A trade-off between predation risk and sibling competition in the begging behavior of Coal and Great Tits

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ABSTRACT. Sibling competition selects nestlings to beg as quickly as possible when a stimulus in the nest entrance is presented. However, predation risk may select for nestlings to properly assess stimuli before begging, because nestlings that beg to erroneous stimuli may signal their position to a predator. The begging behavior of Coal Tit (*Parus ater*) and Great Tit (*Parus major*) nestlings to an artificial stimulus imitating a predator was examined. Sightless nestlings begged to the stimulus, but older nestlings did not. Developmental improvement of the sentient capacity, especially the acquisition of vision, might explain results of this study.

SINOPSIS. **Compromiso ante el riesgo de ser depredado y la competencia entre hermanos en la conducta de pedir comida de individuos de *Parus ater* y *P. major***

La competencia entre hermanos es una fuerza selectiva que favorece a los polluelos que pidan alimento tan rápido como puedan, cuando un estímulo aparece en la entrada del nido. Sin embargo, el riesgo de ser depredado, es una fuerza selectiva que favorece que los polluelos valoren adecuadamente el estímulo de pedir alimento, ya que los que pidan comida ante un estímulo erróneo pueden mostrar su posición a un depredador. En este trabajo se examina la conducta de pedir comida por parte de polluelos de *Parus ater* y *Parus major*, ante un estímulo artificial imitando a un depredador (en este caso el propio investigador). Los polluelos que todavía no habían abierto los ojos solicitaron alimento ante el estímulo artificial, pero no así los polluelos mayores. La adquisición de mejores habilidades sensitivas a lo largo del desarrollo de los polluelos, especialmente de la vista, podría explicar los resultados de este estudio.

Key words: begging behavior, *Parus ater*, *Parus major*, predation risk, sibling competition

Avian chicks beg for food from their parents using calls and postural movements, and parents determine the quantity of food they deliver by the begging behavior of the brood (Stamps et al. 1989; Redondo and Castro 1992; Kilner et al. 1999). Interbrood parent–offspring conflict theory predicts that nestlings must solicit more food than parents are selected to deliver to them (Trivers 1974; Mock and Parker 1997). This is because the genetic relatedness of each nestling with itself is 1, while the relatedness with its parents and siblings is 0.5 or less (Hamilton 1964a,b). As a consequence, nestlings should increase their level of begging to stimulate parents to deliver more food (Mock and Parker 1997). Nevertheless, begging calls may attract predators to the nest, and thus they may be costly for begging chicks (Haskell 1994; Leech and Leonard 1997; Dearborn 1999). Predation thus is a selective force that may mold the evolution of begging calls by nestlings

(Redondo and Arias-de-Reyna 1988; Briskie et al. 1999; Haskell 1999, 2002; Roulin 2001b).

According to intrabrood parent–offspring conflict theory, each chick should beg for a higher share of the food delivered to the entire brood than parents are selected to deliver to it (MacNair and Parker 1979; Mock and Parker 1997). This conflict promotes a strong competition among nestmates. When a parent arrives at the nest with food, the first nestling that begs usually has a greater chance of receiving the food (Leonard and Horn 1996; Hofstetter and Ritchison 1998; Whittingham et al. 2003). Due to nest-mate competition, the parental preference for the first nestling to beg is a selective force favoring nestlings that are alert for the arrival of parents and that beg for food as quickly as possible (Roulin 2001a).

In hole-nesting birds, such as parids (Harrison 1991), predators search holes for possible nests. In a dark nest, defensive behavior by nestlings may be to remain quiet on the nest floor to escape the notice of the predator. However, if nestlings beg as quickly as possible, they

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may confuse predators with an approaching parent and beg for food when the predator peers inside the hole. Some studies have shown that chicks often respond to stimuli other than parents (Clemmons 1995; Budden and Wright 2001; Leonard and Horn 2001), including to potential predators (Leonard et al. 2005). In these cases, begging nestlings may be depredated, while quiet nestlings are not. Nestlings in dark nests have conspicuous flanges (Kilner and Davies 1998; Kilner 1999), and this, together with their calls, makes begging nestlings easily detectable by predators. Moreover, it is possible that many predators, such as martens (*Martes* ssp.) or genets (*Genetta genetta*), reach the nestlings more easily when nestlings stretch their bodies to beg.

