

Barn owl (*Tyto alba*) siblings vocally negotiate resources

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Current theory proposes that nestlings beg to signal hunger level to parents honestly, or that siblings compete by escalating begging to attract the attention of parents. Although begging is assumed to be directed at parents, barn owl (*Tyto alba*) nestlings vocalize in the presence but also in the absence of the parents. Applying the theory of asymmetrical contests we experimentally tested three predictions of the novel hypothesis that in the absence of the parents siblings vocally settle contests over prey items to be delivered next by a parent. This 'sibling negotiation hypothesis' proposes that offspring use each others' begging vocalization as a source of information about their relative willingness to contest the next prey item delivered. In line with the hypothesis we found that (i) a nestling barn owl refrains from vocalization when a rival is more hungry, but (ii) escalates once the rival has been fed by a parent, and (iii) nestlings refrain from and escalate vocalization in experimentally enlarged and reduced broods, respectively. Thus, when parents are not at the nest a nestling vocally refrains when the value of the next delivered prey item will be higher for its nest-mates. These findings are the exact opposite of what current models predict for begging calls produced in the presence of the parents.

Keywords: asymmetrical contest; barn owl; begging; parent–offspring conflict; sibling competition; *Tyto alba*

1. INTRODUCTION

Models of parent–offspring interaction assume that begging is directed at parents, and is the outcome of scrambling competition among siblings for parental attention (MacNair & Parker 1979; Harper 1986; Rodríguez-Gironés *et al.* 1996), or of honest signalling of need towards parents (Godfray 1991, 1995). Basically these models predict that with an increasing level of sibling competition nestlings escalate begging level (Harper 1986; Godfray 1995; Rodríguez-Gironés *et al.* 1996). Parent–offspring conflict is therefore assumed to be expressed mainly when parents distribute food among offspring. However, as would be predicted by the theory of asymmetrical contests (Maynard Smith 1982), siblings may settle contests before parents arrive at the nest with a food item. Applied to the situation of two nestlings, this 'sibling negotiation hypothesis' predicts that the more hungry nestling will contest the next item delivered while the less hungry one will retreat to avoid injuries and/or save energy. Hungry nestlings may behave aggressively and vocalize intensely, and less hungry ones behave submissively and refrain from vocalization.

We tested three predictions of the sibling negotiation hypothesis in the barn owl (*Tyto alba*), where parents are absent from the nest for most of the night, and return on average every hour to bring a single small mammal, which is consumed by one of the two to nine offspring (Taylor 1994). Thus, in large broods some nestlings have to wait hours to be fed. It creates asymmetries in feeding state among siblings; that is the prey item delivered next is of higher value to unfed than to fed nestlings. Despite frequent absence of the parents, offspring vocalize inter-

mittently during the whole night (Bühler & Eppele 1980). The function of those vocalizations is as yet unknown. It is unlikely that vocalization behaviour of the nestlings incurs a predation cost since predation is extremely rare in European populations (two broods predated in a sample of 1031 broods; Taylor 1994).

(a) Predictions of the sibling negotiation hypothesis

In the following, we propose three predictions of the sibling negotiation hypothesis and explain how we experimentally tested them. These predictions are especially relevant for vocalizations made in the absence of the parents because those parents may not be able to hear and be influenced by the calls.

(i) Prediction: vocalization in the presence of a hungry rival

The first prediction posits that a nestling barn owl will refrain from vocalization in the presence of hungrier nest-mates. For a test, we created broods of two randomly chosen siblings by temporarily removing the other brood-mates. One of the two nestlings (thereafter the 'hungry target' nestling) was not provided with food during the daylight hours over two consecutive days, but fed normally by the parents at night. The other nestling was separated and offered dead mice during the daylight hours randomly on one of the days but not the other. At night, we recorded vocalization levels before the first arrival of a parent. Then, we repeated the treatment but alternated the roles of the two siblings.

(ii) Prediction: vocalization after a hungry rival consumed a prey

The second prediction argues that a nestling will increase vocalization level after a hungry nest-mate ate a prey. As for the first experiment, we created broods of two siblings, and provided a randomly chosen nestling with mice during the daylight hours, while its nest-mate was kept without food over the same time-period. We

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then recorded the vocalization of both nestlings at night, before arrival of a parent with the first prey item, and after the parent's departure and the consumption of the prey by the hungry nest-mate.

