individual calls from each nestling in each test period were used to describe the begging calls (average, 8.08; standard error (SE), 0.32 calls).

The response was considered a binary variable assuming 2 values, a response (1) and no response (0), and a response was recorded if the nestling emitted a begging call in a given period. The response level was considered the number of responses to the 9 test periods exhibited by each nestling, and ranged 0-9 responses.

In most of the analyses, the test periods were grouped in 3 phases of deprivation, with the 1st phase including test periods 1, 2, and 3 corresponding to a maximum of a 50 min deprivation period; the 2nd phase including periods 4, 5, and 6 with a maximum of an 80 min deprivation period; and the 3rd phase including periods 7, 8, and 9 with a maximum of 110 min. Within the deprivation phases, values of the variables were averaged for each nestling.

In this study, the term “call variables” is applied to variables at the level of a single call, and “bout variables” are ones measured at the level of the call bout. Call variables used in this study were the call duration (in s), relative peak time [(amplitude peak time - beginning time)/duration of the call], the high frequency of the calls (in Hz, the upper frequency bound of the call), and low frequency of the calls (in Hz). The relative call amplitude was the average of the ratio between the nestling call amplitude and the playback call amplitude (as the maximum power, dB, as a dimensionless sample unit; Charif et al. 2004). This variable measures the nestling call amplitude perceived at the nest entrance, relative to the playback call amplitude.

Three bout variables were measured: bout duration (time elapsed between the 1st and the last begging call emitted by the nestling), 20 s calling rate (number of calls given in the 1st 20 s after the beginning of the playback), and latency (the time elapsed between the beginning of the playback and the 1st nestling call).

Correlations between variable slopes were low ( $|r| < 0.55$ ,  $n = 12$ ) except for the low frequency which was highly correlated with call duration ( $r = -0.72$ ) and the 20 s call rate ( $r = 0.84$ ), and the high frequency which was correlated with the call bout duration ( $r = -0.69$ ). Since the low frequency was correlated with other call variable, it was not included in the analyses to avoid testing correlated variables; a preliminary analysis revealed that it was not influenced by food-deprivation time.

### Temperature

Trials were made at an average nest temperature of 32.9°C (SD, 2.2,  $n = 16$ , range, 29.3-36.7°C), which is approximately the natural range of temperatures inside the nest ( $29.8 \pm 1.8^\circ\text{C}$ , range, 27.3-32.3°C, for 6 broods with 100 samples each, at a 1 s sampling rate) and is within the adult thermoneutral zone (Weathers and Riper 1982). Temperature did not differ between trials in which no nestling responded, 1 nestling responded, or both nestlings responded (analysis of variance (ANOVA)  $F_{2,13} = 0.65$ ,  $p = 0.537$ ). The temperature component of variation with food-deprivation time did not significantly differ from 0 when considering all trials ( $t_{15} = 0.757$ ,  $p = 0.461$ ).

## Statistical analysis

The variation in the ambient temperature in the nest with the deprivation time was examined in each trial by regressing it against the time elapsed from the beginning of the playback test. Then the slopes were compared with 0 using one-sample *t*-tests.

Nestling body mass was linearly related to the tarsus length (mass =  $-3.57 + 1.37$  tarsus,  $n = 32$ ,  $F = 203.7$ ,  $r^2$  adj. = 0.87,  $p = 0.0087$ ), and the regression residuals were used to determine the nestling body condition, after controlling for age and size differences. Based on the body condition, nestlings in each trial were assigned either to the higher- ( $15.54 \pm 2.56$  g) or lower-condition group ( $13.05 \pm 3.84$  g). The classification of nestlings in each trial did not differ either using body weight or condition, except that in 1 nest, the heaviest nestling was not the one in better condition. Thus, either size or condition was used to study the reaction to playbacks, and in this study, we chose to use body condition.

The response of the different nestlings to the deprivation periods corresponds to a repeated-measure experimental design with values of a dichotomous variable (response or no response) for which the Cochran Q test can be applied (Zar 1999).

The variation in calling behavior over the food-deprivation period was examined in several steps, and the effects on the call variables and bout variables were measured separately. In the 1st step, a regression approach was used to study this variation, enabling the use of trials where nestlings only begged in a part of the trial, preventing the exclusion of cases due to empty cells. In the 2nd step, repeated-measures ANOVA was used to confirm the results obtained with the regression analysis.

First for each nestling, the call features were regressed with each test period time to obtain the slope of each variable with the time elapsed. Second, each nestling regression parameter was used in a *t*-test to test for significant changes over time or for differences between large and small nestlings paired by the nest of origin. The slopes of the regression lines were compared with 0 using 1 sample *t*-tests. To determine if large and small nestlings presented behavioral differences with the effect of the food-deprivation period, the slopes of the 2 groups were compared using a paired-sample *t*-test.

