ANIMAL BEHAVIOUR, 2007, 74, 1099–1106
doi:10.1016/j.anbehav.2007.01.027

Nestling barn owls beg more intensely in the presence of their mother than in the presence of their father

ALEXANDRE ROULIN* & LOUIS-FELIX BERSIER†
*Department of Ecology and Evolution, University of Lausanne
†Department of Biology, University of Fribourg

(Received 24 October 2006; initial acceptance 7 January 2007; final acceptance 10 January 2007; published online 4 September 2007; MS. number: 9157)

Nestling begging behaviour may be an honest signal of need used by parents to adjust optimally both feeding rate and within-brood food allocation. Although several studies showed that mothers and fathers can be differentially responsive to nestling begging behaviour with one parent showing a stronger tendency to feed the offspring that beg the most, little information is yet available on whether offspring beg for food at different intensities from the mother than father. In the present study, we investigated in nestling barn owls whether the intensity of vocal begging behaviour in the presence of the mother and in the presence of the father is different. A difference is expected because reproductive tasks are divided between the sexes with fathers bringing more food items to the nest than mothers. The results show that although mothers transfer their prey item to one of the offspring more rapidly than fathers once in their nestbox, nestlings begged more intensely in the presence of their mother than in the presence of their father. To our knowledge, this is the first empirical evidence that offspring vocalize to different levels in the presence of their mother than in the presence of their father.

Keywords: barn owl; begging; parent–offspring conflict; parental care; sexual conflict; sibling negotiation; *Tyto alba*

Theory proposes that family members are in conflict over parental investment with offspring requesting more resources than parents are willing to concede (Trivers 1974; Godfray 1995). Parents are reluctant to provide all the food requested by their offspring because this behaviour would jeopardize parental investment in future breeding attempts (Trivers 1974; Stamps et al. 1978; Parker & Macnair 1979; Parker 1985). Offspring solicit more resources than would be optimal to the parents because an increase in their condition as a result of extra parental investment would outweigh the loss of quality and/or quantity of future siblings in terms of inclusive fitness. For this reason, each nestling is selected to solicit a larger than equal share of the resources (Parker & Macnair 1979; Mock & Parker 1997) by vocalizing and jostling for the position where parents predictably bring food items (McRae et al. 1993; Mock & Parker 1997). Honest signalling models provide a resolution of these family conflicts by proposing that begging signals are costly to produce. In this way, only needy nestlings are willing to beg vigorously giving an opportunity to parents to reliably assess offspring need because misrepresentation of need is selected against (reviewed in Johnstone & Godfray 2002). Experimental studies demonstrated that mainly needy nestlings are willing to beg vigorously (e.g. Mondloch 1995), and that parents feed preferentially needy offspring (e.g. Leonard & Horn 2001) and increase feeding rate when offspring beg more conspicuously (e.g. Ottosson et al. 1997; Burford et al. 1998).

In several taxonomic groups of birds including raptors and owls, sex-roles in reproduction are well defined for instance with males providing most food items and females taking care of the offspring in the nest (Newton 1979; Mikkola 1983). In such a situation, females and males may not be similarly sensitive to offspring begging. At least in passerines, females often feed preferentially late-hatched and thereby needier offspring, and hence females may be more sensitive than males to begging in their decision to which offspring to feed first (Slagsvold

Correspondence: A. Roulin, Department of Ecology and Evolution, Biophore, University of Lausanne, 1024 Lausanne, Switzerland (email: alexandre.roulin@unil.ch). Louis-Félix Bersier is at the Department of Biology, Ecology and Evolution Unit, University of Fribourg, 1700 Fribourg, Switzerland.

0003–3472/07/$30.00/0

1997; Lessells 2002; unfortunately this aspect has not yet been investigated in raptors and owls). In contrast, because males provide most food items to their brood, they may assess the overall offspring begging level to adjust feeding rate, and hence males may be more sensitive than females to offspring begging. Alternatively, because males are already feeding their brood at a high rate, only females may be able to further increase feeding rate in case offspring beg more intensely (e.g. Tolonen & Korpimäki 1996). In this case, females would be more sensitive than males to offspring begging to adjust feeding rate. These examples show that it is difficult to propose a priori predictions regarding which of males and females are more sensitive to begging, and in turn whether offspring should beg more conspicuously towards their mother or father.

