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THERMAL IMAGING OF HOUSE SPARROW NESTLINGS: THE EFFECT OF BEGGING BEHAVIOR AND NESTLING RANK

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Abstract. We used infrared imaging to test whether the energetic cost of begging is observable in changes in body surface temperature (T_s) of young House Sparrow nestlings (*Passer domesticus*), and whether T_s is affected by nestling rank. Begging had a mixed effect on T_s, increasing it slightly at first, but decreasing it when hungry nestlings begged more vigorously. This mixed effect may result from heat production being quickly offset when begging posture and movement enhance heat loss through the skin, and suggests that the energetic cost of begging cannot be inferred from thermal imaging. The analysis of T_s in relation to nestling rank showed that although low-ranked nestlings maintained lower T_s than their larger siblings, their T_s was higher than expected for their body mass. This suggests that nestlings of a lower rank may gain heat from their larger, more developed nestmates.

Key words: body surface temperature, infrared thermal imaging, nestling begging, Passer domesticus, *thermoregulation.*

Imágenes Térmicas de Pichones de *Passer domesticus*: Efectos del Comportamiento de Solicitar y del Rango en la Nidada

Resumen. Utilizamos imágenes infrarrojas de pichones jóvenes de *Passer domesticus* para probar si es posible observar el costo energético de solicitar en los cambios de la temperatura de la superficie del cuerpo (T_s), y si T_s está afectada por el rango del pichón en la nidada. El comportamiento de solicitar tuvo un efecto mixto sobre T_s, aumentándola levemente al principio, pero disminuyéndola cuando los polluelos hambrientos solicitaron con mayor vigorosidad. Este efecto mixto puede deberse a que la producción de calor es rápidamente contrarestada por una pérdida de calor a través de la piel dada por la postura de solicitar y el movimiento, sugiriendo que no es posible inferir el costo energético de solicitar a partir de técnicas de imagen térmica. El análisis de T_s en relación al rango de los pichones en la nidada mostró que a pesar de que los pichones de bajo rango mantuvieron T_s más bajas que sus hermanos de mayor tamaño, la T_s de los pichones más pequeños fue más alta de lo esperado de acuerdo a su tamaño corporal. Esto sugiere que los pichones de menor rango pueden ganar calor de sus compañeros de nido más desarrollados y de mayor tamaño.

The survival of altricial nestlings is affected not only by the amount of food they receive from their parents, but also by their energy expenditure, heat loss, and thermoregulatory ability (Morton and Carey 1971, Dunn 1975, Ricklefs 1979, Olson 1992). These factors may be studied using newly developed infrared imaging techniques, which allow measurement of small changes in the nestlings' surface temperature (T_s) without disturbing their behavior. In this study we used infrared imaging to study the effect of begging behavior and nestling rank on body temperature.

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Begging behavior of young nestlings is considered to be costly in terms of both energy expenditure and the risk of attracting predators to the nest (Harper 1986, Kilner and Johnstone 1997, Briskie et al. 1999). The assumption that begging is costly is fundamentally important for recent models of parent-offspring communication (Godfray 1991, 1995). Although there is still a theoretical debate regarding how high the cost of begging needs to be in order to maintain honesty (Bergstrom and Lachmann 1997, Johnstone 1999), theoretical models implicitly assume that the cost of begging should be borne by the individual, rather than shared equally by the entire brood (Godfray 1995). Accordingly, begging honesty is more likely to be maintained by the energetic cost of begging, for which the signaler alone pays, rather than by the cost of increasing predation risk, which is shared by the entire brood (Rodriguez-Girones et al. 2001). Previous measurements of the metabolic cost of begging have shown that begging increases nestling metabolic rates by 5–28% over their resting metabolic rate (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998). It is unclear, however, whether this increase is biologically meaningful in terms of reducing nestling growth and survival and maintaining begging honesty (Verhulst and Wiersma 1993, McCarty 1996, Bachman and Chappell 1998). Recent research with hand-raised nestlings that were stimulated to beg at different intensities, while being fed at the same rate, has shown that begging may reduce nestling growth rate in some cases, but not in others (Kedar et al. 2000, Rodriguez-Girones et al. 2001).