Raw data for some of the analyses were not

normally distributed (namely, the relative peak time and relative amplitude), but the parametric tests used are robust to deviations to a normal distribution (Zar 1999). In a final procedure, using the raw data, a repeated-measures ANOVA was used with the test periods grouped in the 3 phases of food deprivation, as for the response study. Only the last 2 phases were used in the ANOVA to avoid empty cells, due to low reactions in the 1st phase. In each variable and for each nestling, the results for the test periods within the phase were averaged. Statistical analysis was performed using Statistica 5.0 software (StatSoft 1996) and JMP 5.1.2 (SAS Institute, Cary, NC, USA). Results are shown as the mean  $\pm$  SD.

## RESULTS

### Nestling condition

The response level to the playbacks did not differ between the higher- and lower-condition nestlings (*t*-test for matched pairs =  $-0.737$ , *d.f.* = 15,  $p = 0.473$ ). When considering all nestlings together, no relation was found between the nestling response level and the condition ( $r^2$  adj. = 0.03,  $F_{1,30} = 1.95$ ,  $p = 0.1725$ ). Also, during the experiment, the slopes of the regression lines for the call variables did not differ between higher- and lower-condition nestlings (for all variables, *t*-test for matched pairs  $< 1.18$ , *d.f.* = 6,  $p > 0.18$ ), meaning that nestlings did not differ in their reaction to the deprivation period. Therefore, for the remaining analyses for each nest, the nestling with the best response level to playbacks (number of test periods with calling) was used.

### Response rate

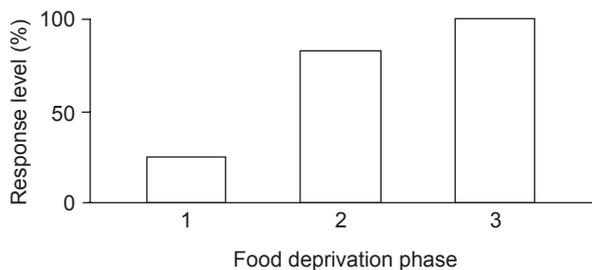
Four trials were excluded, 3 trials with no response from both nestlings and 1 trial with only 1 call. Nestling response to playbacks changed with the deprivation phases (Cochran's Q test:  $Q = 14.889$ , *d.f.* = 2,  $n = 12$ ,  $p = 0.0006$ ), with the number of nestlings calling increasing with the deprivation phase (Fig. 1). This difference was mostly due to the low response level in the 1st deprivation phase (3 responses in 12 trials).

### Vocal begging variables

The study of call-bout variables revealed that nestlings changed their behavior with an increase

in the duration of the deprivation period (Table 1). Moreover, the slope of the regression of the 20 s call rate with hunger level significantly differed from 0 (Table 1), meaning that as the time since satiation increased, there was a significant change in the output of nestling begging vocalizations. Interestingly, the 20 s call rate of nestlings increased with an increase in the food-deprivation period (Fig. 2A), especially from the 2nd to 3rd deprivation phases (with maxima of 80 and 110 min, respectively). The tested nestlings also increased the duration of their calling bouts, but only significantly when the 2nd and 3rd deprivation period were compared (Fig. 2B). Spanish Sparrows' nestlings did not change their calling latency (Table 1).

Nestlings changed some aspects of the call structure with the food deprivation period, namely, the relative call amplitude and high frequency (Table 1). The slope of the relative call amplitude regression with food deprivation differed from 0



**Fig. 1.** Response level as the number of responses to simulated parental feeding visits given by nestlings in 3 increasing phases of food deprivation (1, corresponding to a maximum deprivation period of 50 min; 2, between 60 and 80 min; and 3, between 90 and 110 min).

(Table 1), and significantly increased between the 2nd and 3rd deprivation phases, with nestling's begging becoming louder with an increase in the deprivation phase (Fig. 2C). Also the high frequency changed with the deprivation period (Table 1), with an increasing trend across the 3 phases, but it was only significant in the last 2 phases (Fig. 2D). The food-deprivation period did not affect the call duration (Table 1).

