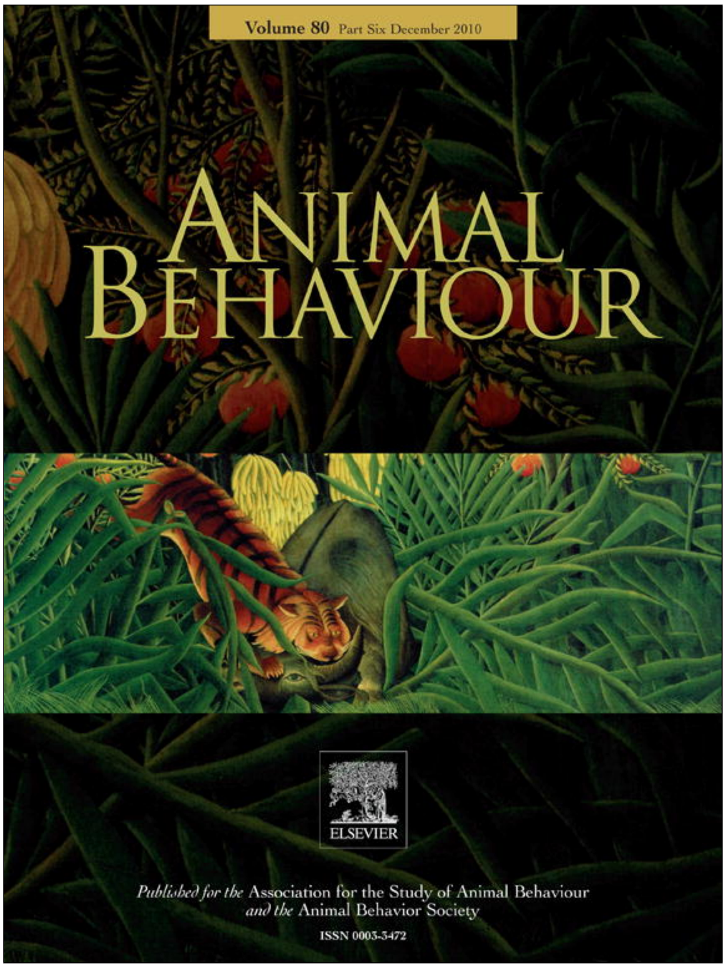
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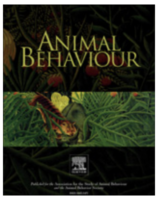

How siblings adjust sib–sib communication and begging signals to each other

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Parents allocate food resources to their offspring in proportion to the intensity of begging behaviour. Begging encompasses several activities including vocalizations that should honestly signal need and jostling for the position in the nest where parents predictably deliver food items. Although siblings are known to adjust begging level to each other, the underlying mechanism remains unknown. We examined this issue in experimental two-chick broods of the barn owl, *Tyto alba*, a species in which siblings communicate vocally with each other in the prolonged absence of parents. The function of sib–sib vocal communication, so-called sibling negotiation, is to resolve conflicts over which individual will have priority of access to the next delivered indivisible food item. We found that when a nestling produced longer negotiation calls and stood closer to the nestbox entrance in the absence of parents, its sibling vocally negotiated at a lower rate. Additionally, when an individual produced more negotiation calls in the absence of parents, its sibling begged less intensely at the parent's return, with begging being the key factor that determined which nestling obtained a food item. We conclude that position in the nest and the duration of negotiation calls produced in the absence of parents influence the rate of producing negotiation calls, which in turn influences the rate at which siblings beg for food from their parents. Adjusting begging behaviour could therefore depend on complex sib–sib interactions taking place in the prolonged absence of parents.