We used infrared thermal imaging in an attempt to detect small variations in the cost of begging in young House Sparrow (*Passer domesticus*) nestlings. We postulated that although the cost of begging may be low, it might be more pronounced under some circumstances, or during short periods. Since heat is produced by metabolic processes and is an inevitable byproduct of biochemical reactions (Bartholomew 1982), thermal imaging, which can measure small instantaneous differences in surface body temperature (T_s), may be a useful tool to study the cost of begging. Bearing in mind the limited thermoregulatory ability of hatchlings (Dunn 1976), and their high ratio of bare-skin surface area to volume, we expected that it might be possible to see a change in T_s during or immediately following begging. Previous studies have shown that begging intensity may vary with the level of a nestling's hunger, rank in the brood, and age (reviewed by Kilner and Johnstone 1997). To test how T_s varies with these factors during begging, we studied thermal images before, during, and after begging, at different levels of hunger, and at different ages in pairs of nestling House Sparrows that differed in rank.

The second aspect of this study dealt with the effect of nestling rank on T_s. Despite many studies on the development of thermoregulation in altricial nestlings (e.g., Dunn 1976, 1979, Olson 1992, Visser and Ricklefs 1993, Pearson 1998), little attention has been paid to the effect of nestling rank within the brood on body temperature and thermoregulatory behavior. While heat production and body core temperature are known to increase with age and mass (O'Connor 1975a), it is not clear how the proximity of larger and warmer brood mates affects the body temperature of younger siblings relative to that expected for their mass and developmental stage. We hypothesized that nestlings of a lower rank benefit from being heated by their larger, more developed nestmates.

METHODS

During spring 1998 we studied House Sparrow nestlings taken from captive and wild breeding colonies located on the campus of Tel-Aviv University, Israel. The nestlings were tested at ages of 2, 4, and 6 days. At 2 days of age, nestlings were completely naked, their eyes were closed, and they were presumably incapable of thermoregulation (Morton and Carey 1971, O'Connor 1975a). At 4 days of age, an initial limited thermoregulatory ability may develop, and at 6 days the nestlings' eyes are open, their wing feathers have begun to emerge, and they usually possess some thermoregulatory ability (Morton and Carey 1971, O'Connor 1975a). The experiments were conducted in a controlled temperature room (34 ± 1°C), within the thermoneutral zone of these birds (O'Connor 1975b). For each experimental session we took the largest (rank 1) and the third-largest (rank 3) nestlings of the same brood (mean ± SD brood size in the study population was 5.2 ± 0.9). We placed the nestlings together in an artificial nest made of synthetic foam, which allowed us to measure their T_s under seminatural conditions. Nestlings were weighed to the nearest 0.1 g (Ohaus C 305-S electronic balance, Pine Brook, New Jersey) and were individually marked by painting their wings with small dots of nontoxic acrylic paint. The same nestlings were tested again at the ages of 4 and 6 days, provided that both pair mates were still available for the experiment. This procedure caused a reduction in sample size with age. The process of bringing the nestlings from their nest to the temperature chamber and taking measurements took 10–15 min.

After 10 min of habituation to the conditions in the temperature chamber, nestlings were fed to satiation (with baby food containing meat and vegetables), and then deprived of food for 135 min. To test the effect of begging behavior on T_s, we stimulated the nestlings to beg by momentarily turning off the light and producing a soft sound, which mimicked a parental visit at the nest. We produced sound that stimulated nestlings to beg continuously for 1 min. To test the relationship between begging intensity and body surface temperature we did begging trials at three levels of hunger defined by time since last feeding (45, 90, and 135 min). Previous work in our laboratory has shown that begging intensity (body posture, sound volume, and the noise component of sound) increases in proportion to these intervals (Delman 1998). A few minutes after the third begging trial, the nestlings were fed, weighed again, and returned to their nests. The experimental procedure did not cause any apparent damage or stress to the nestlings and was carried out under a permit from the animal care committee of Tel-Aviv University.