(iii) *Prediction: vocalization and number of competitors*

The third prediction proposes that nestlings will escalate vocalization in reduced broods but refrain in enlarged ones. These expectations are based on the assumption that a nestling will less often win an asymmetrical contest over a prey item in larger broods (Lotem 1998). For a test, we manipulated brood size for 3 h to alter the number of competitors but not their condition. At night, we recorded the vocalization behaviour of all nestlings before a parent delivered a first prey item.

(iv) *Alternative hypothesis*

Although the three predictions can support the sibling negotiation hypothesis, they may support the alternative hypothesis that parents adjust feeding rate to the amount of calls produced in a nest (e.g. Lotem 1998; Davies *et al.* 1998). For instance, in experimentally reduced broods the remaining nestlings may increase calling rate to compensate for the calls that the removed siblings usually assumed. This non-mutually exclusive hypothesis predicts that parents adjust feeding rate to the begging behaviour of the entire brood, and thus reduce provisioning rate when the amount of calls produced in the nest-box declines. For a test, we either food satiated or did not provide food items to all nestlings, and recorded parental feeding rates.

2. METHODS

(a) *Predictions: vocalization in the presence of a hungry rival and vocalization after a hungry rival consumed a prey*

In western Switzerland, between July and September 1997, we carried out the second experiment in 15 broods, and the first experiment in 12 broods (subsample of the previous 15 broods). The nestlings were 28–44 days old (young fledge at 55 days of age; A. Roulin, unpublished data) and no longer brooded by their mother, and their parents were not in the nest during the daylight hours. In each brood we randomly chose two siblings that differed in age by an average of seven days (range: 2–15 days). This mean age difference was not chosen for any particular reason. To impose an asymmetry in food value between the two siblings, we manipulated their hunger state. From 09.00 to 21.30 they were kept separately in a box with either three dead mice (food-satiated nestling) or without prey (hungry nestling). As in natural conditions, where parents store surplus prey items in the nest-box during the night, and nestlings consume some of them during the daylight hours (A. Roulin, unpublished data), the food-supplemented nestlings consumed on average 1.7 mice (34 g). A one-month-old nestling consumes on average 4.2 prey items per 24 h (Taylor 1994) and thus our manipulation should have strongly affected the hunger level of the provided nestlings.

From 21.30 to 23.30, we temporarily removed their siblings from the nest-box and placed back the two experimental siblings in their original nest. During the 2 h we recorded the vocalization activity of the two experimental siblings with an infrared-sensitive video camera and a microphone. Calls could unambiguously be assigned to one of the two siblings, since they were ringed on different legs and most calls were sequentially

produced and accompanied by opening of the beak. At night, 15 min before a parent brought the first prey item, we counted the number of calls produced during the first 14 min. In the second experiment, after the departure of the parent (range of time in the nest-box: 3–70 s) and after the hungry nestling ate the prey (mean time between arrival of the parent and the consumption of the prey = 7 min, range: 1–18 min), we counted the number of calls produced during the subsequent 14 min. For each of these two periods, five calls were randomly selected per individual and digitized at 22.05 kHz and 8 bits using the software Canary (Charif *et al.* 1995). From the acoustic waveform of these calls, we measured the contained energy flux density (J m^{-2}), and multiplied the mean energy flux density of the five calls by the number of calls produced by the nestling during the 14 min. This value was then divided by 14 and $(\log + 1)$ transformed for normality before statistical analyses. This last value is referred to as the 'vocalization index'. Given that paired comparisons within broods and individual nestlings were performed, no amplitude calibration among nest-boxes was required (Charif *et al.* 1995).

In the first experiment 12 two-chick broods were considered, and since every nestling was tested the sample size was 24. In the second experiment 15 two-chick broods were used and only one nestling per nest tested. Sample size was therefore 15. One can note that in nine out of the 15 two-chick broods the tested nestling was older than its nest-mate.

