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Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the barn owl, *Tyto alba*

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ABSTRACT

When siblings differ markedly in their need for food, they may benefit from signalling to each other their willingness to contest the next indivisible food item delivered by the parents. This sib–sib communication system, referred to as 'sibling negotiation', may allow them to adjust optimally to investment in begging. Using barn owl (*Tyto alba*) broods, I assessed the role of within-brood age hierarchy on sibling negotiation, and in turn on jostling for position where parents predictably deliver food (i.e. nest-box entrance), begging and within-brood food allocation. More specifically, I examined three predictions derived from a game-theoretical model of sibling negotiation where a senior and a junior sibling compete for food resources (Roulin, 2002a; Johnstone and Roulin, 2003): (1) begging effort invested by the senior sibling should be less sensitive to the junior sibling's negotiation than vice versa; (2) the junior should invest less effort in sibling negotiation than its senior sibling but a similar amount of effort in begging; and (3) within-brood food allocation should be directly related to begging but only indirectly to sibling negotiation. Two-chick broods were created and vocalization in the absence (negotiation signals directed to siblings) and presence (begging signals directed to parents) of parents was recorded. In support of the first prediction, juniors begged at a low cadence after their senior sibling negotiated intensely, probably because negotiation reflects prospective investment in begging and hence willingness to compete. In contrast, the begging of senior siblings was not sensitive to their junior sibling's negotiation. In contrast to the second prediction, juniors negotiated and begged more intensely than their senior sibling apparently because they were hungrier rather than younger. In line with the third prediction, juniors monopolized food delivered by their parents when their senior sibling begged at a low level. The begging cadence of both the junior and senior sibling, the junior's negotiation cadence, the difference in age between the two nest-mates and jostling for position were not associated with the likelihood of monopolizing food. In conclusion, sibling negotiation appears to influence begging behaviour, which, in turn, affects within-brood food allocation. Juniors may negotiate to challenge their senior siblings, and thereby determine whether seniors are less hungry before deciding to beg for food. In contrast, seniors may negotiate to deter juniors from begging.

Keywords: begging, hatching asynchrony, parent–offspring conflict, sibling competition, sibling negotiation, *Tyto alba*.

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INTRODUCTION

Conflicts between family members over parental investment (Trivers, 1974) are thought to have promoted the evolution of honest offspring signals of need allowing parents to adjust optimally the feeding rate (Godfray, 1991; Ottosson *et al.*, 1997) and within-brood food distribution (MacNair and Parker 1979). If parent–offspring communication plays an important role in within-brood food allocation (e.g. Leonard and Horn 1998), the begging strategies used by individual chicks may be influenced by communication between siblings, so-called 'sibling negotiation', which takes place in the prolonged absence of parents (Roulin, 2002a; Johnstone and Roulin, 2003).

When siblings differ markedly in their need for food but not in competitive ability, the outcome of sibling competition is predictable, since a needier nestling is likely to be more willing to compete for access to indivisible food resources. The indivisibility of the food a parent brings in a single feeding visit is crucial (e.g. Mock, 1985) because then investment in sibling competition will be paid back to only one of the competitors. In such circumstances, a game-theoretical model showed that selection may favour siblings who advertise their need for food to each other in the absence of parents, allowing them to later adjust their effort to scramble competition and begging signals directed to parents (Johnstone and Roulin, 2003). In the absence of parents, needy nestlings may indicate to siblings their willingness to compete strongly for the next food item by using visual (e.g. wing flapping), physical (e.g. move and push siblings to assess competitiveness) or vocal signals. In contrast, less needy siblings may indicate that they will retreat from any contest, since they have less to lose from not getting the food item (e.g. Johnstone, 1999). This sib–sib communication system may allow needy nestlings to obtain food resources at a lower cost, compared with when sibling negotiation does not occur. This assumes that the costs of negotiating are lower than the costs of extra effort in sibling competition when siblings have not negotiated beforehand. Less needy nestlings may also avoid wasting energy in a competition where the likelihood of winning is low (Roulin, 2002a).

In the development of the sibling negotiation hypothesis (Roulin, 2002a), much emphasis was placed on the importance of asymmetry in food need between siblings. The importance of this factor overshadowed discussion of the potential importance of hatching asynchrony. In many bird species, hatching asynchrony leads to a distinct age hierarchy among the siblings in a brood (Magrath, 1990), and hence the last-hatched nestlings (so-called juniors) are less competitive and fed less than their first-hatched siblings (so-called seniors; see, for example, Price and Ydenberg, 1995; Price *et al.*, 1996; but see Stamps *et al.*, 1989). For this reason, juniors are expected to invest more energy in non-aggressive scramble competition to compensate for their poorer competitive ability (Bengtsson and Rydén, 1981; Godfray, 1995; Price and Ydenberg, 1995; Price *et al.*, 1996; Hofstetter and Ritchison, 1998; Cotton *et al.*, 1999; but see Nuechterlein, 1981; Lotem, 1998). Even if hatching asynchrony affects offspring begging and within-brood food allocation by creating among-sibling asymmetries in competitive ability and need, its role in sibling negotiation is still unclear. However, a recent game-theoretical model showed that competitive asymmetries between siblings may play a role in how individuals invest in negotiation (Johnstone and Roulin, 2003). In this model, offspring vary in their need for food, and before the arrival of a parent they honestly signal to each other their current need (i.e. they negotiate). This information influences their subsequent competitive behaviour in the presence of parents, which plays a central role in which chick has priority of access to food resources, since the parents lack full control of food allocation. Two major results came out of this model, which assumes that parents do not adjust feeding rate to offspring behaviour. First, seniors' begging will be less sensitive to variation in juniors' need than vice versa (Fig. 1). Information on need can be gathered from nestling calling activity in the absence of parents. This prediction is intuitively appealing because seniors can rely on their size advantage to monopolize food resources. Second, a junior should invest less effort in negotiation than its senior sibling because seniors respond less strongly to juniors' need than vice versa. In contrast, effort invested in begging is predicted to be similar between juniors and seniors (Johnstone and Roulin, 2003).