When the fitness benefits derived per unit of begging effort directed to the mother and father are not the same, nestlings may beg differentially from one of the two parents. For example, if mothers are more likely than fathers to feed the offspring that beg most intensely, offspring should beg more vigorously towards their mother than towards their father. A study in the great tit, *Parus major*, showed that experimentally food-deprived nestlings indeed compete more intensely for the within-nest location where the mother rather than the father usually feeds the nestlings (mother's and father's feeding locations are not the same; Kölliker et al. 1998). To our knowledge, this is the unique published study reporting that nestlings behave differently in the presence of their mother than in the presence of their father. However, to date there is still no empirical study testing whether offspring produce more begging vocalizations towards their mother or their father. This may frequently be the case because in several species mothers and fathers respond differentially to begging (Kölliker et al. 1998; Krebs 2001; Quillfeldt et al. 2004; but see Price 1998; Whittingham et al. 2003).

Here we investigated whether in the barn owl nestlings beg for food differentially from their mother than from their father. Before offspring are two-week-old, the male hunts most food items and transfers them to the mother who distributes them among the offspring; later the male provides about two-thirds of the prey items and delivers them himself to one of the offspring. Because father and mother can be easily recognized once at the nest (they differ in size and behaviour), we predict that nestlings beg differently in the presence of the mother than in the presence of the father (to which parent nestlings should beg at the highest level is difficult to predict). To examine whether this behaviour depends on offspring need, as shown in the great tit where nestlings compete more intensely to be fed by their mother than by their father only when food-deprived (Kölliker et al. 1998), we measured begging levels in experimentally food-deprived and food-satiated broods. To better understand why nestlings may beg more vigorously towards one of the two parents, we recorded the total amount of time spent by parents at the nest and the amount of time taken by mother and father to transfer a food item to one of the offspring once at the nest. A parent that takes less time may be less sensitive to begging in its decision to which offspring to feed first or, alternatively, it may be highly sensitive to begging and rapidly assess which chick to feed first. We also recorded nestling vocalization in the absence of parents (so-called sibling negotiation), a behaviour that is highly sensitive to food need with nestlings vocalizing more intensely when more hungry (Roulin et al. 2000). Therefore, vocalization behaviour in the absence of parents should indicate whether brood food need differs before the arrival of the mother and father.

METHODS

Study Organism

Although being nocturnal on the European continent, barn owl parents store food in their nest allowing offspring to spread consumption of meals over 24 h (Roulin 2004a). This bird is medium-sized with breeding males weighing on average 315 g and breeding females weighing 333 g (Baudvin 1986). This size dimorphism implies that males are less noisy than females when entering their nest cavity (in our study area owls land on a perch installed just beside nestboxes) potentially implying that offspring can recognize which parent is feeding them. Males frequently produce specific calls when they are very close to the nest, perhaps to indicate their identity. In the nest, females often produce another type of call apparently to induce sibling competition (personal observation). A barn owl brood contains between one and nine nestlings, and nestlings take their first flight around 55 days of age. Nestling age can be estimated by measuring the length of the flattened wing from the bird's wrist to the tip of the longest primary (Roulin 2004a). Before offspring are two weeks of age, the father gives food item to his partner who distributes them to the offspring, and afterwards the mother delivers one third of the prey items to the offspring and each parent gives itself its prey item to one of the offspring (Roulin 2002; Durant et al. 2004). Mothers and fathers deliver similar-sized prey items (Durant et al. 2004). Male and female nestlings vocalize in the absence and presence of parents to similar levels, and juniors vocalize in the absence and presence of parents to higher levels than their senior siblings mainly because they are more hungry rather than because they are smaller (Roulin 2004b). Based on the same experimental data set as the one used in the present paper, we have already shown that in the absence of parents nestlings vocalize more intensely when food-deprived compared with when food-satiated; in the presence of parents, nestling begging rate is not associated with offspring need (Roulin et al. 2000; Roulin 2001). In the presence of parents all nestlings vocalize (Bühler & Epple 1980; personal observation).

Begging in the Presence of Mother and in the Presence of Father

The study was performed in a population of barn owls located in western Switzerland, from June to August 1997.