(b) *Prediction: vocalization and number of competitors*

The third experiment was carried out between May and July 1998. Seven pairs of nests of 29-day-old nestlings (range: 24–35 days) were randomly selected. The natural size of these broods ranged from three to eight nestlings. During the daylight hours parents were naturally absent from the nest. At 20.00 we reduced or enlarged brood size by half by transferring between one and four randomly chosen nestlings between two nests. For instance, after transferring two from a brood of four nestlings, the reduced has two nestlings and the enlarged six. A brood of eight nestlings was enlarged only by one nestling to stay within the natural range of brood sizes recorded in the study area from 1987 to 1998 (A. Roulin, unpublished data). In control-I broods we handled nestlings at 20.00 in a way similar to that in reduced broods but without altering brood size. The size of control-II broods remained unchanged, but at 20.00 between one and four nestlings were exchanged between the two nests (the exact number corresponds to the number of nestlings used to enlarge the brood). We exchanged nestlings other than those transferred from a reduced to an enlarged brood. This cross-fostering was done to control for potential effects on nestling vocalization behaviour of mixing nestlings of two origins and of transferring nestlings between nests, as was the case in the enlarged broods. At 23.00 all nestlings were placed back in their original nest. All 14 broods underwent each treatment, and the order of the manipulations was alternated. From the video, starting 15 min before a parent brought a first prey item, we counted the number of calls produced by all nestlings during the first 14 min. We divided this number by the manipulated brood size to calculate calls per nestling per minute before statistical analyses.

(c) *Alternative hypothesis*

The experiment was conducted between June and August 1997. We selected 26 broods containing 36-day-old nestlings (range: 18–49 days). At 09.00 we put in the nest-box twice as

many dead laboratory mice as the number of nestlings (treatment 'food satiated'). Each nestling ate on average 1.1 mice during the daylight hours, and the remaining mice were left in the nest-box. The next day we removed prey items left in the nest-box at 09.00 (treatment 'hungry'). We alternated the order of the two manipulations.

From 21.30 to 05.30 we recorded, with an infrared-sensitive camera fixed in the nest-box 24 h beforehand, the number of prey items brought to the nest by both parents. With a microphone we recorded the vocalization behaviour of the nestlings during the same time-period. In the absence of the parents the total number of calls produced during 30 s by all nestlings was counted every 15 min. We then calculated the mean number of calls per minute produced during the whole night. We recorded parental feedings and vocalization behaviour of the nestlings in the same way as explained above (see §2(a)). Thus, for every nest we could compare parental provisioning rate in relation to vocalization behaviour of the offspring when they were food satiated or hungry.

(d) Statistics

Throughout, statistics are two-tailed and the significance level is 0.05. All *t*-tests are paired. Means are followed by \pm s.e. Statistical analyses were performed with the SYSTAT statistical package (Wilkinson 1989).

3. RESULTS

(a) Test of the prediction: vocalization in the presence of a hungry rival

Nestlings vocalized more when hungry than when food satiated (mean vocalization index: 2.7 ± 0.2 versus 1.1 ± 0.3 ; $t_{23} = 6.2$, $p < 0.001$). When one of the two siblings was food satiated, the nestling that vocalized most intensely ate the prey delivered by a parent in 23 out of 24 cases (binomial test, $p < 0.001$), and in ten out of 12 cases ($p = 0.038$) when they were both kept without food during the daylight hours. In five out of these 12 cases the older nestling begged more intensely and ate the first item delivered by parents. This suggests that the age difference between two nest-mates had a weak influence on which nestling begged more intensely and got the first item of the night.

In the absence of the parents, stronger vocalization by one of the two nestlings therefore predicted that it will be fed first. A nestling may also potentially use the nest-mates' vocalization behaviour to assess whether it has a dominant or subdominant role in the contest over the next prey item delivered, and consequently vocally escalate or retreat. In support of the first prediction, the hungry target nestling vocalized more during the night when its nest-mate was food satiated than during the night when it was hungry ($t_{23} = 3.01$, $p = 0.006$; figure 1), thus escalated in vocalization level when the value of the next prey item declined for its nest-mate.

(b) Test of the prediction: vocalization after a hungry rival consumed a prey

The hungry nestling vocalized significantly more than its food-satiated nest-mate (3.3 ± 0.3 versus 1.7 ± 0.4 ; $t_{14} = 7.8$, $p < 0.001$), and decreased vocalization level by half after it ate the first prey item ($t_{14} = -4.6$, $p < 0.001$). In line with the second prediction, we found that the experimentally food-satiated nestling now increased vocalization