Using two-chick barn owl (*Tyto alba*) broods, I examined how hatching asynchrony affects vocalization in the absence (hereafter 'sibling negotiation') and presence (hereafter 'begging') of parents, jostling for the position where parents deliver food (i.e. nest-box entrance) and within-brood food allocation. Calls produced in the absence of parents are used by nestlings as negotiation signals, as shown by Roulin *et al.* (2000) in an experimental study. In two-chick broods, a target nestling negotiated less intensely in the absence of parents when its rival was more hungry, but this escalated after the rival had been fed by a parent to indicate that it was now willing to compete vigorously. This observation is consistent with the idea that nestlings compete intensely only when the likelihood of winning a contest over food resources is high. Even though parents may assess vocalizations in their absence to adjust feeding rate, the primary function of these calls may be to resolve sibling conflicts over the impending food resources. This statement is based on an experiment in which all nest-mates were food-supplemented. Although vocalization behaviour in the absence of parents was strongly altered by this experiment (vocalization behaviour in their presence was not affected; Roulin, 2001b), parents did not modify their food provisioning rate. All these findings are the exact opposite of what current models predict for begging calls directed to parents (Roulin *et al.*, 2000), justifying a different

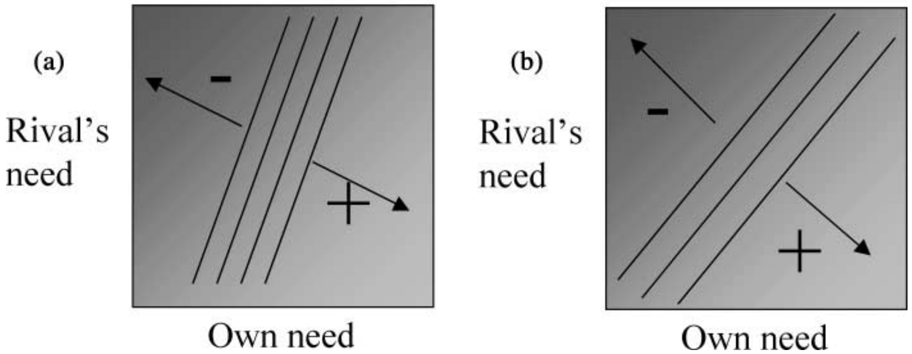

Fig. 1. Theoretical prediction of the effort invested in begging by a senior (a) and junior sibling (b) in relation to own and nest-mate's need. With increasing nest-mate's need, nestlings are expected to decrease effort in begging (arrow ' – ', dark shading), whereas nestlings are expected to increase effort with a decrease in nest-mate's need (arrow ' + ', pale shading). The model predicts that juniors are more sensitive to a change in nest-mate's need than seniors, as shown by the steeper slope of the 'senior' than 'junior' line. In this model, each individual is informed about their nest-mate's need after a period of sib–sib communication that takes place in the prolonged absence of parents, a process referred to as 'sibling negotiation' (adapted from Johnstone and Roulin, 2003).

terminology for vocalizations produced in the absence (i.e. sibling negotiation) and presence (i.e. begging) of parents. In the present study, I examined the following three predictions.

1. *Begging effort invested by seniors should be less sensitive to juniors' negotiation than vice versa*. If the function of sibling negotiation is to deter nest-mates from begging and competing, mainly juniors should adjust begging to their nest-mates' investment in negotiation (Fig. 1; Johnstone and Roulin, 2003). This prediction is based on the fact that seniors can secure food resources more easily given their greater physical competitiveness. Being informed via sibling negotiation that seniors are willing to beg, and hence compete intensely at the parents' arrival, juniors may save energy by retreating from a contest for which the likelihood of winning is low.
2. *Juniors should invest less effort in negotiation than seniors but a similar effort in begging*. If juniors are more sensitive to their nest-mates' need for food than senior siblings (Fig. 1), they should refrain from negotiating more often when a nest-mate is hungry (Johnstone and Roulin, 2003). This prediction is derived from prediction 1.
3. *Within-brood food allocation should be directly related to begging effort but only indirectly to sibling negotiation*. The probability that an individual monopolizes a food item delivered by its parents should be related to the effort invested in begging rather than in negotiation. This prediction is derived from the sibling negotiation hypothesis, which postulates that the primary function of sibling negotiation is to allow nestlings to adjust optimally effort in begging, which, in turn, determines the outcome of a contest (Roulin, 2002a). From prediction 1, I also expect seniors' rather than juniors' begging to predict within-brood food allocation, because the seniors' investment in begging determines the level at which juniors beg, and not the other way round.