We monitored nestling T_s throughout the experiment using an infrared thermal camera (Inframetrics model 760, North Billerica, Massachusetts) connected to a

VCR (Sony SLV-X730), and positioned 1 m above the nestlings. To detect changes in T_s as a result of begging we analyzed thermal images sampled (a) 1 min before each begging trial, (b) halfway through each begging trial (i.e., 30 sec after trial initiation), (c) at the end of each begging trial, and (d) 1 min after each begging trial. Considering the small body mass of sparrow nestlings of this age (4–16 g), changes in core temperature should be reflected at the surface very rapidly and it is unlikely that a change generated during begging could reach the nestlings' skin only after our last sampling (2 min after begging initiation). We confirmed that no such late effect occurred by observing the continuous video recording taken by the infrared camera throughout the experiment. To obtain a baseline measurement we also analyzed two thermal images taken at the beginning of each experiment, 1 min before and 1 min after the nestlings were fed to satiation. All thermal images sampled from the video were converted to digital images (using Adobe Premier® software) and stored for subsequent analysis. Using Adobe Photoshop® software, we extracted a circle from each image that included most of the back surface of the nestling, and that was approximately perpendicular to the photographing angle. We matched the circle's color with a prepared scale of color images based on photographs of a flat surface of known temperature. All thermal images were taken with the camera adjusted for a total span of 5°C divided into 20 shades (i.e., a resolution of about 0.25°C). However, because each circle was composed of a mosaic of pixels of two or three adjacent shades (in different proportions), matching its average appearance with those of the prepared scale allowed detection of relative differences of 0.1°C. A larger error in absolute accuracy is expected due to the lack of a precise value for the spectral emissivity of nestling skin (Floyd and Sabins 1987). It is important to note, however, that considering the short intervals between images taken before, during, and after begging trials, errors in absolute accuracy would be unlikely to obscure an increase in temperature following begging. There was also significant positive correlation between our measurements of T_s and conventional measurements of cloacal temperature (Ovadia 2001: $r = 0.99$, $n = 20$, $P < 0.001$, $y = 0.8(x) + 3.9$, cloacal temperature was constantly higher by about 0.6°C; see also Thomas et al. 1993 for similar results).

STATISTICAL ANALYSES

We used a repeated measures ANOVA (SPSS Inc. 2002) to analyze changes in T_s in relation to three main effects and the interactions among them. The three main effects were (a) *begging*: differences within a begging trial (before, halfway through, at the end, and 1 min after begging), (b) *hunger*: differences among begging trials conducted 45, 90, and 135 min since last feeding, and (c) *rank*: differences within each pair of nestlings (rank 1 versus 3). The two initial baseline measurements (before and after feeding) were not included in the statistical model. We repeated the analysis for each age group separately. The small sample size for age 4 and 6 days (5 and 4 pairs respectively) resulted in low statistical power, but provided qualitatively similar results to those obtained with 2-day-old nestlings (10 pairs). To further analyze the effect of nestling rank on T_s while controlling for body size, we used the residuals from the regression relating T_s to mass. For this analysis, for each individual, we used its average T_s of the first (before begging) measurements taken in each of the three begging trials to represent T_s.

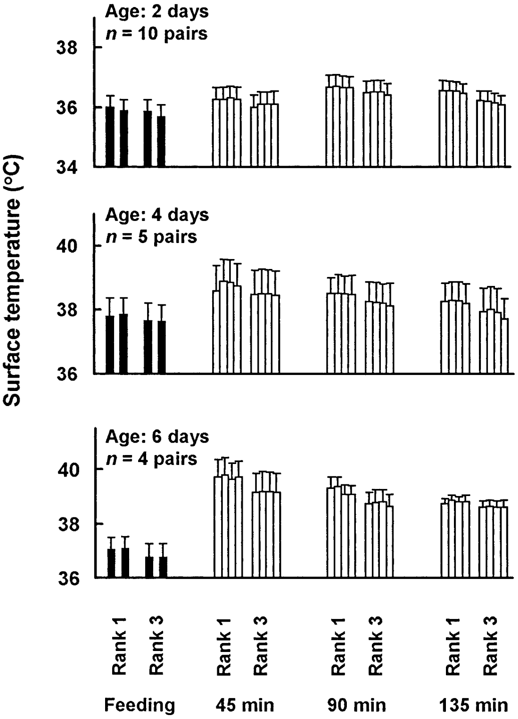

FIGURE 1. Surface temperature (mean $T_s \pm$ SE) of large (rank 1) and small (rank 3) House Sparrow nestmates immediately before and after feeding in the laboratory (black bars), and during begging trials conducted 45, 90, and 135 min after feeding (white bars, left to right: 1 min before begging, halfway through begging, end of begging, and 1 min after begging).