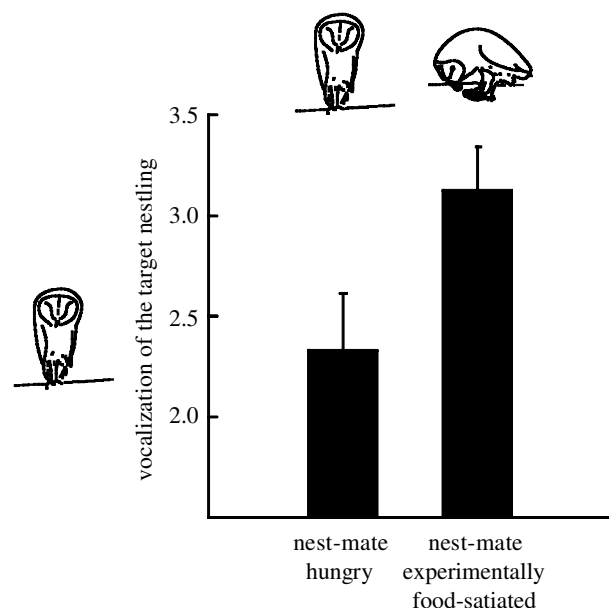


Figure 1. Vocalization index of a hungry target nestling at night before the first arrival of a parent. The vocalization level produced by the hungry target nestling (bird without prey on the left) on two subsequent nights when its nest-mate was either hungry or food satiated (bird without prey versus bird with prey on the top).

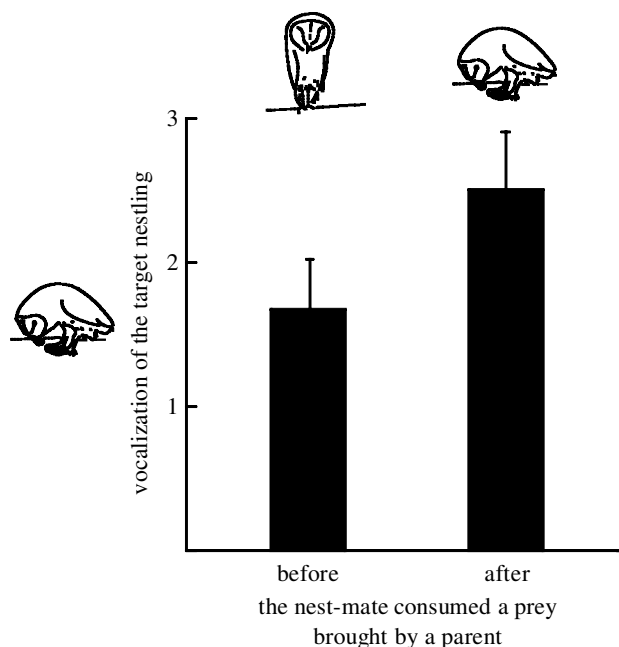


Figure 2. Vocalization index of a food-satiated target nestling (bird with prey on the left) at night before the first arrival of a parent with a prey, and after its hungry nest-mate ate this prey (bird without prey versus bird with prey on the top).

level significantly (repeated measures ANCOVA, $F_{1,13} = 6.3$, $p = 0.026$, controlling for the time-lapse between the two recordings, $F_{1,13} = 1.0$, $p = 0.34$; figure 2).

(c) Test of the prediction: vocalization and number of competitors

As expected the number of calls per nestling was higher when brood size was reduced compared with the

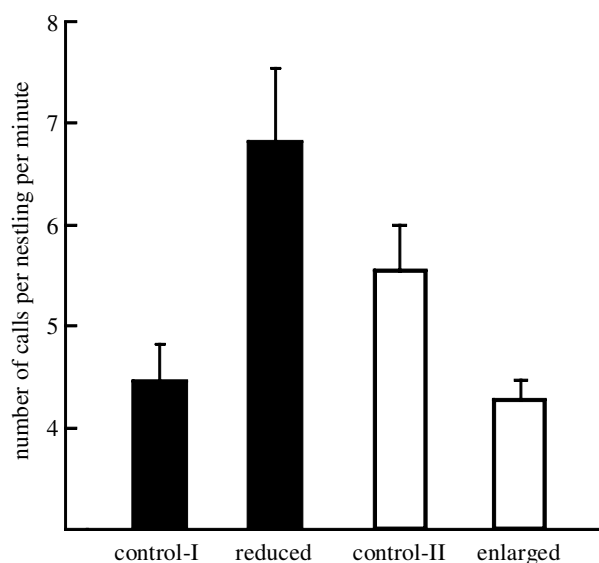


Figure 3. Mean number of calls per nestling per minute (\pm s.e.) when brood size remained unchanged (control-I) versus when it was reduced, and when some nestlings were cross-fostered without altering the size of the brood (control-II) versus when brood size was enlarged.

situation where brood size remained unchanged ($t_{13} = 3.01$, $p = 0.01$; figure 3). In addition, the number of calls per nestling was lower when brood size was enlarged, compared with the situation where some nestlings were cross-fostered but brood size remained unchanged ($t_{13} = -3.85$, $p = 0.002$; figure 3). This agrees with the third prediction that the effort a nestling allocates to vocalization in the absence of the parents declines with increasing number of competitors.