METHODS

Study organism

The present study was conducted in a Swiss population of barn owls breeding in nest-boxes ($1.0 \times 0.6 \times 0.5$ m) fastened to barn walls. This species is suited to the study of sibling negotiation because negotiation signals are costly in terms of energy, with each nestling producing on average 1786 calls per night (Roulin, 2002a), in terms of time, with investment in sibling negotiation being traded off against other activities such as preening (Roulin, 2002a), and in terms of predation risk, because loud vocalizations may attract stone martens, congenerics to commit infanticide (Birrer and Hüsler, 2003) and fledglings that switch nest to parasitize investment of unrelated parents (Roulin, 1999). The fact that nestlings produce so many calls per night in the absence of parents implies that nestlings do not call for irrelevant stimuli such as the noise made by wind or rain (e.g. Leonard and Horn, 2001; Roulin, 2001a). Among-sibling asymmetry in food need is large because only one nestling is fed per parental visit. Parents deliver one prey item every 45–60 min (each chick consumes only three voles per night), and hence during long periods not all siblings are food satiated. In captive owls fed *ad libitum*, daily food intake increases from 63 ± 5 g (mean ± standard deviation) at 20 days of age to 80 ± 10 g at 31 days, followed by a spontaneous decrease to 60 ± 9 g at 60 days (Durant and Handrich, 1998). The species is sexually dimorphic in size with female nestlings being 6% heavier than male nestlings (Roulin *et al.*, 1999). As eggs are laid every 2–3 days and the female starts to incubate her clutch soon after the first egg is laid, an age hierarchy is established among the offspring (Roulin, 2002b). In large broods (mean brood size = 4.1; range = 1–9), the first-hatched nestling can be up to 25 days older than the last-hatched sibling (personal observation). Late-hatched nestlings have impaired growth when rearing conditions are poor and frequently die when food supply decreases, as shown by brood size manipulation experiments (Roulin, 1998; Roulin *et al.*, 1999). Most brood reduction events take place in the first 3 weeks after hatching. Death of nestlings generally occurs by starvation, with siblicide being rare, although cannibalism is frequent (Roulin, 2002b). During the first 2–3 weeks after hatching, the mother broods the offspring and distributes small mammals among them. Then, offspring are able to swallow entire prey items, and she progressively helps her partner collect food. In Switzerland, the annual proportion of hatchlings that fledge varies between 0.54 and 0.89 (mean = 0.77; personal observation). Fledging occurs at 55 days of age, and nestlings return to the nest until independence at an age of 70–85 days (Roulin, 1999). Extra-pair paternity is rare in the barn owl, with only one extra-pair young identified out of 211 nestlings from 54 broods (Roulin, 2004). In the presence of parents, each nestling produces on average 30.4 calls per minute (range = 16–88) and in their absence 3.7 calls per minute (range = 2–10) with a frequency of 6–10 kHz (Bühler and Epple, 1980; Roulin, 2001b). The acoustic waveform generated with the program Canary (Charif *et al.*, 1995) showed that calls produced in the absence and presence of parents are similar (personal observation).

Prediction 1: begging effort invested by seniors should be less sensitive to junior siblings' negotiation than vice versa

Experiment 'temporary two-chick broods'

To investigate the first prediction, I created 74 two-chick broods (13 in 1997, five in 1998, 47 in 2000 and nine in 2001) to determine whether juniors' begging is associated with seniors' negotiation. I used exclusively two-chick broods because in larger broods it is difficult to assign begging calls to individuals. However, results based on two-chick broods may be representative of larger broods, since usually only one or two nestlings negotiate intensely while their nest-mates are much less vocal (Bühler and Epple, 1980; personal observation). In the evening at 21.30 h, two siblings were randomly chosen per nest and their nest-mates temporarily placed in a large plastic can (diameter = 0.6 m; height = 0.8 m) at some distance from the nest until midnight. The age of the two focal nestlings was estimated by measuring the length of the flattened wing from the bird's wrist to the tip of the longest primary (Roulin, 2004), a trait that is weakly sensitive to food supply (Durant and Handrich, 1998). The mean age of seniors was 40 days (range = 18–59) and that of juniors 33 days (range = 15–56), and their mean age difference was 7 days (range = 1–22).

An infrared-sensitive camera and a microphone were installed in nest-boxes without any apparent signs of distress to either the adults or nestlings. Siblings were ringed on a different leg to make them easy to distinguish on video footage. Vocalization behaviour in the absence of parents, referred to as 'sibling negotiation', was recorded in the following way. In the 15 min preceding the first parental feeding visit of the night, I counted the number of calls produced by both nestlings in the first 14 min – that is, before the nestlings were aware of the presence of a parent in the surroundings of the nest-box, the nestlings suddenly behaving differently once they realized that a parent was close to the nest. Calls were easy to assign to one of the two individuals, because nestlings open their bill while calling, and calls of different individuals are easily distinguishable by the human ear (personal observation). I was able to record begging behaviour in the presence of parents in only 50 of the 74 broods, because it was sometimes difficult to assign calls to individuals. Therefore, I considered only broods for which I could assign calls to each individual chick with certainty. I counted calls between the moment when a parent entered the nest-box and gave its prey to one of the two offspring, and divided this number by the amount of time during which the calls had been produced (on average 9.1 ± 1.2 s). The latter value, denoted 'begging', was used in the statistical analyses.