When parents are delivering food to dependent young, they have to decide which to feed first, a source of conflict between parents and offspring (Trivers 1974; Godfray 1995). Although parents may have a preference for some young (Smiseth et al. 2003), sibling competition may limit the extent to which parents can reach and feed specific offspring (Tanner et al. 2008). The honest-signalling model predicts that parents should give priority to hungry individuals that produce the most conspicuous begging signals. Indeed, from the offspring's point of view, the benefit of obtaining additional resources should compensate for the cost of signalling only if it is hungry (Godfray 1991, 1995). Although the prediction that parents provision young in relation to the intensity of offspring calling rate, and thus need, has been verified (Leonard & Horn 2001; Smiseth et al. 2003), it is usually unclear whether parents or offspring control within-brood food allocation (Porkert & Spinka 2006; Tanner et al. 2008). Siblings compete and, if they are not equal in strength, the stronger nestlings have an advantage in monopolizing parental attention. For instance, in bluethroats, *Lusciniaa svecica*, although seniors and juniors adopt similar begging behaviour when food is limited, parents preferentially feed seniors (Smiseth et al. 2003). Moreover, in many situations parents deliver food from a given position at the nest rim or at the cavity entrance, inducing siblings to compete intensely for the most profitable nest location (Budden & Wright 2005). Commonly, the strongest or most hungry young occupy the best place, which confers an advantage in monopolizing parental food resources (Dickens et al. 2008). Under the scramble competition model, competitive asymmetries between siblings predict which individual is fed by parents not only because the strongest young are better able to supplant siblings in physical competition, but also because the cost of begging may be lower for large than small individuals (Martinez-Padilla et al. 2004). Accordingly, a recent study in the great tit, *Parus major*, showed that within-brood food allocation is under nestling control rather than the result of active parental choice (Tanner et al. 2008; see also Kilner 1995). Thus, the observation that parents give priority to offspring that beg conspicuously is consistent with both the honest-signalling and scramble competition models (Royle et al. 2002). As both models can explain how food is shared among the progeny, an important aspect to tackle is the extent to which parents and offspring are in control. However, this may not be an easy task because investment in competitive behaviour and begging signals can be positively correlated (Leonard et al. 2003).

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Assessing the vocal behaviour of each nestling in a nest is technically difficult in many species, and thus researchers have often considered begging posture as an index of begging signals. Although some studies have considered vocal displays, few of them have considered both begging posture and vocalizations to examine their relative importance in within-brood parental food allocation. In the few studies that have done so, begging posture appeared to influence the probability of being fed more than vocal displays (Kilner 1995; Lichtenstein & Sealy 1997; Ostreiher 2001; Rodriguez-Girones et al. 2001a; Leonard et al. 2003; Whittingham et al. 2003; Ploger & Medeiros 2004; but see Roulin 2004). In birds, jostling for the nest position where parents predictably deliver food can involve pushing each other (McRae et al. 1993; Boersma & Davis 1997; Kölliker & Richner 2004), flapping wings to prevent siblings moving (Grim 2008), extending the neck to be closer to a parent that delivers food (Teather 1992; Hofstetter & Ritchison 1998) or beating siblings to intimidate them (Drummond 2006). Jostling for position and vocalization behaviour are not independently expressed. An individual that vigorously vocalizes usually also physically competes, which in turn can induce siblings to escalate begging behaviour (Smith & Montgomerie 1991; Leonard & Horn 1998; Johnstone 2004). Vocal and posture signals may also strategically compensate for each other: in the tree swallow *Tachycineta bicolor*, nestlings vocalized at higher rates when experimentally confined to the back of the nestbox (Leonard et al. 2003). However, how nestlings adjust vocalizations and posture in relation to the competitive ability, posture and vocal signals of their siblings remains to be examined.

The barn owl, *Tyto alba*, is particularly interesting for investigating how nestlings adjust signalling levels to each other's vocalizations and posture. Nestlings not only vocally request food from their parents (i.e. 'beg') but also vocally inform their siblings about their hunger level. This latter process, denoted 'sibling negotiation', takes place in the prolonged nocturnal absence of parents and allows each individual to adjust investment in begging behaviour optimally once the parents have returned to the nest with a food item (Johnstone & Roulin 2003). In the absence of parents, the hungriest individual vocalizes at a high rate, a behaviour that appears to induce less hungry siblings to retreat momentarily from the contest, as their chances of monopolizing food are low (Roulin et al. 2000; Roulin 2004).