We might expect that the response of nestlings to stimuli should reflect a tradeoff between the level of sibling competition and the risk of predation. One prediction of this hypothesis is that sightless younger nestlings should beg to inappropriate stimuli provoked by potential predators more often than older nestlings. This would be because, due to their poor sensory development (Bengtsson and Rydén 1981; Choi and Bakken 1990), sightless nestlings have more difficulty in determining whether a stimulus is caused by a parent or a predator, and some studies have shown that younger nestlings beg in response to erroneous stimuli more frequently than do older nestlings (Clemmons 1995; Budden and Wright 2001). Second, older nestlings, which are larger, are more easily caught by predators, and they should therefore be more careful in the presence of a predator.

The objective of my study was to test the begging responses of two species of parids, the Coal Tit (*Parus ater*) and the Great Tit (*P. major*), to a simulated predator. I performed a simple experiment in which I imitated a foraging predator. I assumed that nestlings viewed me as a predator because parids react to humans as they do to real predators (for example, they frequently attack researchers studying nests; G. Moreno-Rueda, pers. obs.).

METHODS

This study was done during the breeding seasons of 2003 and 2004 in the Botanical Garden of La Cortijuela (37°05′N, 3°29′W), situated at 1800 m in the National Park of Sierra Nevada, southeastern Spain. The study area was a mixed woodland of pine (*Pinus* spp.) and oak (*Quercus* spp.), separated by pastureland and shrubbery. Various species of parids nest in this area (Moreno-Rueda 2002–2003). About 3–5% of nest boxes have predation each year. Predators in the study area are various carnivores, Green Woodpeckers (*Picus viridis*), and the ant *Camponotus cruentatus* (Moreno-Rueda 2004; G. Moreno-Rueda, unpubl. data).

Parids are insectivorous hole-nesting birds (Cramp 1998). The typical clutch size in my study area is 5–6 eggs for the Coal Tit and 4–6 eggs for the Great Tit (G. Moreno-Rueda, unpubl. data). Brood size in nests used in this study was 5.39 (SD = 0.81, range = 4–8) chicks for the Coal Tit ($N = 44$ nests) and 5.27 (0.96, 4–6 chicks) for the Great Tit ($N = 15$ nests). When clutches were near to hatching, I checked the nest each day until hatching occurred. Thus, I knew the exact age of nestlings when the experiment was performed. Fledging age is about 16–19 d for the Coal Tit and 16–22 d for the Great Tit (Harrison 1991). In this study, I used only broods 0–15 d old (day 0 being the day when the first nestling hatched). To analyze differences in the response to the treatment with age, I grouped broods into eight age ranks: 0–1, 2–3, 4–5, 6–7, 8–9, 10–11, 12–13, and 14–15 d old (Fig. 1). Nestlings open their eyes at about 7–8 d for the Coal Tit and at about 8–9 d for the Great Tit (Harrison 1991). For this reason, I considered as younger (sightless) nestlings those of the first four age categories (0–7 d old) and older nestlings as those 8–15 d old.

Nests were checked between 1–3 h after sunrise. Nests in which parents were present when I checked the nest box were excluded from analyses. With a pole, I silently lowered each nest box from its location in the tree. Then, upon opening the front of the nest box, I recorded whether or not any chick begged. I considered a nestling to beg when it gaped and/or called. I did not consider any nest when nestlings begged before I opened the nest box. If I detected alarm calls by adults, I excluded that nest from analysis. Each brood counted only once in the analyses. Although hunger may affect the response to erroneous stimuli (Leonard et al. 2005), I did not control for hunger, and I assumed that hunger did not vary with age.
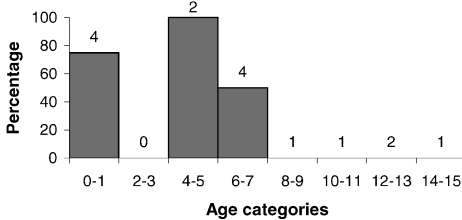
A)
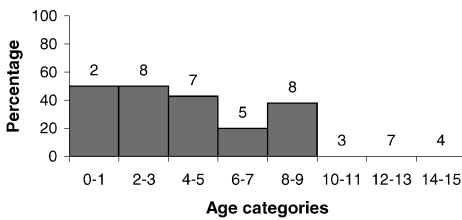
B)

Fig. 1: Percentage of nests treated in which at least one nestling begged for food when the nest-box was opened, according to the age of the brood (in days). On bars the sample size (number of nests treated). A) coal tits, B) great tits.

Data are presented as percentages or frequencies of broods where at least one nestling begged in response to the experimental stimulus. To examine the relationship between the response and age, I used Spearman rank correlations, chi-square tests, and logistic regression (Siegel and Castellan 1988). All tests were two-tailed.