To establish whether juniors' and seniors' jostling behaviour is associated with effort invested in sibling negotiation and begging, I calculated the proportion of time each individual was closer to the nest-box entrance during the 15 min preceding the first parental feeding visit of the night. Mean location was easily determined because nestlings often remained several minutes at the same place. I was able to determine this proportion in 65 broods (in nine nests the camera was unable to record this information). I monitored the location of the nestlings in their nest over 15 min rather than only just when a parent arrived with a small mammal because nestlings cannot accurately predict when this will occur. Therefore, a mean nestling location in the nest calculated over a long time period better reflects nestlings' willingness to be close to the nest-box entrance.

Prediction 2: juniors should invest less effort in negotiation than seniors but a similar effort in begging

To test the second prediction, I performed three experiments referred to as 'temporary two-chick broods', 'target chick in the presence of a younger versus older sibling' and 'manipulation of food supply of a target nestling'.

Experiment 'temporary two-chick broods'

To determine whether, independently of age, senior and junior siblings negotiate and beg at different levels, I analysed data collected in the same 74 two-chick broods as the ones used to test the first prediction. To remove age-related variation in vocalization behaviour, I extracted residuals from a second-order curve between negotiation and age, and between begging and age. I used second-order models because the level of vocalization may increase in intensity from birth to the period of maximal food intake at 31 days of age (Durant and Handrich, 1998), and then decrease to stop at independence around 70 days. Sex was determined using molecular techniques (Roulin *et al.*, 1999). The day on which vocalizations had been recorded, senior and junior siblings in 69 broods were weighed to the nearest gram (nestlings in five broods were not weighed by error). To derive a nestling body condition index, I extracted residuals from a second-order curve of body mass of all nestlings on their age (body mass = $-30.65 + 16.70 \times \text{age} - 0.18 \times \text{age}^2$; $F_{2,135} = 175.36$, $P < 0.001$; Fig. 2). Each chick appears only once in this analysis. Residuals were not associated with age (Pearson correlation: $r = 0.00$, $n = 138$, $P = 1.00$), and hence a difference between junior and senior siblings in body condition index is not biased by the fact that seniors were older. This index can reflect variation in the amount of food that has been processed since birth, but also short-term variation in hunger depending on the time span

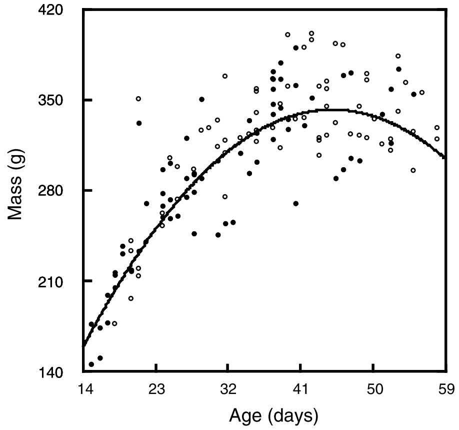

Fig. 2. Relationship between nestling body mass and age. Open circles represent seniors and filled circles juniors. Second-order curve is drawn.

since the last meal. To determine whether juniors jostle more for position than their senior nest-mates, I assessed whether they are more often close to the nest-box entrance. To obtain a better estimate of the effort invested in jostling for position, I also counted the number of steps each nestling took between the moment when the parent entered the nest-box and the moment when it gave its food item to one of the two offspring. I was able to count steps in 45 of 65 broods only, since the camera was not always placed in a position to record this information. A single step represents approximately 3 cm.

Experiment 'target chick in the presence of a younger versus older sibling'

In 2000, I examined experimentally whether nestlings adjust sibling negotiation when competing with an older versus a younger sibling. From each of eight broods, I selected one target nestling aged 38 days on average (range = 27–47). In the evening at 21.30 h, this nestling was left in its nest-box with a sibling that was either older (mean age = 44 days; range = 30–50) or younger (mean age = 32 days; range = 23–41) than itself. Its other nest-mates were temporarily placed in a large can at some distance from the nest until midnight. The target nestling was on average 5.8 days older (range = 2–11) than its junior sibling, and 6.5 days younger (range = 2–13) than its senior sibling. In four of the broods, I paired the target nestling with the senior on the first night and with the junior on the following night. In the remaining four broods, I reversed the order of these manipulations. Starting 15 min before the first parental visit of the night, I recorded the number of calls produced by the target nestling in the subsequent 14 min. This period began on average 102 min after the two-chick broods had been created (range = 31–245 min). This amount of time was probably long enough for nestlings to adjust to the experimental set-up, since in a similar experiment nestlings altered their behaviour (Roulin *et al.*, 2000). Unfortunately, it was not possible to record vocalizations in the presence of parents in all eight broods, which precluded any analysis of the effect of this experiment on begging.

