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Begging in the absence of parents: a "quick on the trigger" strategy to minimize costly misses

Roi Dor,[a] Hilla Kedar,[a] David W. Winkler,[b] and Arnon Lotem[a]
[a]Department of Zoology, Tel-Aviv University, Israel and [b]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY, USA

Nestling begging in the absence of parents may reflect "false alarms" due to cognitive constraints or signaling activity toward nest mates (sibling negotiation). According to signal detection theory, cognitive constraints should result in both false alarms (begging in the absence of parents or to inappropriate stimuli) and misses (failure to beg during parental visits). In our study of house sparrows, nestling begging in the absence of parents comprised up to 50% of the begging events at the nest and was more frequent at an early age and among hungrier (lower ranked) nestlings. In contrast, the probability of begging during parental visits was constantly high (80% or more), suggesting that the rate of misses must have been low even at an early age. These results have 2 main implications. First, the observation that begging in the absence of parents decreases with nestling age favors the cognitive constraints hypothesis over functional explanations such as the sibling negotiation hypothesis. Second, the low proportion of "misses" among young nestlings suggests that nestling respond to their cognitive constraints by using low decision criteria (a "quick on the trigger" strategy) that increases the frequency of false alarms but minimizes costly misses. *Key words:* cognitive constraints, false alarm, nestling begging, *Passer domesticus*, signal detection theory. *[Behav Ecol 18:97–102 (2007)]*

Nestling begging has been studied extensively as a signal of need in parent–offspring communication (Kilner and Johnstone 1997; Budden and Wright 2001a; Wright and Leonard 2002). In this context, begging behavior has been studied primarily as a behavior that is directed at the parents and triggered by parental stimuli. Recently, however, there has been increasing interest in the phenomenon of nestling begging in the absence of parents (Roulin et al. 2000; Budden and Wright 2001b; Leonard and Horn 2001; Leonard et al. 2005). This behavior appears maladaptive because it bears the same costs as begging in the presence of parents (energetic or increased predation risk) but with no apparent benefit.

One possible explanation for parent-absent begging was suggested by Roulin et al. (2000) based on their work on the barn owl (for theoretical analysis, see also Roulin 2001, 2004; Johnstone and Roulin 2003). These authors suggested that begging in the absence of parents is a form of communication between the siblings that determines which nestling will get the next food item that will be delivered to the nest. Although there is supportive evidence for this "sibling negotiation hypothesis" from the barn owls, it is not yet clear whether it can also explain parent-absent begging in small passerines. Another functional explanation for parent-absent begging is that such begging can be used to communicate hunger to the parents near the nest (Maurer et al. 2003). This behavior may allow the parents to learn about nestlings' need from a distance, without revealing the nest's location to a predator (Maurer et al. 2003). An alternative view to these functional explanations is that begging in the absence of parents represents errors in the execution of begging behavior as a result of cognitive constraints (Clemmons 1995; Budden and Wright 2001b; Leonard and Horn 2001; Leonard et al. 2005).

Cognitive constraints and signal detection theory

The cognitive constraints hypothesis can be conceptualized best by applying signal detection theory (SDT) (Green and Swets 1966) to the case of nestling begging (see also Leonard et al. 2005). According to SDT, signals are presented in a complex environment, surrounded by noise or competing stimuli that may overlap with the signal itself. The problem can be illustrated graphically by a typical SDT model (Figure 1a) that reduces the problem to one dimension (e.g., color, size, or sound level) and 2 stimuli (correct and incorrect). The curves in the figure describe the probability density functions on the perceived dimension of the 2 stimuli. The amount of overlap between them sets the discrimination constraints (or sensitivity in SDT terminology). In the case of nestling begging, the correct stimulus that should trigger begging behavior may be the image of the visiting parent or the sound of its feeding call, whereas the incorrect stimulus may be a shadow of a moving cloud or a call of another bird at a distance. The amount of overlap between the 2 stimuli may be high at an early age and likely to diminish as nestlings improve their eyesight and perceptual abilities (see Figure 1b). To take an action, a nestling must use some decision criteria χ, which implies that it begs in response to any stimulus with a perceived dimension that is greater than χ (see Figure 1a). This would result in 4 possible outcomes (with their respective SDT terms). If the signal dimension is greater than χ, the nestling may correctly beg to a visiting parent (hit) or incorrectly beg in the absence of a parent (false alarm). If the signal dimension is smaller than χ, then the nestling may correctly ignore nonparental stimuli (correct rejection) or incorrectly ignore a parent visiting the nest (miss). Note that by modifying the size of χ, a nestling changes the probability that different outcomes take place. For example, by lowering the decision criteria to χ' (Figure 1c), it can eliminate the risk of misses but at a cost of making many more false alarms. The optimal decision criterion depends on the relative payoff of the 4 outcomes and on the probability density functions of the 2 stimuli (see details in Wiley 1994; Bradbury and Vehrencamp 1998; and some extensive SDT animal behavior applications in Getty 1997; Rodriguez-Girones and Lotem 1999; Johnstone 2002).