RESULTS

Two-day-old nestlings showed significant effects of rank and begging ($F_{1,9} = 14.3$, $P < 0.01$; $F_{3,27} = 3.8$, $P = 0.02$, respectively), a highly significant interaction between hunger level and the effect of begging ($F_{6,54} = 5.6$, $P < 0.001$), and a significant interaction between rank, hunger, and begging ($F_{6,54} = 2.4$, $P < 0.05$; Fig. 1). The highly significant interaction between hunger level and the effect of begging on T_s is indicated in Figure 1 by the slight increase in T_s during the first begging trial (45 min) as opposed to the decrease in T_s during the third begging trial (135 min). Although the increase in T_s during the first begging trial was small (maximum mean difference of 0.1°C), applying the model again with only the first begging trial data indicated that this slight increase was nevertheless significant ($F_{3,27} = 5.6$, $P = 0.01$). Analysis of data for 4- and 6-day-old nestlings was based on a

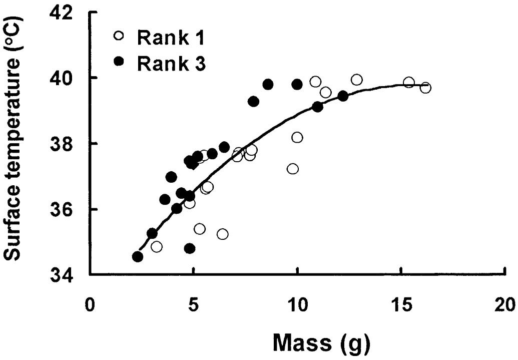

FIGURE 2. Surface temperature of large (rank 1) and small (rank 3) House Sparrow nestmates in relation to body mass (regression equation: $y = -0.028x^2 + 0.89x + 32.78$; $r^2 = 0.74$, $P < 0.001$). A nestling's T_s is the average of the first (before-begging) measurements taken in each of the three begging trials.

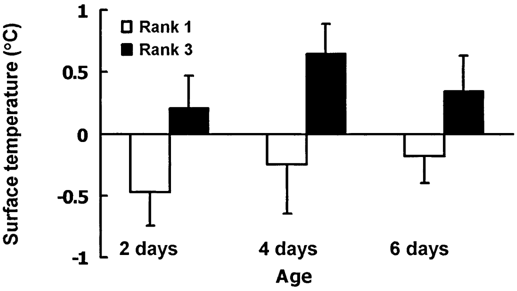

FIGURE 3. The residuals of T_s (°C ± SE) taken from the regression of T_s on body mass (see Fig. 2) of large (rank 1) and small (rank 3) House Sparrow nestmates. Paired t-tests: age 2 days: $n = 10$, $t = 4.4$, $P < 0.01$; 4 days: $n = 5$, $t = 4.9$, $P < 0.01$; 6 days: $n = 4$, $t = 1.5$, $P > 0.1$.

smaller sample size but still showed a significant effect of rank in both cases ($F_{1,4} = 10.5$, $P < 0.05$; $F_{1,3} = 15.2$, $P < 0.05$). The effect of begging was not significant ($F_{3,12} = 1.8$, $P > 0.2$; $F_{3,9} = 3.06$, $P = 0.08$, for days 4 and 6 respectively), but Figure 1 hints at the possibility of a similar mixed effect of begging.

The fact that low-ranked nestlings had lower T_s than their larger siblings was expected considering that nestling body temperature increases with body mass and with age (O'Connor 1975a). However, after controlling for body size, using the residuals from the regression relating T_s to mass (Fig. 2), the T_s of low-ranked nestlings was almost always (18 of 19 cases) higher than in their larger sibs (Fig. 3).