Experiment 'manipulation of food supply of a target nestling'

To test experimentally whether negotiation strategies employed by seniors and juniors are different when the food supply of a target sibling is manipulated, I reanalysed the data collected in 1997 (Roulin *et al.*, 2000). This allowed me to measure for juniors and seniors the change in negotiation effort between the night when their sibling was unwilling (i.e. when experimentally food-supplemented) and the night when it was willing (i.e. when experimentally food-deprived) to contest the first prey item delivered by their parents. From each of 12 broods, I randomly selected two siblings, of which the older was the 'senior' (mean age = 36 days; range = 29–44) and the younger the 'junior' (mean age = 29 days; range = 21–39). The mean age difference between them was 7 days (range = 2–15). On one day, the senior was kept in a large can between 09.00 and 21.30 h with three dead laboratory mice ('food-supplemented' treatment), whereas its junior sibling was kept in another can without any food ('food-deprived' treatment). On another day, the senior was food-deprived and its junior sibling food-supplemented, and on another day both individuals were food-deprived. The food-supplemented individual consumed on average 1.7 mice (34 g). The three treatments were performed on three successive days and their order was randomized. At 21.30 h, the two siblings were returned to their nest-box, and their nest-mates, which had remained in the nest during daylight hours, were removed until 23.30 h. During this period, energy invested in negotiation (denoted 'negotiation index') by the senior and the junior siblings, which were ringed on opposite legs and hence recognizable on the video footage, was recorded. At night, 15 min before a parent brought the first prey item, I counted the number of calls during the first 14 min. Five calls were randomly selected per individual, and digitized at 22.05 kHz using the Canary software (Charif *et al.*, 1995). From the acoustic waveform of these calls (Fig. 3), the mean energy flux density of the five calls was multiplied 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. Because I performed paired comparisons within broods and individual nestlings, no amplitude calibration among nest-boxes was required (Charif *et al.*, 1995).

Prediction 3: within-brood food allocation should be directly related to begging but only indirectly to sibling negotiation

Experiment 'temporary two-chick broods'

I investigated the relationship between vocalization behaviour, jostling for position and within-brood food allocation in 64 of the same 74 two-chick broods used to test the first and

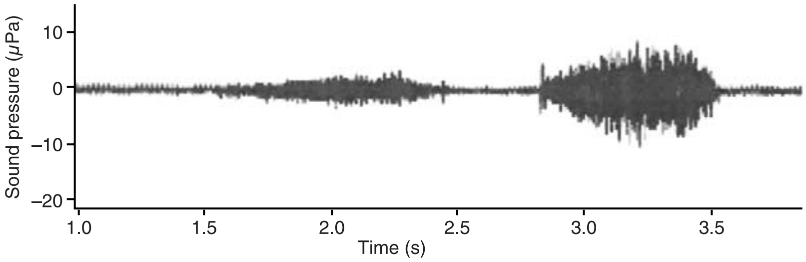

Fig. 3. Acoustic waveforms (sound pressure in μPa in relation to time in seconds) of calls produced in the absence of parents by an experimentally food-supplemented nestling (on the left) and food-deprived sibling (on the right).

second predictions. In the other 10 broods, I was unable to determine whether the junior or senior sibling consumed the first prey item of the night delivered by their parents. To determine whether negotiation and begging intensities, as well as jostling for position, are associated with the probability of being fed, I applied a stepwise backward procedure of a logistic regression with a binomial error distribution. For the dependent variable, 1 was assigned when the junior sibling was fed first and 0 for when the senior sibling was fed first. I fitted a full model that included all the explanatory variables – that is, vocalization in the absence (negotiation) and presence (begging) of parents of both junior and senior siblings, as well as their age difference. To take into account the intensity with which siblings jostled for the position where parents deliver food (i.e. nest-box entrance), I calculated 'mean location of senior sibling' minus 'mean location of junior sibling'. The latter value describes the extent to which seniors block the nest-box entrance and was introduced as an independent variable in the logistic regression. The significance of each variable was tested using the chi-squared distributed change in both deviance and number of degrees of freedom when it was dropped from the full model including all significant and non-significant terms. The logistic model that contained only significant terms was called the 'final model'.

Statistical analysis

All tests were two-tailed and P-values less than 0.05 were considered to be significant. The results are reported as the mean ± one standard error.

RESULTS

Prediction 1: begging effort invested by seniors should be less sensitive to junior siblings' negotiation than vice versa

Experiment 'temporary two-chick broods'

In temporary two-chick barn owl broods, juniors begged less intensely when the senior sibling negotiated more intensely beforehand (junior's begging as the dependent variable in a three-way ANOVA, senior's negotiation: $F_{1,46} = 8.69$, $P = 0.005$, standardized $\beta = -0.40$). The junior's negotiation ($F_{1,46} = 3.70$, $P = 0.06$, $\beta = 0.25$) and the intensity with which its senior sibling begged ($F_{1,46} = 0.60$, $P = 0.44$, $\beta = -0.10$) did not contribute significantly to the model. In a similar model, the senior's begging was significantly related only to the senior's negotiation (three-way ANOVA: $F_{1,46} = 3.90$, $P = 0.05$, $\beta = 0.31$; junior's negotiation: $F_{1,46} = 0.26$, $P = 0.61$, $\beta = -0.08$; junior's begging: $F_{1,46} = 0.60$, $P = 0.44$, $\beta = -0.13$). The proportion of time the junior nestling was closer to the nest-box entrance than its senior sibling was not significantly associated with the junior's and senior's negotiation (four-way ANOVA: $F_{1,39} = 1.42$, $P = 0.24$ *vs* $F_{1,39} = 0.07$, $P = 0.80$) and begging ($F_{1,39} = 0.94$, $P = 0.34$ *vs* $F_{1,39} = 0.04$, $P = 0.85$). A similar result was seen for the proportion of time the senior nestling was closer to the entrance (all P-values > 0.25). In conclusion and as predicted, investment by juniors in begging, but not in jostling for position, was sensitive to the senior's negotiation, whereas the senior's begging was not associated with the junior's negotiation.

