Young of several species of birds and mammals produce behavioral displays directed towards their parents during their growing period in order to obtain food or other resources. Several explanations have been proposed to explain these widespread begging behaviors. While early ethologists considered begging as a signal that simply communicates offspring need to the parents, Trivers (1974) suggested that the offspring use begging in an attempt to extract more resources than the parents are willing to provide (Smiseth and Lorensten, 2001). Later, Godfray (1991, 1995) suggested that parents respond to offspring solicitation behavior because it reflects the actual condition of their young (honest signaling), with progeny in greater need begging more strongly than those that are in good condition. The suggestion is that at equilibrium, begging serves to advertise some component of offspring condition which parents are otherwise unable to assess directly. To be honest, theo-
tical models of honest signaling predict that begging intensity reflects offspring need that parents provide resources in relation to offspring begging intensity, and that producing the signal entails some cost (Kilner and Johnstone, 1997).

Regarding the first condition, some works in birds give support for the relationship between offspring condition and begging intensity (Redondo and Castro, 1992; Price and Ydenberg, 1995). In mammals, Weary et al. (1997) showed that some features of piglets’ vocalizations vary with their need for resources.

Ctenomys talarum is a small herbivorous subterranean rodent that lives in a system of closed galleries parallel to the soil surface. Pups of C. talarum are born with little hair, closed eyes, and depend exclusively on their mother to obtain milk and maintain their body temperature. They start to open their eyes and eat grass between the second and third week of life. As they increase in size and grow hair, they also develop the physiological and behavioral mechanisms necessary to control body temperature.

During the nestling period, pups of C. talarum emit a very conspicuous call which elicited maternal care (Schleich and Busch, 2002). In a semi-natural enclosure (Zenuto et al., 2001) the pups emitted these care-eliciting cries during the first weeks after birth, when they were not capable of maintaining their body temperature and eating solid food. As pups kept growing, and concomitant with the development of their thermoregulatory capacity and independent walking and eating, there was a decrease in the number of care-elicitation cries emitted by the pups, suggesting that begging calls in C. talarum pups truly reflect offspring need (Schleich and Busch, 2002).

However, as explained before, to be considered as honest calls, variation in the emission of care-eliciting cries must reflect variation in the pup’s condition. Although the behavioral response of C. talarum’s pups during the nestling period give some support for this correlation (Schleich and Busch, 2002), the analysis was done using the whole litter, and no study was done to evaluate the individual pup vocal response to isolation at different ages or physical condition. Moreover, the previous study on vocalization of C. talarum pups (Schleich and Busch, 2002) was carried out at ambient temperature. It is known that cool temperatures are one important threat to the survival of juveniles of species with altricial development. For that reason, reduction in ambient temperatures could increase pups’ need and affect vocalization rate between pups in different physical condition, differences that could not be noticeable at thermoneutrality.

Therefore, the aim of this study was to study the vocal behavior of isolated pups at different ages and at different ambient temperatures, to provide additional information about the relationship between pups’ physical condition and vocalization intensity in order to understand the significance of the care-elicitation calls of C. talarum pups. I expected pups to decrease vocalization intensity at older ages, to vocalize more at low temperatures, and that pups in worst physical condition (lower body weight) vocalize more than pups in better condition.

Pregnant females of Ctenomys talarum were captured using plastic live traps in the sandy dunes of Mar de Cobo, Buenos Aires Province, Argentina. Captured individuals were carried to the laboratory and housed individually in plastic boxes. Wood shavings were provided as nesting material. Animal room temperature was maintained at 24 ± 1 °C, and photoperiod was light/dark 12:12. Relative ambient humidity ranged from 50% to 70%. Animals were fed with mixed grasses, carrots, lettuce, corn, and sunflower seeds ad libitum. Water was not provided since C. talarum does not drink free water.