Address correspondence to R. Dor. E-mail: dorroi@post.tau.ac.il.
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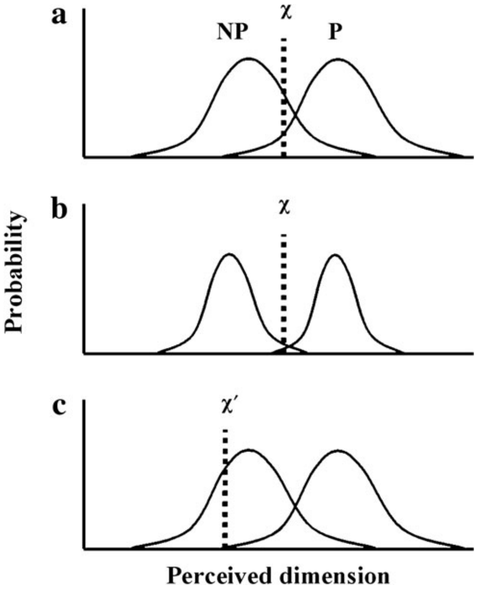

Figure 1
An SDT illustration of nestling begging response to parental (P) and nonparental (NP) stimuli. The figure describes the probability density function of each stimulus (the probability of encountering the stimulus in the perceived dimension). The use of decision criterion χ would result in responding to NP stimuli with a perceived dimension greater than χ (false alarm) and in not responding to P stimuli with a perceived dimension smaller than χ (miss). The probabilities of false alarms and misses vary according to the location of χ and the shape of the probability density functions. For further explanation see text.

Explaining the evidence

Although there are some limitations to the use of SDT in experimental studies of nestling begging (see discussion by Leonard et al. 2005), SDT provides a theoretical framework for the cognitive constraints hypothesis, which helps to make current explanations of empirical data more explicit. For example, in both black-capped chickadees *Poecile atricapilla* and southern gray shrikes *Lanius meridionalis*, the frequency of begging in the absence of parents decreases with age (Clemmons 1995; Budden and Wright 2001b). This reduction was explained by the developing sensory and cognitive abilities of the growing nestlings as well as by their increasing experience with the correct and incorrect stimuli (Clemmons 1995; Budden and Wright 2001b). In SDT terms, this would result from a reduction in the amount of overlap between the curves. This reduction becomes possible when the perception of each signal becomes more accurate and therefore could be represented by a narrower density function (Figure 1b). Note, however, that because there are no data concerning the rate of "misses" in these studies, we cannot tell whether such improvements in cognitive abilities also reduced the rate of misses as suggested by Figure 1b.

Different results were reported from tree swallows (*Tachycineta bicolor*) where the frequency of begging in the absence of parents increases with age (Leonard and Horn 2001). This opposite result can still be explained by SDT because SDT also predicts a change in the decision criteria depending on the relative cost of misses versus false alarms. As pointed out by Leonard et al. (2005), in tree swallows, begging and sibling competition intensifies with age and a nestling's probability of being fed may be affected by its fast response to the arriving parent. This sets a high cost for misses, whereas the cost of false alarms may actually become lower because older nestlings can maybe bear the energetic cost of extra begs more easily (see also Kilner 2001). Under these conditions, older nestlings may correctly adopt lower decision criteria that minimize misses but cause many false alarms (as in Figure 1c).

