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Parent–offspring conflict and the coordination of siblings in gulls

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Offspring solicit food from their parents by begging behaviours. Studies on birds suggest that these displays are 'honest signals of need' and adults provide food according to the begging level. However, siblings may compete for parental resources and the begging intensity is expected to change with brood size. Here, we show that in the black-headed gull (*Larus ridibundus*) an increase of the numbers of siblings can result in a decrease of individual begging cost through nestlings' synchronized signalling. This is in accordance with some mathematical models. As parents respond to the total solicitation emerging from the nest, the probability to get food increases with the number of chicks begging together. The more siblings there are, the more they coordinate their begging while decreasing the number of individual begging bouts. Intra-brood synchronization of begging enables chicks to reduce their effort and hence exerting an important role in parental–offspring negotiation.

Keywords: begging behaviour; parent–offspring conflict; animal communication; black-headed gull

1. INTRODUCTION

Many animal offspring solicit parental care by begging behaviour (Wright & Leonard 2002). This behaviour has recently received attention because of its relevance to the 'parent–offspring conflict' theory, which suggests that young demand may be greater than is optimal for the parents (Royle *et al.* 2002). Theoretical models have put forward that this conflict may have a stable resolution: parents respond with food provisioning in proportion to begging intensity, which represents an honest cue expressing the need of the young (Kilner & Johnstone 1997). Some studies in birds support this assertion (Budden & Wright 2001). However, conspicuous begging signals should also be selected considering that parents and siblings constitute a complex communication network where multiple signallers compete for parental resources and thus the siblings may modify their begging effort in response to the level of competition (Budden & Wright 2001). A central question is: does the begging intensity of a chick increase with the number of competitors present in the nest? The answer to this question is controversial. A theoretical model predicts that when multiple signallers compete for the attention of a receiver, individual equilibrium signal costs will be lower (Johnstone 1999). However, in tree swallows *Tachycineta bicolor*, Leonard *et al.* (2000) show that begging intensity increases with brood size. In other respects, a particular situation is the case where the parent has no control over food allocation between chicks. In this case, and according to the 'sibling competition' model (Rodriguez-Gironés 1999; Rodriguez-Gironés *et al.* 2001), the amount of food consumed by chicks is determined by their relative begging efforts. In one of its versions, this model shows the possibility that if a chick of a two sibling brood invests in signalling, the two nest-mates will share the benefits of this effort, while only one of them is paying the costs. In this perspective, the more competitive chick will then invest less in signalling while receiving a larger share of the food than its sibling (Rodriguez-Gironés *et al.* 2001). This model leads to the hypothesis that signalling plays a minor role in the pattern of allocation of resources. Unfortunately, this model does not explore the effect of brood size on begging behaviour.

Here, we investigate how brood size modulates chicks' solicitation behaviour in the black-headed gull, *Larus ridibundus*, a semi-altricial bird with a brood size of one to three siblings (Cramp & Simmons 1983). When a parent returns to the nest, its chicks recognize its calls and start begging before the adult lands (Charrier *et al.* 2001*a*; Mathevon *et al.* 2003). Begging behaviour is also exhibited when the parent is in the nest. Parents respond by regurgitating on the ground (Fjeldsa 1978).

Through comparing the intensities and the rates of begging behaviour among chicks from nests of different brood sizes, here we show the first empirical evidence, to our knowledge, that an increase of the numbers of siblings can somewhat counter-intuitively result in a decrease of individual begging cost through nestlings' synchronized signalling.

2. MATERIAL AND METHODS

The observations were made from a floating hiding place (localization of the colony: Etang de la Ronze, Plaine du Forez, France; May to June 2001 and 2002). Chicks were banded for individual identification.

We made 34 observation sessions (nine on nests with one chick, 14 on nests with two chicks and 11 on nests with three chicks; session duration of 1 h). To limit the effect of age, we focused on chicks aged from 8 to 15 days (mean age ± s.d.: nests with one chick: 11.1 ± 2.6 days; with two: 11.0 ± 2.2 days; with three: 11.0 ± 2.1 days).

The begging behaviour of the gull chick is characterized by the following sequence: approach to the parent, hunched postures (HP) and parental beak stimulations (BS) (Fjeldsa 1978). During this sequence, begging calls are emitted. Whenever a chick begged, we obtained the score of its begging behaviour by noting the number of HP and of BS, and the rate (low (LO), medium (ME) or high (HI)) of calls. The five scores were defined as follows.

1 = (no HP + 1 BS) or (1 HP + no BS) + LO.
2 = (1 HP + 1 BS) or (no HP + 2 BS) or (2 HP + no BS) + LO or ME.
3 = (1 HP + 2 BS) or (2 HP + 1 BS) or (2 HP + 2 BS) + ME.
4 = (1 to 3 HP + 3 BS) or (3 HP + 1 to 3 BS) + ME to HI.
5 = (1 to more than 3 HP + 4 or more BS) or (4 or more HP + 1 to more than 3 BS) + HI.