(d) *Test of the alternative hypothesis*

Although the number of calls per minute produced by the entire brood was about double when nestlings were hungry compared with food satiated (14.7 ± 1.5 versus 8.2 ± 1.2 ; $t_{25} = 6.61$, $p < 0.001$), parents did not significantly reduce feeding rate in food-saturated broods compared with unfed broods (10.7 ± 1.1 versus 8.7 ± 1.1 prey items per night; $t_{25} = -1.45$, $p = 0.16$). These results are in the same vein as those showing that parents fed at similar intensities both experimentally enlarged and reduced broods (Roulin *et al.* 1999). Although we cannot conclude that parents do not adjust feeding rate to the begging behaviour of their offspring, our experiment suggests that when a nestling reduces calling rate after a meal, its nest-mates may not need to increase calling rate to ensure parental care.

4. DISCUSSION

Results of the first two experiments showed that a nestling refrained from vocalization in the absence of the parents when the value of the prey item next delivered would be higher for its nest-mate. The third experiment showed that nestlings refrained from vocalization when brood size (and thus sibling competition) was larger and escalated when it was smaller. Similar experiments in passerines provided different results for begging vocaliza-

tions produced in the presence of the parents. When parents arrived at the nest, passerine nestlings begged more intensely or did not adjust begging level in the presence of more hungry nest-mates (Smith & Montgomerie 1991; Cotton *et al.* 1996; Price *et al.* 1996; Leonard & Horn 1998). Thus, passerines fitted predictions of the honest signalling and scramble competition hypotheses (MacNair & Parker 1979; Harper 1986; Rodríguez-Gironés *et al.* 1996; Godfray 1991, 1995) whereas barn owls vocalizing in the absence of the parents fitted predictions of the sibling negotiation hypothesis. The applicability of our findings to other species will best be discussed once empiricists have considered species other than passerines or begging calls produced at the post-fledging period when dependent young vocalize both during and between parental visits (e.g. Frumkin 1994).

When the value of the prey item next delivered was higher for its nest-mate, a nestling barn owl could have refrained from vocalization for at least two reasons.

First, because a less hungry nestling could be at risk of physical aggression from nest-mates, it refrained from vocalization to signal to nest-mates that it would not contest the next prey item. This possibility was proposed by Forbes (1991) to explain the submissive behaviour of junior nestlings in the osprey (*Pandion haliaetus*). In the barn owl, aggressive interactions among siblings occur only during periods of decreased food availability (A. Roulin, unpublished data). Since we did not deprive nestlings of food, overt sibling competition was not expected to arise. This first explanation may therefore not hold.

Second, in the presence of a hungrier nest-mate a nestling has little chance of getting the next delivered prey item, and thus it may refrain from vocalization to save energy (Leech & Leonard 1996). In one night each nestling barn owl produces on average 1750 calls when parents are not at the nest (A. Roulin, unpublished data), and each call is between 0.3 and 0.9 s with an intensity of 6–10 kHz (Bühler & Epple 1980). Calling behaviour may therefore entail energetic costs, and nestlings would probably optimize calling rate to the expected benefit; that is, nestlings should vocalize intensely only when the chance of getting a prey item becomes non-negligible. Experiments were conducted when nestlings were older than one month, an age at which brood reduction rarely occurs (Taylor 1994). Consequently, if a nestling did not get the first prey item delivered by a parent, it was quite predictable that it would get the next one. Therefore, refraining from vocalization to save energy should have no dramatic effect on the probability of being fed later.

In conclusion, we propose that in the absence of the parents, nestling barn owls negotiate via begging vocalization which one will have priority access to the next delivered prey item. The nestling that values the next delivered item more highly may beg vigorously, and its nest-mates assess this signal before deciding whether to enter in or retreat from sibling competition. This communication system may allow nestlings to determine when they have a chance of getting a prey item, and thus when they should vocally and behaviourally compete. It now remains to discover how such a signalling system is evolutionarily stable, how cheating (i.e. to not vocalize but compete for prey items) cannot invade populations, and the applicability of our findings to other species.

We are grateful to Jean-Charles Daiz, Martin Epars and Laurent Hirt for technical assistance, and the Service vétérinaire du canton de Vaud for the authorization to feed young barn owls and manipulate brood sizes. The constructive criticism of Rebecca Kilner, Rufus Johnstone, Tore Slagsvold and two anonymous referees helped us to greatly improve a previous version of the manuscript.

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