Interestingly, the ideas of Leonard et al. (2005) goes further than using cognitive constraints as an explanation for false alarms. It also implies that nestlings strategically respond to this constraint by setting a lower decision criterion that causes many false alarms but prevents costly misses. However, Leonard et al. (2005) did not analyze the relative frequency of false alarms and misses to make this point more explicit. Part of the problem in doing this is that misses cannot be measured directly. Nestlings may not beg in response to parental stimuli simply because they are not sufficiently hungry or motivated, not just because they fail to detect the parental stimuli. Another problem is that the rate of false alarms (frequency of occurrences over time) cannot represent the actual error probability because no information is available on the frequency of the incorrect stimuli at the nest (e.g., a moving cloud or incidental noise). However, an upper limit for the rate of misses can be derived from the observed rate of "hits" (the rate of begging responses to parental stimuli). For example, if nestlings beg in response to parental stimuli in 80% of the cases, their rate of misses could not be higher than 20%. Comparing this potential rate of misses with the observed frequency of false alarms may nevertheless be informative. This is because a change in their relative magnitude may indicate a change in the nestlings' decision criteria.

In this study, we explore possible changes in the frequency of false alarms and misses in house sparrow nestlings in an effort to understand how begging decision criteria may be determined. To that end, we monitored begging in the absence of parents as well as begging in the presence of parents and analyzed their frequency in relation to nestling age, relative rank, and the level of hunger. We show that the pattern of false alarms and misses in this population is consistent with the cognitive constraints hypothesis as well as with the idea that nestlings apply a "quick on the trigger" strategy to minimize misses.

METHODS

Data collection and video recordings were carried out during April–July 1999 and 2000 in a colony of free-living house sparrows breeding in nest-boxes on Tel-Aviv University campus. Each box was composed of 2 sections separated with a clear glass plate, one section for the nest itself and another for a camera. The colony was monitored throughout the breeding season to determine the exact dates of egg laying and hatching (hatching day was marked as day 0). The study was carried out under an animal care permit from Tel-Aviv University Animal Care Committee (No. L-01-05).

We monitored nestling behavior in 16 nests by taking 3-h videos when nestlings were at the ages of 3, 4, and 6 days (nestlings usually fledge at the age of 14–15 days). We used infrared video cameras (Boxwatch, Ltd, UK) placed in the camera section of the nest-boxes and connected via a 30-m cable to a VCR (Sony EV-C500E) located indoors. To minimize disturbance, we set up the video camera on the evening before the recording started (i.e., on the evening of day 2). In each day of the experiment, 30 min before video recording, nestlings were individually marked with black (or white) nontoxic acrylic paint on their back, weighed to the nearest 0.1 g using Ohaus C 305-S electronic balances, and their wing length was measured with a caliper to the nearest 0.1 mm. Nestling relative rank within a brood was determined based on mass (rank 1 given to the heaviest chick and rank 4 to the lightest) or when mass differences were smaller than 0.1 g, according to wing length.

Video analysis

For every begging event, we recorded the time, parent's sex, nestling begging, and meal size for each nestling. We analyzed 2 kinds of begging events: begging occurring in response to parental stimuli (during parental visits—"correct detections" or hits) and begging in the absence of a parent (hereafter false alarms). Parental stimuli included feeding calls, noise when entering the nest-box or darkening of the box when entering the nest. Events of begging in the absence of parents were defined as events that were not triggered by known parental stimuli. All begging events were recorded when at least one nestling in the brood begged for at least 3 s. Events that could not be attributed to one of these 2 categories, such as begging at the parents' departure stimuli ("intermediate" events, Budden and Wright 2001b), were omitted from the analysis. Although these events could be considered as errors to some extent, they are directed to parents and could affect parental behavior. For each begging event, each nestling was given a score of 1 if it begged and 0 otherwise.

During a parental visit the parents can feed one or more nestlings. For each parental visit, each nestling that was fed was given a meal size score in proportion to the parent's bill: 1) small food item that was not noticeable outside the bill, 2) noticeable food filling half the bill, and 3) noticeable food filling the entire bill. Based on the videos, we also calculated for each begging event the time since the last receipt of food by each nestling.