After birth, vocalization rate of isolated pups was measured in 15 min trials at 2-3, 6-7, 10-11, and 15-16 days of pups’ age. For this, each pup (n = 9, five females and four males from three different litters of three pups each) was taken out from its nest and immediately isolated in a small chamber were the recordings were obtained. Pups were always in close contact with their mother before starting the
VOCAL BEHAVIOR OF *Ctenomys talarum*’s PUPS

experiments, reducing this way initial differences in body temperature or food supply due to differential exposition to maternal body heat and milk provision. Trials at thermoneutrality (25 °C) were done at days 2, 6, 10, and 15; while trials at cold temperatures (19° C) were conducted 3, 7, 11, and 16 days after pups were born. Body weight of pups from birth to 16 days old was obtained before recordings.

The duration of resting and vocalization periods (i.e. begging period) was obtained using a unidirectional microphone (Shure 16A, 50-15,000 Hz) localized 10 cm from the pups and recorded on chromodioxide tapes using a cassette-tape recorder (Marantz PMD 222, frequency sensitivity 40-14,000 Hz). The duration of each begging period was determined to the nearest 1 s. Silent and calling periods were obtained during the same trial.

In addition to the study of the individual response of the pups to isolation, I also analyzed if in each litter and for every day and temperature, the pup that presented lowest body weight was the one that spent more time vocalizing during the isolation period. To evaluate the development of homeothermy during the growing period, body temperature of pups was measured before and after each trial (to calculate Δ*Tb*) as pharyngeal temperature, with an YSI probe model 93k73545-402 connected to a thermistor Cole-Parmer Instrument Company model 8402-10. A two-way repeated-measures ANOVA was used to test the null hypothesis of no differences in time spent begging at different temperatures and ages, and to test the null hypothesis of no differences in Δ*Tb* (difference between body temperature before and after each measurement) of pups at different temperatures and ages. A Tukey’s test a posteriori was used to identify differences when results showed statistical differences (SigmaStat 3.0).

The time that the pups spent begging during isolation maintained constant during the first days after birth (until 10-11 d) and decreased at 15-16 days (*Fig. 1*; n = 9, df = 3, F = 4.24, 2-3 days vs. 15-16 days p = 0.031, 6-7 days vs. 15-16 days p = 0.02, two-way RM ANOVA, Tukey test). However, no statistical differences in the time spent begging were observed between pups at ambient or cold temperatures (*Fig. 1*; n = 9, df = 1, F = 0.002, p>0.05, two-way RM ANOVA). In *Table 1*, it is shown for each litter how many times the pup with lowest body weight was the one that spent more time vocalizing. In twelve analyzed periods, at thermoneutrality the pup with lowest body weight of each litter vocalized only

![Fig. 1. Time spent (mean ± SE) by *Ctenomys talarum* pups begging during the isolation period (in seconds) at different ages and temperatures (● 25° C; ■ 19° C).](image)

**Table 1**

<table>
<thead>
<tr>
<th>Litter</th>
<th>Day 2</th>
<th>Day 3</th>
<th>Day 6</th>
<th>Day 7</th>
<th>Day 10</th>
<th>Day 11</th>
<th>Day 15</th>
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</table>
six times more than the others, while at low temperatures the number rose to nine times.

Single pups showed higher $\Delta T_b$ at early ages (2-3, 6-7 days old) than those observed at more advanced age (15-16 days old) (Fig. 2, n = 9, df = 3, F = 8.23, p = 0.002, two-way RM ANOVA). $\Delta T_b$ of pups at cold temperatures were higher than at thermoneutrality (Fig. 2, n = 9, df = 1, F = 66.33, p = 0.001, two-way RM ANOVA), although not statistically significant interaction with pups’ age was observed (Fig. 2, n = 9, df = 3, F = 1.3, p > 0.05, two-way RM ANOVA).