### DISCUSSION

Spanish Sparrow nestlings increased their response level to simulated parental visits when subjected to increasing food-deprivation periods. This result concurs with most studies addressing the relation between begging and hunger level (e.g., Kacelnik et al. 1995, Price and Ydenberg 1995, Kilner 1997, Leonard and Horn 1998). The study also found that for the studied condition differences, nestlings did not differ in their response level to the experimental manipulation of their hunger level. These results are contrary to what might be expected, since different-sized nestlings should have different sensibilities to changes in their short-term needs (Trivers 1974). This result occurred in the absence of nest mates, i.e., without competition, and other studies showed that the behavior of manipulated nestmates can affect the begging of unmanipulated focal nestlings. Also, the absence of an effect might have been due to differences in the condition between the 2 groups not being large enough to elicit a differential behavioral reaction within this experimental framework, especially if this difference corresponds to a small difference in the

**Table 1.** Effects of the food-deprivation period on different variables of nestling vocal begging behavior in Spanish Sparrows. The component of variation in the call with deprivation time (slope of the linear regression equation of the variables with time for each nestling) was tested for differences with 0

	Slope mean ± SD (n = 12)	t-value (d.f.)	p
Call latency (s)	-0.280 ± 0.95	-1.021 (11)	0.329
20 s call rate (calls in 20 s)	11.210 ± 11.34	3.425 (11)	0.006
Call bout duration (s)	12.690 ± 8.34	5.270 (11)	0.0003
Call duration (s)	0.010 ± 0.02	1.811 (11)	0.097
Relative peak time	0.030 ± 0.06	1.789 (11)	0.101
High frequency (Hz)	250.800 ± 203.83	4.262 (11)	0.001
Relative amplitude	0.018 ± 0.013	4.720 (11)	0.0006

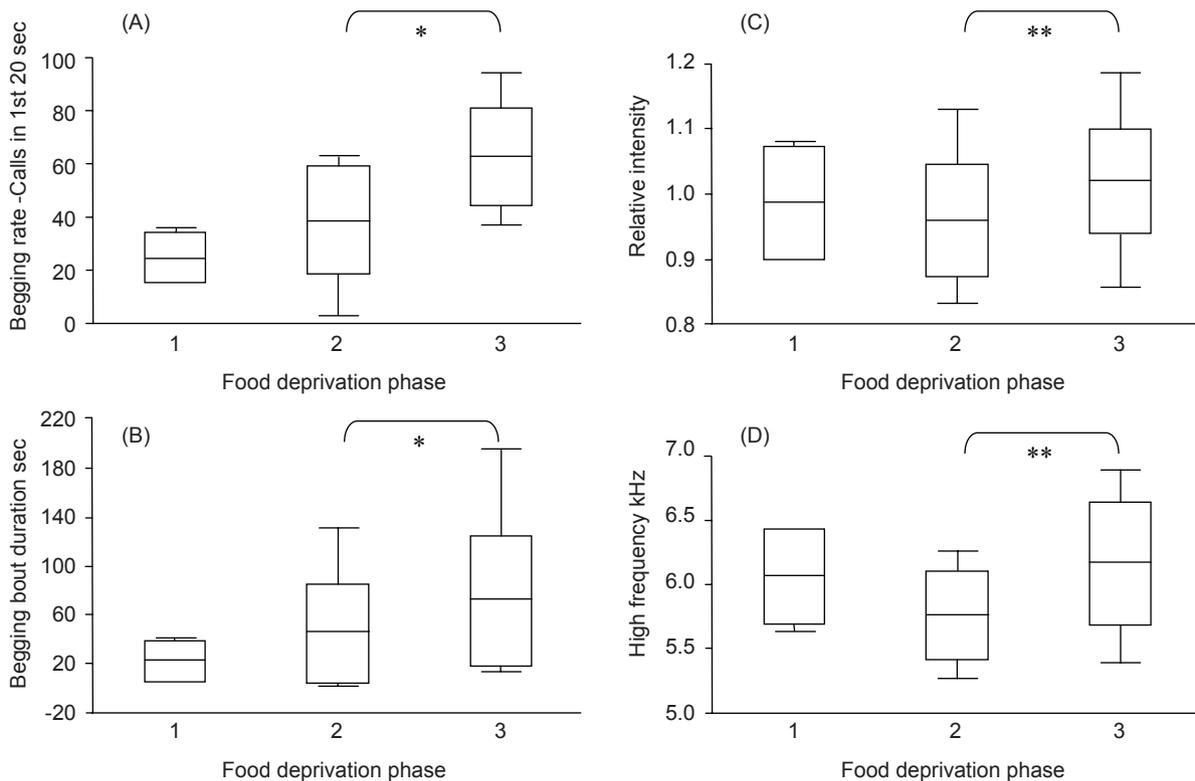
long-term need.

We expected that the observed temperature variation would not influence the results obtained for the hunger signaling, since it was within the adult thermoneutral zone (Weathers and Riper 1982) and above the egg physiological development zero temperature, and its variation was low and near the lower limit of optimal development (respectively, 26 and 36°C for eggs according to Lundy 1969 in Conway and Martin 2000).