Prediction 2: juniors should invest less effort in negotiation than seniors but a similar effort in begging

Experiment 'temporary two-chick broods'

In two-chick broods, the relationship between negotiation and age followed a second-order curve (regression based on mean sibling values: $F_{2,71} = 5.24$, $P = 0.008$; Fig. 4a), as did that between age and begging ($F_{2,71} = 4.41$, $P = 0.018$; Fig. 4b). Therefore, to determine whether junior and senior siblings negotiated and begged at different levels independently of age, I extracted residuals from these second-order curves, where siblings were used as independent data points. Male and female nestlings had similar residual negotiation and begging values (Student's t-test: $t_{146} = 0.85$, $P = 0.40$ *vs* $t_{99} = 0.17$, $P = 0.87$), and hence I did not control for this variable in subsequent analyses. In a repeated-measures ANCOVA, juniors negotiated at a higher level than their senior siblings (junior and senior values as repeated measures: $F_{1,66} = 7.26$, $P = 0.009$; Fig. 5a), but both juniors' and seniors' body condition indices become non-significant (covariates: $F_{1,66} = 1.45$, $P = 0.24$ *vs* $F_{1,66} = 0.69$, $P = 0.41$). In a similar analysis, juniors begged at a higher level than their senior siblings (repeats: $F_{1,45} = 4.65$, $P = 0.036$; Fig. 5b), and again body condition did not explain any of the variation (covariates: $F_{1,45} = 0.21$, $P = 0.65$ *vs* $F_{1,45} = 0.18$, $P = 0.67$). Because juniors were in poorer condition than their senior siblings (paired t-test: $t_{68} = 2.26$, $P = 0.027$), I examined whether the factor 'body condition' was non-significant in the above analyses because all the variation was taken up by the factor 'seniority'. In line with this proposition, nestling body condition was significantly correlated with sibling negotiation (Pearson correlation on mean sibling values: $r = -0.24$, $n = 69$ nests, $P = 0.046$), but not with begging ($r = -0.08$, $n = 48$, $P = 0.57$).

Senior and junior nest-mates were located equally as often close to the nest-box entrance (junior and senior values as repeated measures in an ANOVA: $F_{1,33} = 0.30$, $P = 0.59$). In the same model, the juniors' body condition explained a significant part of the variation ($F_{1,33} = 12.74$, $P = 0.001$), with juniors in poorer condition being closer to the nest-box entrance. In contrast, the variables seniors' body condition ($F_{1,33} = 2.20$, $P = 0.15$), juniors' and seniors' negotiation ($F_{1,33} = 3.31$, $P = 0.08$ *vs* $F_{1,33} = 1.32$, $P = 0.26$) and begging ($F_{1,33} = 0.002$, $P = 0.97$ *vs* $F_{1,33} = 0.85$, $P = 0.36$) did not explain any significant part of the variation in jostling for position. Seniors did not take more steps towards a parent that entered the nest with a prey (mean 0.69 *vs* 0.80 steps; Wilcoxon matched-paired signed-rank: $z = 0.22$, $n = 30$, $P = 0.83$). In conclusion, juniors negotiated and begged more intensely than their senior siblings, but did not jostle more vigorously, probably because they were in poorer condition or hungrier rather than because they were younger.

Experiment 'target chick in the presence of a younger versus older sibling'

Target chicks negotiated at a similar rate when paired with an older (10.2 ± 3.3 calls per minute) and a younger (10.0 ± 2.5 calls per minute; paired t-test: $t_7 = 0.09$, $P = 0.93$) sibling. This suggests that relative size difference *per se* does not affect sibling negotiation.

Experiment 'manipulation of food supply of a target nestling'

In the presence of a food-deprived junior or senior sibling, a target nestling reduced its effort in negotiation (Roulin *et al.*, 2000) to a similar extent as when the sibling was