Under honest signaling models, to be considered as honest, begging calls must meet the predictions proposed by theoretical models. The first one states that the intensity of begging must reflect the individual’s true need, with begging intensity negatively correlated with offspring condition (Kilner and Johnstone, 1997). Previous works in birds gave support for this prediction. Redondo and Castro (1992) and Price and Ydenberg (1995) showed that magpie and yellowheaded blackbird nestlings beg harder when they are deprived of food and reduce their begging when fed. Price and Ydenberg (1995) also demonstrated that when hunger level was controlled, chicks in poor condition begged more than chicks in good condition. Leonard and Horn (1998), working with nestling tree swallows, also found that begging intensity increased in broods in which all of the nestlings had been food deprived. Regarding mammals, Weary and Fraser (1995) measured the vocalizations of isolated piglets and found that piglets that had missed nursing or were growing slowly relative to their birth weights vocalized more than litter-mates that had just been fed or were growing relatively well.

Since during the first two weeks of life it is not possible to isolate altricial pups of *C. talarum* for long periods, I could not analyze the vocal response of fed or food deprived pups of this species of subterranean rodents. Instead, I measured the vocal behavior of pups with similar access to food but that differed in their body weight, a common indicator of physical condition. The results of this work show that, congruently with the observations obtained in semi-natural conditions (Schleich and Busch, 2002), the time that the pups spent begging during isolation decreased at the end of the second week of life, concomitantly with the development of independent walking and eating, and with the development of the thermoregulatory capacity. However, unexpectedly, no differences in the time spent vocalizing between pups of *C. talarum* under ambient or cold temperatures were observed. Cold temperatures usually increase the vocalization rate of young birds and mammals. For example, Evans (1994) showed that young white pelicans increased calling as their body temperature fell, suggesting that this vocalizations may represent honest signals of need. In mammals, piglets isolated in a cold enclosure called more than litter-mates isolated at thermoneutrality (Weary et al., 1997), while some species of rodents vocalize more when isolated at cool air temperatures (Blumberg and Alberts, 1990). The lack of effect of cold temperatures on the vocalization intensity of *C. talarum* pups is against the supposed honest condition of their begging calls, since a reduction in ambient temperature, which would lead to an increase in the pup’s need, did not increase the emission of care-elicitation vocalizations. However, if we analyze the vocal behavior of each pup in each litter at both temperatures, the response pattern is rather different, since at low temperatures the number of times that the pup with lowest body weight vocalized more increased with respect to thermoneutrality. During isolation periods (when the mother left the

![Fig. 2. $\Delta T_b$ (Tb°C initial - Tb°C final; mean ± SE) of pups of *Ctenomys talarum* at different ages and temperatures (●25°C; ■19°C).](image)
nest area or when one of the pups strayed away from the nest area), pups in worst condition (lower body weight) would suffer more the physiological consequences of the isolation (decrease of body temperature, higher at low temperatures), causing an increase in the emission of care-elicitation calls. Therefore, it seems that begging intensity in *C. talarum* pups may reflect physical condition, a factor connected with long-term need.

However, although the number of times that the pup with lowest body weight vocalized more was higher than the one expected by chance and even increased at low temperatures, occasionally this pattern was not observed and the pups in better condition vocalized more. This suggests the possibility that other factors, besides physical condition, may also influence the vocal behavior of pups of *C. talarum*. It has been shown that changes in the social and physical environments are stressful factors that can also affect the begging behavior and weaning of young animals (Weary et al., 2007). Both maternal and littermate separation, together with taking out the pups from the nest and move them to a strange environment, could have also affected the vocal behavior of *C. talarum*’s pups. Certainly, more studies, increasing the number of litters analyzed and investigating the maternal response to their offspring calls are needed to fully elucidate the role of begging in *C. talarum*. Until now, the results obtained in the successive works about the begging behavior of this species of subterranean rodent are contradictory, since while some studies provide some evidence supporting the honest condition of these signals (Schleich and Busch, 2002; this study), others present data against this possibility (no significant energetic costs associated with the emission of begging calls; Schleich and Busch, 2004), showing the complexity of the parent-offspring relationship in this rodent and the difficulty of extrapolating predictions of models generally developed for birds to other groups of animals.

**LITERATURE CITED**


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