Data analysis

We monitored a total of 16 nests of 4 ($n = 10$) and 3 ($n = 6$) nestlings, but because of brood reduction and technical problems, we have repeated measurements of all ages for only 11 nests. To insure a well-matched data set with equal representation of all ranks and ages, we further reduced the data set to the 7 nests that had 4 nestlings observed at all the 3 ages. The data from all other nests show qualitatively similar trends and are available at: http://www.tau.ac.il/~lotem/roi_files/Supplementary%20data%20for%20BE%20paper.htm.

Statistical analysis was performed using the SAS system for mixed models (Littell et al. 1996) with SAS software version 8.1. This statistical method allowed us to construct the appropriate mixed models with nests as random effect, nestling rank as a fixed effect, nestling age as the repeated measure, and additional variables as possible covariates for each chick (nestling mass, average meal size, average time from the last meal) or brood (parental visit rate at the nest). Degrees of freedom were calculated following the Kenward–Roger method for SAS proc mixed with repeated measurement (Littell et al. 1996). The dependent variable in the model was either the number of false alarms per hour (false alarms rate) or the proportion of begging during parental visits (hit rate). We used an arcsine square root transformation for the data of both variables and Statistica software version 6.0 to verify homogeneity of variances and normality of the residuals (using Levene's and Kolmogorov–Smirnov's tests, respectively). In a later stage of the analysis, as new questions came up, we used the same procedure for analyzing the average meal size and the probability of receiving food first as dependent variables (see below).

RESULTS

Begging in the absence of parents

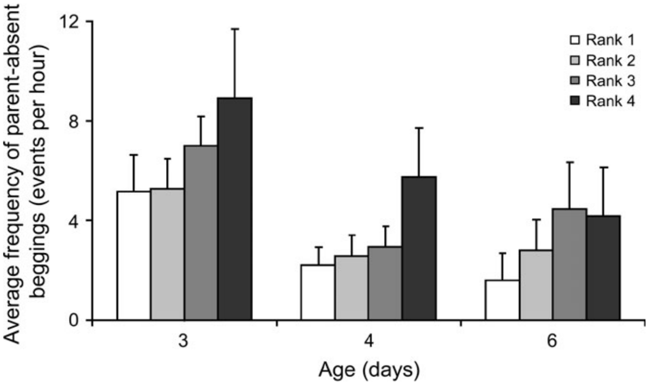

Figure 2
The effect of age (days) and rank (rank 1 = heaviest) on the average (±SE) rate (events per hour) of begging in the absence of parents.

Nestling begging in the absence of parents (false alarms) composed a substantial proportion of total begging events at the nest. It was especially common at day 3 (54% of total begging events) and was still common at the age of 4 and 6 days (34% and 30% of total begging events, respectively). The rate of false alarms (number of events per hour) decreased with age as well as with nestlings' mass rank at the nest (Figure 2) (SAS proc mixed model: $F_{3,15} = 5.69$, $P < 0.01$; $F_{2,23} = 15.86$, $P < 0.0001$ for age and rank, respectively, with no significant age × rank interaction: $F_{6,28.9} = 0.27$, $P = 0.940$).

We further extended our statistical analysis by including the following possible confounding variables as covariates in the model: nestlings' mass, average time from the last meal for each chick, average meal size for each chick, and parental visit rate at the nest (visits per hour). We started by including all covariates in the model and then removed nonsignificant covariates by backward elimination, one at a time, and largest P values first. The final model showed a significant effect of age ($F_{2,22.5} = 14.62$, $P < 0.0001$) and average meal size ($F_{1,51.6} = 5.18$, $P = 0.027$) on false alarm rate (i.e., decreasing with age and average meal size) but no significant effect of nestling rank ($F_{3,8.12} = 2.38$, $P = 0.145$). This suggests that the effect of rank on the rate of false alarms (Figure 2) may be explained by a situation in which low-ranked nestlings had received smaller meals and were therefore hungrier (see further analysis below).

Begging in the presence of parents

The probability of begging during parental visits was constantly high (Figure 3) and was not affected significantly by nestling age or rank (SAS proc mixed model: $F_{2,23} = 2.4$, $P = 0.11$; $F_{3,18.8} = 0.58$, $P = 0.64$, for age and rank, respectively). Including the 4 covariates mentioned above in the model did not change this result but showed a significant effect of average meal size ($F_{1,38.9} = 5.33$, $P = 0.026$), indicating that the probability of begging during parental visits was higher when hungrier. All other covariates included in the model were nonsignificant, although "average time since the last meal" was on the verge of significance ($F_{1,44} = 3.35$, $P = 0.074$) in a way consistent with the expected effect of hunger.