DISCUSSION

THE EFFECT OF BEGGING ON SURFACE TEMPERATURE

T_s of the nestlings increased during the first 45 min of the experiment, especially at 4 and 6 days of age. However, this increase cannot be attributed to begging activity because it was already apparent 1 min before the start of the first begging trial. Spontaneous begging was rare during the first 45 min of the experiment. The lack of increase in T_s in later trials, when spontaneous begging was occasional, indicates that spontaneous begging probably did not increase T_s. A possible explanation for the increase in T_s during the first 45 min may be that heat production resulted from the heat increment of postfeeding digestion (Musharaf and Latshaw 1999). Alternatively, the nestlings' rate of heat production was relatively high at the beginning of the experiment, which resulted in an increase in body temperature in the warm environment of the temperature-controlled room (34°C). Over time, a nestling may reduce its rate of heat production either as a delayed response to the warm environment, or perhaps as a method of saving energy after fasting (e.g., Macleod et al. 1993, Merkt and Taylor 1994, Choshniak et al. 1995).

The effect of begging on T_s was tested by analyzing differences in T_s within each begging trial. The results of this analysis indicated that T_s increased during the first begging trial but decreased in the third begging trial, when nestlings were hungrier. The mixed effect of begging on T_s may be explained by an increase in both heat production and heat loss through begging that leads to different outcomes under different levels of hunger. Hungry nestlings beg more intensely and are also likely to move more, to open their gape more frequently, and to stand erect (reviewed by Kilner and Johnstone 1997). Previous work in our laboratory has shown similar results for House Sparrow nestlings (Delman 1998, Kedar et al. 2000). Thus, when hungry nestlings increase their begging effort, they not only produce more heat but also increase evaporative heat loss from the wet surfaces of their buccal cavity, and increase convective loss through the skin as a result of movement and exposed posture. Although begging intensity was not measured during the present experiment, the increase in begging activity with hunger was clearly evident. It is possible, therefore, that during the first begging trial, when begging activity was moderate, the magnitude of heat production was still greater than the magnitude of heat loss. However, when begging became more intense during the second and third begging trials, the amount of heat loss due to body movements and exposed posture outweighed the amount of heat produced, resulting in the mixed effect of begging illustrated by Figure 1.

The mixed effect of begging on T_s suggests that using thermal imaging to study the energetic cost of begging may not be feasible. Although surface body temperature is affected by heat production, it is very probably also sensitive to body movement and posture. The delicate balance between heat production and heat loss that determines T_s may be difficult to predict. The increase in the T_s of 2-day-old nestlings during the first begging trial is consistent with other recent evidence that begging has some energetic cost (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998, Soler et al. 1999). However, like previous studies, our data cannot resolve the controversy over how high or low the cost of begging is in terms of fitness, and how likely it is that its cumulative effect can stabilize begging honesty (Verhulst and Wiersma 1997, Johnstone 1999, Rodriguez-Girones et al. 2001).

NESTLING RANK AND SURFACE TEMPERATURE

Low-ranked nestlings had lower T_s than their larger siblings. This result was expected, considering that nestling body temperature increases with body mass and with age (O'Connor 1975a). The increase in T_s with mass is a combined result of physical (i.e., surface to volume ratio) and biological factors (age and developmental stage in relation to the onset of homeothermy). However, after controlling for body mass, using the residuals from the regression relating T_s to mass, the T_s of low-ranked nestlings was nearly always higher than in their larger siblings. Hence, while large nestlings had higher T_s than their smaller nestmates, the smaller nestlings had higher T_s than expected for their body mass. This suggests that lower-ranking nestlings can be warmed by their larger, more developed nestmates.

It has been shown that nestlings can reduce their exposed surface area by up to 40% by huddling (Webb and King 1983), and that huddling can bring the brood to ''effective homeothermy'' earlier than the onset of ''physiological homeothermy'' in an individual (Dunn 1975). Our results illustrate that the advantage of huddling may be especially high for the younger brood mates. Due to their lower T_s, young brood mates can absorb heat from their larger siblings, and maintain body temperature that is higher than expected for their mass.

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