RESULTS

In 12 of 44 nests of Coal Tits (27.3 %), some nestlings begged when I opened the nest box. This frequency varied with nestling age, with a negative correlation between age and the percentage of nests where at least one nestling begged ($r_s = -0.41$, $P < 0.01$; Fig. 1A). Only in three of 22 nests with older nestlings did any nestling beg when the experiment was performed, while in nine of 22 nests with sightless nestlings at least one chick begged ($\chi^2_1 = 4.13$, $P < 0.05$). The probability that at least one chick would beg when the experiment was performed varied with age (logistic regression, $\chi^2_1 = 8.39$, $P < 0.01$). The inclusion of brood size did not significantly change the model ($\chi^2_2 =$

9.92, $P < 0.01$, difference = 1.53, $P = 0.22$). Brood size when nestlings were blind was not significantly correlated with the frequency of nests in which at least one chick begged ($r_s = 0.22$, $P = 0.32$, $N = 22$).

A similar pattern was found for Great Tits ($r_s = -0.65$, $P < 0.01$; Fig. 1B). In this species, in no nest with older nestlings did any chick beg (0 of 5), while in 7 of 10 nests with sightless nestlings at least one chick begged ($\chi^2_1 = 6.56$, $P = 0.01$). The logistic regression model revealed that the probability that at least one chick begged was determined by the age of the brood ($\chi^2_1 = 6.90$, $P < 0.01$). Older nestlings that did not beg for food when stimulated usually remained immobile on the floor of the nest watching me, while younger nestlings that did not beg appeared to be sleeping in the nest.

DISCUSSION

My results suggest differences in anti-predator behavior with age in the Coal Tit and the Great Tit. Young, sightless nestlings begged food from extraneous individuals arriving at the nest entrance, revealing their position to a possible predator. However, older nestlings appeared to distinguish whether an individual arriving at the nest entrance was a parent or a possible predator, and responded to a possible predator by staying near the bottom of the nest. These behavioral differences with age are presumably related to the development of the perceptual senses of nestlings. Other studies have shown that nestlings diminish their begging response to stimuli other than parents as they grow older (Clemmons 1995; Budden and Wright 2001).

When nestlings receive a stimulus, they must identify it and determine whether it is related to food if they are to beg as quickly as possible and thereby increase their likelihood of being fed. However, the process of assessing the stimulus requires time. As nestlings develop, they increase their sentient abilities (Bengtsson and Rydén 1981; Choi and Bakken 1990), and the time needed to assess the stimulus diminishes with age. My results (Fig. 1) suggest an abrupt change in the response of nestlings, coinciding with the opening of their eyes. Nestlings may use different strategies in sibling competition when they are sightless versus when they can see. Sightless nestlings could spend more time

assessing each stimulus, reducing the mistakes committed, but selection for shorter latency appears to favor speed of response. Older nestlings have adequate sentient ability, especially the vision, to make quick assessments of stimuli and more proper responses. This would explain results in this and other studies on begging to erroneous stimuli (Clemmons 1995; Budden and Wright 2001; Leonard and Horn 2001). Similarly, some studies have found that nestling responsiveness to parental alarm calls increases with age (Kleindorfer et al. 1996). However, Leonard et al. (2005) found that the responses of Tree Swallow (*Tachycineta bicolor*) nestlings to acoustic stimuli from a potential predator (in relation to those from parents) did not diminish with age. A possibility is that the response to acoustic stimuli changes little with age, while the response to visual stimuli changes more abruptly.

Thus a trade-off may exist in the begging behavior of parids, and the results of this study suggest that the resolution of this trade-off may vary with age. Both sibling competition and predation risk might affect the evolution of latency in this way. The nestling that begs more quickly is more likely to be fed (Leonard and Horn 1996; Hofstetter and Ritchison 1998; Whittingham et al. 2003). However, a nestling making a mistake may show its position to a predator. Because partial nest predation occurs in birds (Halupka 1998), a prudent nest-mate would be favored by natural selection. That predation risk shapes the evolution of begging calls has been previously suggested (Redondo and Arias-de-Reyna 1988; Briskie et al. 1999; Haskell 1999, 2002). Predation risk might also determine the time spent by nestlings in assessing stimuli and, therefore, the latency of nestlings. Nestlings from species or populations with high predation risk should have longer latencies than do species or populations with low predation risk. Comparative studies are needed to explore this hypothesis.

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