Nestling rank and meal size

As mentioned above, our analysis of the rate of false alarms suggests that the effect of rank (Figure 2) may be explained by a situation in which low-ranked nestlings received smaller meals. This was indeed confirmed by analyzing average meal size as the dependent variable in our statistical model (see Figure 4 and statistics therein). One interesting interpretation

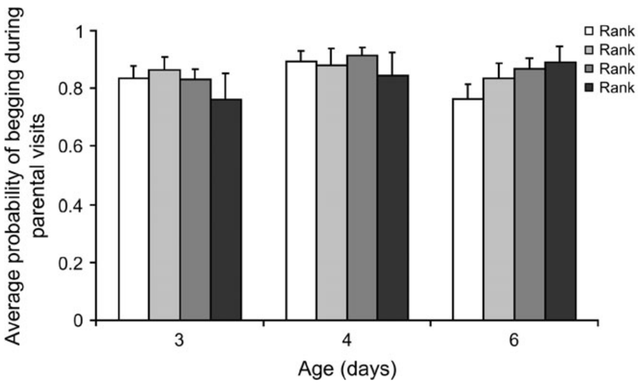

Figure 3
The effect of age (days) and rank (rank 1 = heaviest) on the average probability (±SE) of begging during parental visits.

of these results would be that parents fit the size of the food item brought to the nest to the size of the nestling. However, further analysis supported an alternative explanation, namely, that during parental visits, low-ranked nestlings received lower proportions of first feedings compared with high-ranked nestlings (see Figure 5 and statistics therein) and that the "leftovers" given as second (or third) feedings are usually of a smaller size (average meal sizes of first and second feedings were 1.51 ± 0.36 and 1.11 ± 0.25, respectively [describing average ± standard deviation of 81 and 63 observations where a nestling received at least one first or second meal during a video session]).

DISCUSSION

The effect of age, rank, and hunger on begging in the absence of parents

In this study of house sparrow nestlings, begging in the absence of parents comprised a substantial proportion of total begging events at the nest (50–30%). This proportion is somewhat higher than that reported in other passerine species (Clemmons 1995; Leonard and Horn 2001; Budden and Wright 2001b). The rate of begging in the absence of parents (events per hour) decreased with nestling age, and this reduction was especially pronounced between days 3 and 4 (see Figure 2). A similar age effect was found in black-capped chickadees (Clemmons 1995) and in southern gray shrikes (Budden and Wright 2001b), and it is most consistent with the idea that begging in the absence of parents represents detection errors (false alarms) as a result of cognitive constraints (for discussion, see Clemmons 1995; Budden and Wright 2001b). Our study provides additional support for this idea because a sharp reduction in the frequency of false alarms was observed between days 3 and 4, which is when house sparrow nestlings open their eyes (Dor R, personal observation).

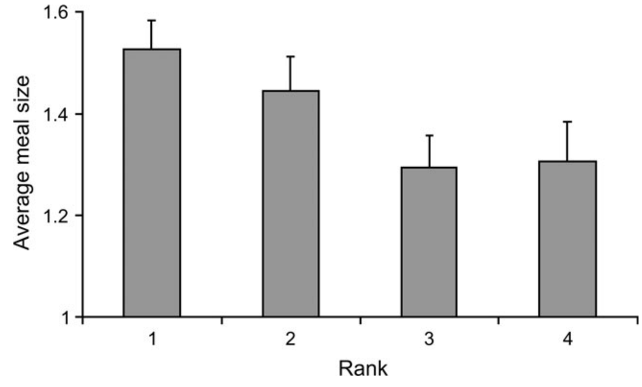

Figure 4
Average (±SE) meal size (for meal size score see Methods) in relation to nestlings' rank (rank 1 = heaviest) ($F_{3,18.3} = 4.65$, $P = 0.014$, SAS proc mixed model with age as repeated measurements, rank and nests as fixed and random effects, respectively. No significant effect was found for age or age × rank interaction).