Each begging event was characterized by its occurrence time, the number of chicks begging together, the total begging intensity (summation of the begging score of each begging chick) and the parental response (regurgitation or not). We assessed, separately for nests with one, two and three chicks, the average individual begging intensity (AIB) by calculating the mean of the scored individual

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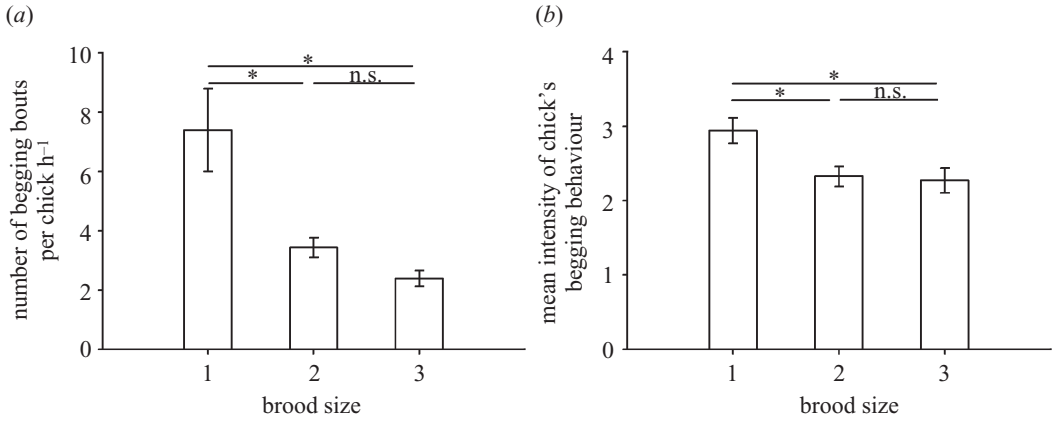

Figure 1. Relation between brood size and (*a*) number of begging bouts per chick h^{-1}, and (*b*) mean intensity of chick's begging behaviour. $^{*}p < 0.05$ (Mann–Whitney test).

begging intensities, and the mean number of begging behaviour by chick and by hour (MBH). Their product (AIB times MBH) represents an index of the individual begging cost (begging units h^{-1}).

We used non-parametrical statistics (Kruskall–Wallis one-way ANOVAs and Mann–Whitney *W*-tests). When a non-significant result ($p > 0.05$) was found, a power analysis was performed (GPower analysis; Faul & Erdfelder 1992).

3. RESULTS

(a) *The begging effort decreases with brood size*

The number of begging bouts exhibited by any given chick per hour decreases with increase in brood size. A chick alone, with one, or with two siblings, begs 7.4 ± 1.4, 3.4 ± 0.3 and 2.4 ± 0.3 times h^{-1} ($H_2 = 20.41$, $p < 0.05$), respectively (figure 1*a*). Moreover, nestlings do not necessarily beg simultaneously and the average occurrence of begging events is greater in nests with a single chick (7.4 ± 1.4 begging events h^{-1}) than in nests with two chicks (5.01 ± 0.55; $W = 158$, $p < 0.05$) and than in nests with three chicks (4.33 ± 0.76; $W = 67$, $p < 0.05$). The averaged occurrence of begging events is not significantly different between nests with two or three chicks ($W = 127$, $p = 0.30$), but as the power of the test is low (0.17), one cannot say that both occurrences do not differ at all.

Solitary chicks beg on average more intensively than chicks with siblings ($H_2 = 8.53$, $p < 0.05$; figure 1*b*) and the individual begging cost decreases with the increase of sibling number (21.4 begging units h^{-1} for a single chick, 7.9 for a chick with one sibling, and 5.4 for a chick with two siblings).

(b) *Parents respond to the total solicitation level emerging from the nest*

During a begging event, the total begging intensity emerging from the nest increases with the number of siblings begging together, i.e. synchronized siblings, as a result of summation of individual begging behaviour intensities ($H_2 = 83.9$, $p < 0.05$). In nests with one chick, parents respond proportionally to the begging intensity of the chick ($H_4 = 19.5$, $p < 0.05$). In nests with two and with three siblings, parents respond to the begging level of the whole brood (nests with two chicks: $H_9 = 65.7$, $p < 0.05$; three chicks: $H_9 = 30.9$, $p < 0.05$; all brood sizes pooled: $H_9 = 111.4$, $p < 0.05$; figure 2). The probability of eliciting regurgitation thus increases with the number of synchronized siblings ($H_2 = 78.6$, $p < 0.05$): 17% of the begging bouts of a solitary chick elicit parental regurgitation; in the case of two siblings, when one chick begs alone, elicited parental response is 23% of the begging bouts versus 87% when both chicks beg together; in the case of three siblings, one-chick begging bouts resulted in 13.5% parental regurgitation, whereas synchronized beggings of two or three siblings succeed in 55% and 100%, respectively.