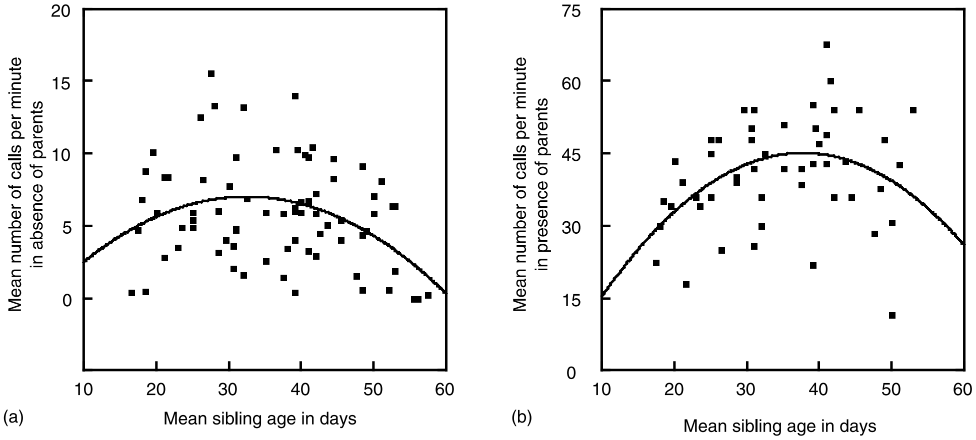

Fig. 4. Relationship between age and number of calls per minute produced (a) in the absence of parents (i.e. sibling negotiation) and (b) in the presence of parents (i.e. begging) in two-chick barn owl broods. Each data point represents mean sibling values. Second-order curves are presented: (a) $-2.39 + 0.58 \times \text{age} - 0.009 \times \text{age}^2$, $F_{2,71} = 5.24$, $P = 0.008$; (b) $-0.17 + 0.05 \times \text{age} - 0.0006 \times \text{age}^2$, $F_{2,71} = 4.41$, $P = 0.018$.

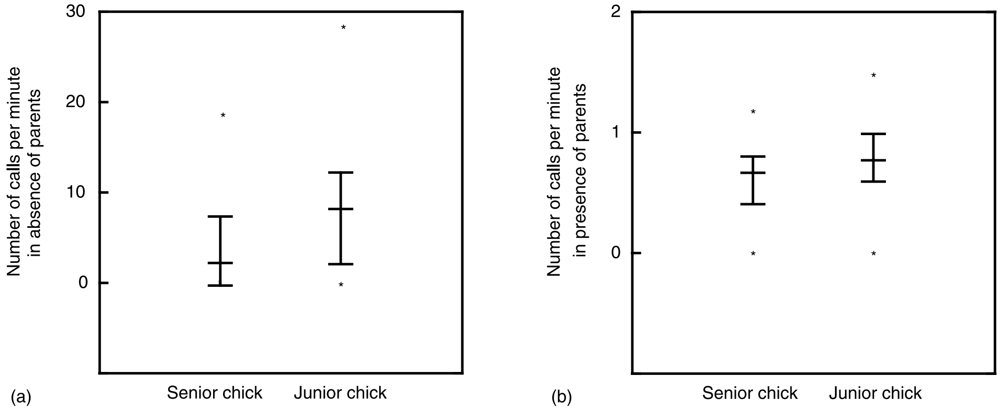

Fig. 5. Number of calls per minute produced in the absence (a) and presence (b) of parents by senior and junior barn owl siblings. Calls in the absence of parents were counted during the first 14 of the 15 min preceding the first parental feeding visit of the night. Calls in the presence of parents were counted between the moment when the parent entered the nest-box and gave its prey to one of the two offspring. Horizontal lines represent median, 25% and 75% quartiles. Asterisks show outliers.

food-supplemented (difference in negotiation indices: 0.89 ± 0.48 *vs* 0.77 ± 0.27; paired *t*-test: $t_{11} = 0.22$, $P = 0.83$). The same result was seen when considering negotiation effort as the difference in number of calls ($t_{11} = 0.47$, $P = 0.65$). As for the previous experiment, these results suggest that relative size difference *per se* does not affect sibling negotiation.

Prediction 3: within-brood food allocation should be directly related to begging but only indirectly to sibling negotiation

Experiment 'temporary two-chick broods'

In temporary two-chick broods, juniors ate the first delivered prey item of the night in approximately 50% of cases (34 of 64 nests; binomial test: $P > 0.50$). Prey monopolization by juniors mainly occurred when their senior sibling begged at a low cadence (logistic regression in Table 1). In contrast, the age difference between the two chicks, the difference in mean location to the nest-box entrance between senior and junior siblings, the intensity with which juniors negotiated and begged as well as seniors negotiated did not predict prey monopolization by juniors (Table 1). Because begging effort is positively correlated with sibling negotiation (see results under prediction 1), begging appears to influence within-brood food allocation directly, whereas sibling negotiation may have an indirect effect by influencing begging behaviour.

DISCUSSION

Investment in sibling negotiation and begging in relation to asymmetry in food need and age

In contrast to a game-theoretical model of the sibling negotiation hypothesis (Johnstone and Roulin, 2003), in temporary two-chick broods juniors negotiated and begged more intensely than their senior sibling. This result can be interpreted in at least two ways. First, juniors negotiated and begged more vigorously because they were hungrier or had processed less food since birth (Wilson and Durkin, 1987; Roulin, 1998; present study). In that case, the net benefit of signalling food need to nest-mates and parents may be greater

Table 1. Logistic regression of the probability that junior barn owl nestlings monopolized the first prey item of the night delivered by a parent

	Change in			
Parameter	Deviance	d.f.	*P*	Estimates of coefficients
Full model	43.59	43		
Final model	54.85	48		
Constant		1		
Senior's begging cadence	5.66	1	<0.04	3.91
Rejected term				
Senior's negotiation cadence	0.55	1	>0.50	0.08
Junior's negotiation cadence	1.16	1	>0.50	−0.09
Junior's begging cadence	3.01	1	>0.10	2.64
Age difference between senior and junior	0.00	1	1.00	0.006
Difference between senior and junior in mean location to nest-box entrance	0.37	1	>0.50	0.01

Note: The final model is the model with all predictor variables that explained a significant part of the deviance. Rejected terms did not explain a significant part of the deviance.

for juniors than seniors. Nestling body condition index was not associated with sibling negotiation and begging levels in statistical models including the factor seniority. However, because juniors were in poorer condition than their senior sibling, the effect of body condition was probably hidden by this factor. Consistent with this explanation is the finding that the mean sibling body condition index was negatively correlated with sibling negotiation but, however, not with begging. This is in line with results of another study showing that manipulation of food supply altered effort invested in negotiation but not in begging (Roulin, 2001b). This is also consistent with another result of the game-theoretical model of sibling negotiation, showing that negotiation is more sensitive than begging to variation in food need (Johnstone and Roulin, 2003).