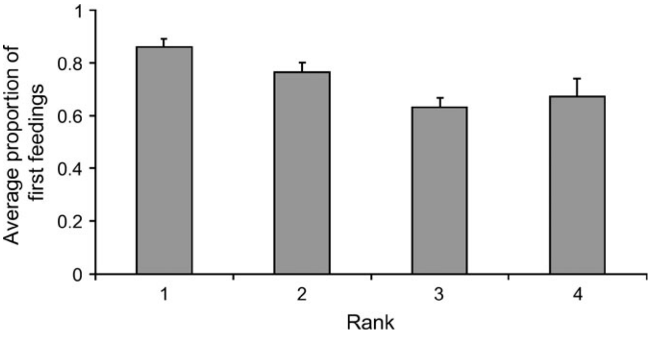

Figure 5
The average proportion (±SE) of cases where nestlings of different ranks (1 = heaviest) were fed first during parental visits. ($F_{3,13.1} = 8.82$, $P < 0.01$, SAS proc mixed model with age as repeated measurements, rank and nests as fixed and random effects, respectively. No significant effect was found for age or age × rank interaction).

Our study provides the first analysis of parent-absent begging in relation to nestling rank, showing that low-ranked nestlings produce more false alarms. One possible explanation is that this is because they are in fact younger and smaller and therefore lagging behind in their physiological and cognitive development. In other words, the rank effect may represent the age effect but on a smaller scale (because age was determined in whole days, differences in rank may still represent smaller differences in age). However, our analysis of potential covariates provides no support for this explanation and instead suggests an alternative one. The covariate "nestling mass" (that could possibly reflect small-scale differences in chronological or biological age) was not significant, and instead, there was a significant effect of average meal size on false alarm rate. We further showed that low-ranked nestlings were less likely to receive the first feedings during parental visits and, consequently, tended to receive the secondary smaller meals (Figures 4 and 5). These results suggest that low-ranked nestlings were more likely to produce false alarms simply because they were hungrier than their older nest mates. The effect of hunger on the rate of false alarms was indicated in previous studies (Price and Ydenberg 1995; Leonard and Horn 2001; Budden and Wright 2001b; Leonard et al. 2005) and has been suggested to reflect an adaptive shift in the nestlings' begging decision criteria. This is because, for a hungry nestling, the difference between the potential benefits from correct begging and the cost of false alarms may be greater than for well-fed nestlings.

False alarms or functional begging?

The sibling negotiation hypothesis (Roulin et al. 2000; Johnstone and Roulin 2003) may provide an alternative interpretation of our results. However, if parent-absent begging is a form of negotiation between the siblings, it is not clear why it decreases with age, whereas the motivation to beg in parental visits does not decrease in a similar manner (Figure 3). Furthermore, according to this hypothesis, parent-absent begging is supposed to predict which nestling will get the next food item (Roulin et al. 2000). In our study, however, lower ranked nestlings did most false alarm begging but were less likely to