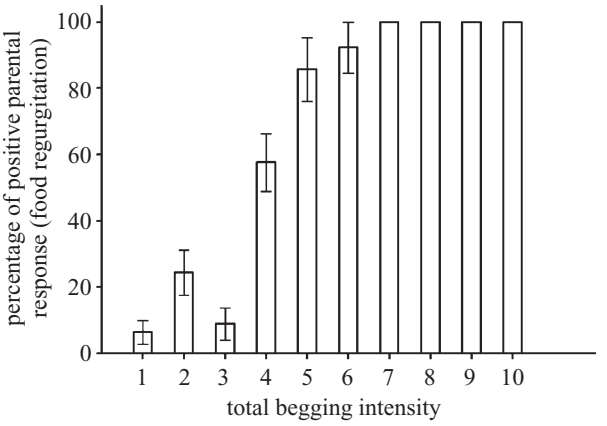

Figure 2. Parental response to the whole brood begging level (all brood sizes pooled).

(c) *Offspring synchronization increases with brood size*

In two-chick nests, 61% of the begging events are exhibited by a single chick while the other 39% are displayed by both chicks. These proportions are unlikely to be explained by chance only. Indeed, if we consider that the duration of a begging event is *ca*. 1 min, we can roughly test the independency of chicks' begging behaviours using a 2×2 table of contingency ($n = 60$ min, each chick spending $3.06/2 = 1.53$ min begging alone and 1.95 min begging with its sibling). It appears that the begging behaviours of both chicks are not independent of each other ($p < 0.05$, χ^2-test of independence, $\chi^2_{\text{obs}} = 17.06 > \chi^2_{0.05,1\text{d.f.}}$).

In three-chick nests, only 31% of their begging behaviours are demonstrated by a single chick, whereas all other begging events are synchronized either between two chicks (42%) or all three (27%) (on a total of 4.33 begging events per hour; i.e. 1.34 were performed by a chick alone, 1.82 by two chicks and 1.2 by three). We can also roughly test the independency of a chick's begging behaviour in front of each of its siblings' behaviours ($n = 60$ min, each chick spending $1.34/3 = 0.45$ min begging alone and $1/3 \times 1.82 + 1.2 = 1.81$ begging with the considered sibling). It appears that the begging behaviour of a chick is not independent from the begging behaviour of each of its siblings ($p < 0.05$, $\chi^2_{\text{obs}} = 37.74 > \chi^2_{0.025(\text{Bonferroni correction})1\text{d.f.}}$).

The more in number they are, the more the nestlings tend to synchronize their begging behaviours. As chicks enhance their probability to solicit parents when synchronized, the more siblings there are, the more efficient in securing parental regurgitation begging becomes.

4. DISCUSSION

The prior question of this work was if gull offspring should beg more often and more intensively as the number of siblings and its inherent level of competition increase. Our results show that this seems not to be the case in the black-headed gull. In this species, the begging effort of a given chick decreases with the number of siblings. Although this observation is somewhat counter-intuitive and contrary to the one made in the tree swallow (Leonard *et al.* 2000), this is in accordance with the prediction made by some previous mathematical models (Johnstone 1999; Rodriguez-Gironès *et al.* 2001). Black-headed gull chicks seem to demonstrate a dynamic adjustment of their signalling behaviour. When competition is likely to increase (according to the number of siblings), nestlings seem to join their begging behaviours: as their parents respond to the whole-brood begging intensity, the synchronized siblings gain the ability to get more food from parents. Although we have no idea how much food a particular chick was eating (some chicks with siblings are likely to eat less than singletons owing to competition during food sharing), this synchronization appears to be efficient and may allow chicks to maximize the return of begging effort while decreasing individual begging cost: thus increasing direct fitness.

A characteristic feature of the black-headed gull feeding behaviour is that parents regurgitate food on the nest ground: they do not allocate food individually to each chick. This kind of feeding pattern seems to be absent in passerine species. As most of the research studies on begging behaviour have been done on passerines, it is not surprising that no other example of siblings synchronization has been described.

The present finding provides empirical support that coordination among siblings may act as a powerful force during intra-familial conflicts between young and parents. This behaviour may constitute a novel aspect of the behavioural plasticity occurring in parent–offspring relationships (Kedar *et al.* 2000; Charrier *et al.* 2001*b*). We propose that the coordination phenomenon should be more widely taken into account to enhance the understanding of the mechanisms and the evolution of the parent–offspring communication network.

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