Second, juniors have a poorer resource-holding potential and may try to compensate for this by investing more effort in negotiation in an attempt to deter more competitive siblings from a contest. The latter possibility is, however, not consistent with the experimental tests. Target nestlings produced a similar number of calls whether paired with an older or a younger sibling, suggesting that short-term variation in hunger level has a greater impact on negotiation than within-brood age hierarchy. Furthermore, in the absence of parents, target nestlings negotiated more intensely when their sibling was food-supplemented rather than food-deprived, probably because the likelihood of monopolizing the next delivered food item is greater (Roulin *et al.*, 2000). However, the difference in negotiation effort between the two nest-mates' food states did not differ significantly between target juniors and seniors. This suggests that if nestlings tend to reduce their level of negotiating when their nest-mates are hungry compared to when they are satiated, the extent of this reduction does not differ dramatically between juniors and seniors. Although the sample sizes of these two experiments were small, I tentatively suggest that nestlings did not drastically adjust negotiation effort in relation to the size of their nest-mate, but rather to their respective need for food. This would not be surprising since if the function of sibling negotiation is to signal each others' need for food (Roulin, 2002a), sibling negotiation should be more sensitive to asymmetry in hunger than age. Asymmetry in hunger can indeed change to a large extent throughout a single night, whereas within-brood age hierarchy remains the same. Further tests of the game-theoretical prediction that independently of need seniors invest more effort in sibling negotiation than juniors (Johnstone and Roulin, 2003) should be carried out in broods in which seniors and juniors have the same need for food. This may be the only experimental design that can properly nullify among-sibling asymmetry in food need, allowing researchers to examinee the effect of among-sibling asymmetry in age on sibling negotiation.

Effect of hatching asynchrony and sibling negotiation on begging and within-brood food allocation

Juniors monopolized the first prey item of the night delivered as often as seniors. Because of their poorer competitiveness, juniors may therefore have to invest more effort in negotiation and begging to derive the same amount of food as seniors. In support of this proposition, juniors monopolized food mainly when seniors did not beg intensely, an outcome that juniors can predict from a senior's low investment in negotiation. This is consistent with the proposition that seniors have a better control over food allocation, and hence are frequently able to derive a larger than equal share of the resources (if this was not the case at the first feeding of the night, it may be at subsequent feedings). This control may take the form of aggression directed towards juniors, exclusion of juniors from positions near the food source or elevation of begging more than juniors, since seniors may pay lower costs of negotiating and begging. The suggestion that seniors have a better control over food access is further supported by the fact that although juniors were in poorer condition than their senior nest-mates, juniors were not able to monopolize more food items.

Two observations suggest that sibling negotiation allows nestlings to deter siblings from begging rather than from jostling for position. First, juniors begged at a lower extent when their senior sibling negotiated intensely beforehand. Second, jostling for position was not associated with sibling negotiation and begging. The result that juniors, but not seniors, begged less intensely when their nest-mate negotiated vigorously fits the prediction of the game-theoretical model of the sibling negotiation hypothesis (Johnstone and Roulin, 2003).

CONCLUSIONS

The results of the present study lead to the following four propositions. First, juniors invest more effort in sibling negotiation and begging than their senior sibling probably because they are hungrier or in poorer condition. This finding does not fit the game-theoretical model of the sibling negotiation hypothesis (Johnstone and Roulin, 2003). Second, negotiation effort is more sensitive to asymmetry in hunger between two siblings than to their size difference. Third, begging rather than sibling negotiation determines within-brood food allocation, potentially implying that parents do not assess calls produced in their absence to allocate food among their offspring. Fourth, within-brood food allocation is under the control of seniors, leading juniors to adjust begging effort in relation to their nest-mate's investment in sibling negotiation as predicted by the game-theoretical model (Johnstone and Roulin, 2003). In other words, need for food may influence sibling negotiation (but also begging), which, in turn, partly determines investment in begging by juniors. To get access to the food parents bring to the nest, seniors may rely on both their size advantage and sibling negotiation to deter their junior nest-mates from competing. In contrast, juniors may use information about the seniors' need for food before deciding to compete over prey access, information that is acquired via sibling negotiation. Juniors would then beg intensely only if seniors negotiated to a limited extent, indicating that seniors will not contest the next delivered prey item. Juniors may therefore negotiate not to deter their senior siblings to compete, but to determine whether they are more hungry than their siblings. By vocally challenging each other in the absence of parents, juniors may determine how hungry they are compared with their senior siblings, and seniors may deter their junior siblings from begging. These suggestions should be tested further by investigating vocalization behaviour at successive parental feeding visits in broods of natural sizes.

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