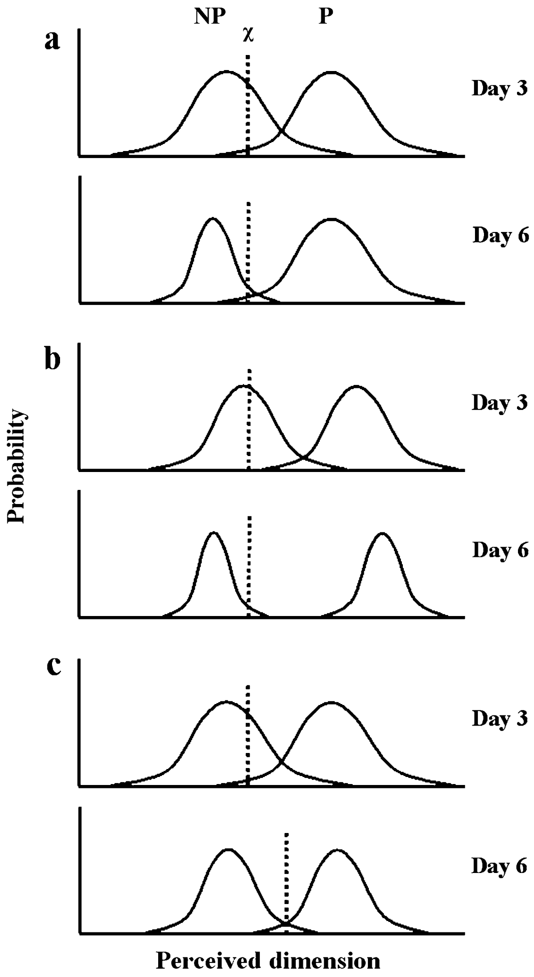

Figure 6
Three possible scenarios (a–c) for explaining the results of our study in SDT terms (see text for explanations). Figures details are as in Figure 1.

receive the first feedings (Figure 5) or to be fed at all (Kedar 2003). Finally, although the sibling negotiation hypothesis cannot be rejected completely, it should be noted that empirical support for this hypothesis came from a study on nestlings that were much older than those studied here and probably more developed in their cognitive ability (Roulin et al. 2000; Roulin 2001, 2004). As mentioned earlier, another functional explanation for parent-absent begging is that it is directed to a parent that might be in the vicinity of the nest (Maurer et al. 2003). In this light, however, it is difficult to explain the reduction in false alarms with age, especially between days 3 and 4. If nestlings improve their cognitive abilities with age, they should become better in detecting parental presence outside the nest rather than vice-versa.

Misses, false alarms, and nestlings' decision criteria

The constantly high rate of begging in the presence of parents (hits in SDT terms) implies that the rate of misses could not be higher than 20% (see Figure 3) and was probably much lower (the significant effect of meal size on begging in parental visits suggests that at least some lack of response was due to satiation). The overall picture from our data is that the frequency of false alarms (over time) was high at an early age and decreased later on, whereas the probability of misses was already low at an early age. In other words, it seems that young nestlings did not differ from older ones in recognizing the correct parental stimuli but made frequent errors in recognizing the incorrect stimuli. An intuitive explanation for this might be that recognizing the parent, when it is there, is simply easier, perhaps because they give specific indications of their presence, such as calls. However, this argument can also work the other way around: if recognizing the parent is easy due to some key distinguishing features, why not refrain from begging in the absence of these features?

Thinking about these problems in terms of SDT might help to clarify the discussion. We use Figure 6 to illustrate 3 possible scenarios. In Figure 6a, nestlings do not change their decision criteria with age, but their improved perception narrows the distribution of the nonparental stimuli, thereby reducing the rate of false alarms while keeping a constant low rate of misses. The second scenario (Figure 6b) is similar but assumes that both distributions narrow with age. Note that for this we must assume that there were no misses to begin with (that all nonresponses to parental stimuli were due to low motivation or satiation, otherwise we cannot explain their constancy). In the third scenario (Figure 6c), both distributions narrow with age (as expected by improved perception), but nestlings also shift their decision criteria to the right, thus lowering their frequency of false alarms while maintaining the same low rate of misses. A general feature in all the 3 scenarios described in Figure 6 is that the decision criteria of the young nestlings (day 3) were biased to the left. In other words, any attempt to explain our results seems to suggest that young nestlings used low decision criteria that resulted in high rates of false alarms and low rates of misses. In other words, nestlings seem to behave as if they are quick on the trigger with their begging response. As mentioned earlier in this paper, such a bias may be expected when the cost of misses is considerably higher than the cost of false alarms. Although it is not yet clear how costly begging is (see discussions in Verhulst and Wiersma 1997; Rodriguez-Girones et al. 2001; Kilner 2001; Wright and Leonard 2002), our results suggest that for young sparrow nestlings, the cost of extra begging is probably much lower than the cost of missing a feeding opportunity during parental visits.

Finally, among the 3 scenarios described in Figure 6, we believe that the most reasonable is the third one (Figure 6c). First, it is more realistic to expect that the improved perception with age would affect the distribution of both stimuli, not only one. Second, it seems adaptive for the nestlings to shift their decision criteria upward following this change: this upward shift should allow them to reduce the rate of false alarms when it becomes possible, while still minimizing the risk of costly misses.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/ and http://www.tau.ac.il/~lotem/roi_files/Supplementary%20data%20for%20BE%20paper.htm.

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