Results confirmed that information on nestling need might be encoded in variables of calling behavior, including both call and bout variables. As the food-deprivation period increased, nestlings begged more often, extended their calling bout, increased the call amplitude, and used higher frequencies. From the bout variables, as expected, the initial call rate (20 s call rate) presented a significant effect of the deprivation period. The call rate was confirmed as a signal for need (Leonard

and Horn 2001a, Sacchi et al. 2002) that parents use to feed nestlings (Leonard and Horn 2001b); although in recent studies, it was found that the relation between hunger and the call rate can be affected by factors like brood size, the presence of nestmates, or movement confinement (Leonard et al. 2003, Marques et al. 2006). The bout duration also increased with the deprivation period but only between the 2nd and 3rd phases.

The begging latency did not vary with the food-deprivation period, which is in accordance with results from Sacchi et al. (2002), suggesting that although hungrier, Spanish Sparrow nestlings do not compete by begging sooner. Although in some species call latency is affected by the hunger level (Marques et al. 2008), this difference might be the result of a species' life history traits. The absence, in most variables, of a stronger reaction in the 1st phase of the deprivation time might have been due to an over-satiation effect in this study, with 5% of their weight being too much food,



**Fig. 2.** Variations in nestling vocal begging with the food-deprivation phase (of 3 periods corresponding to a maximum of 50, 80, and 110 min of food deprivation, only the last 2 were used in the test): A, begging rate; B, begging bout duration (\* repeated-measures MANOVA  $F_{2,8} = 7.07$ ,  $p = 0.017$ , univariate tests repeated-measures ANOVA  $F_{1,9} = 14.23$ ,  $p = 0.0044$ , and ANOVA  $F_{1,9} = 6.90$ ,  $p = 0.0275$ , respectively); C, relative intensity; and D, high frequency (\*\* repeated-measures MANOVA  $F_{2,7} = 13.19$ ,  $p = 0.0042$ , univariate tests repeated-measures ANOVA  $F_{1,8} = 13.47$ ,  $p = 0.0063$ , and ANOVA  $F_{1,8} = 23.61$ ,  $p = 0.0013$ , respectively); line, mean; box, mean  $\pm$  SD; whiskers, maximum and minimum.

surpassing the aimed satiation and inhibiting the hunger response.

The call variable that changed with the deprivation period was the high frequency, and it only presented an increasing trend between the 2nd and 3rd phases of food deprivation. This effect in frequency was detected in the hunger signaling of older Tree Swallows *Tachycineta bicolor* (Leonard and Horn 2006) but not in younger ones (Leonard and Horn 2001a). These results are of particular interest since they illustrate a difference in the information value of a high frequency both at the species level and between species, importantly emphasizing that not only bout variables, but also call variables might convey information about hunger. In this framework, high frequency might differentially reveal a nestling's needs across species. The duration of the call in this study did not change with the food-deprivation period, contrary to what was found for Barn Swallows *Hirundo rustica*, Tree Swallows, and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus* (Price et al. 1996, Leonard and Horn 2001a, Sacchi et al. 2002, Marques et al. 2008). Interestingly, this result contests the assumption that call duration is a direct component of begging intensity, and in Spanish Sparrows, this might result from the relatively long nestling calls and a possible risk of call overlap (Marques et al. 2006). The relative call amplitude changed with the deprivation period, although only significantly increasing between the 2nd and 3rd phases, and nestlings seemed to beg louder when hungrier. Surprisingly, at least in Tree Swallows, parents might not use amplitude to decide which nestling to feed (Leonard and Horn 2001b), and nestlings seem to use call amplitude in a situation of high ambient noise to help the parents perceive their calls (Leonard and Horn 2005).

The results presented in this study support the idea that nestling vocal begging behavior encodes information about their needs, and that not all of the studied variables may convey such a message. Vocal call variables which are important for conveying information are the initial call rate (20 s rate), duration of the begging bout, call amplitude, and a high frequency of the call. These results confirm the view of begging as an honest signal, namely that begging should reflect a nestling's needs (Kilner and Johnstone 1997). However, when allocation of food resources is determined by competitive begging scrambles between siblings, the scramble competition model predictions are similar to models of honest

signaling of need, and consequently it will be difficult to distinguish between the 2 models based on empirical observations of the reactions of chicks to feeding by parents (Parker et al. 2002, Royle et al. 2002). Nevertheless, as shown in a recent study, the relation between begging behavior, namely the vocal component, and hunger can change when including other factors in the study, like the presence of nestmates and movement confinement (Leonard et al. 2003). Those factors influence vocal begging and might alter the information value of some of the signal components to parents. Particularly interesting would be to test these differences by manipulating both the need and the competitive environment within the nest.

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