In a previous study (Roulin et al. 2009), we analysed the temporal dynamics of vocal interactions between two barn owl siblings in the absence of parents. Although nestlings produced longer calls when hungrier, we nevertheless found substantial within-individual variation in the duration of calls in the very short term (i.e. within minutes) owing to social interactions that are independent of hunger level, since food need cannot vary so quickly. When a nestling increased (versus decreased) call duration, its sibling produced longer (versus shorter) calls, and hence call duration fluctuated over time. This suggests that siblings challenge each other vocally in the very short term to assess each other's motivation. The aim of that study was to investigate the pattern of temporal fluctuation of call duration, while in the present study our goal was to determine how siblings adjust the behaviours that are usually associated with the likelihood of obtaining food, that is, call duration, call rate and physical competition with each other both in the absence and in the presence of parents. This is a key aspect to understand how different signalling components interact and their relative role in how food is shared among the siblings. Thus, although we reanalysed some of the data published in 2009 (we nevertheless doubled the data set by using unpublished data), the analyses and goals of the present study were fundamentally different.

Vocalization rate and call duration in the absence of parents are closely associated with hunger level (Roulin et al. 2001, Roulin et al. 2009), and hence the honest-signalling model predicts that siblings adjust calling rate to each other's vocalization in both the absence and the presence of parents. This model predicts that a nestling would reduce vocal signalling and retreat from the competition for prey if its sibling increases its vocalization rate and/or call duration. Under the scramble competition model, a nestling would adjust calling rate in both the absence and the presence of parents in relation to sibling behaviour associated with jostling to be close to the nestbox entrance. This model predicts that the individual standing closer to the nest position where parents predictably deliver food would induce its sibling to refrain from vocalizing.

METHODS

Study Organism

The barn owl is medium-sized with a body mass of 241–515 g and predates small mammals in the open landscape at night. As eggs are laid every 2.5 days and females start to incubate the clutch once the first egg has been laid, there is a pronounced within-brood age hierarchy. The mother feeds the offspring with food items brought by the father until the offspring are about 2 weeks of age, when the mother begins to hunt for the brood. At the age of 3 weeks, nestlings are thermoindependent and are able to consume food without the mother's help. For this reason, she is no longer present in her nest during daylight hours, coming back only at night to feed her young. This situation is convenient for manipulating nestlings' hunger level during the day without disturbing the parents. At night, about every hour, parents deliver a single prey item per nest visit, which is consumed by a single nestling. This implies that at each parental visit only the individual that obtains the food item is paid back for all the effort invested in sib–sib vocal communication, begging calls directed to parents and scramble competition. Barn owl siblings are rarely aggressive to each other.

General Methods

The study was performed in 1997, 2000 and 2001 in western Switzerland on a population of wild barn owls breeding in nestboxes (1.0 × 0.6 m and 0.5 m high) located on barn walls. We created 74 two-chick broods, as in larger broods the vocal behaviour and position of each individual in the nest are difficult to record (between 1986 and 2008, mean ± SE brood size of 764 broods that produced at least one fledgling was 4.3 ± 1.4 with a difference in age between the first and the last nestling being 1–39 days). In the evening from 2130 to 2400 hours, we removed from the nest all but two individuals, randomly chosen. Thus, two individuals remained in their nest while their nestmates were temporarily placed in a large ventilated plastic can (diameter = 0.6 m; height = 0.8 m) at some distance from the nest until midnight, when they were put back in their nest. Focal nestlings were thus in a natural, unmanipulated state of hunger. We estimated the age of the two focal nestlings by measuring the length of the flattened wing from the bird's wrist to the tip of the longest primary (Roulin 2004). The oldest nestling, referred to as 'senior', was 40 days (range 18–59) and the 'junior' sibling 33 days (range 15–56). Age difference between the two siblings was 7 days (range 1–22). For comparison, in 44 natural two-chick broods observed between 1990 and 2009, the range of age difference between siblings was 1–12 days (unpublished data).

We installed an infrared-sensitive camera and a microphone in nestboxes without any apparent signs of distress to either the adults or nestlings. The two siblings were ringed on a different leg

Table 1
Behaviour of junior and senior barn owl siblings in the absence of parents during the first 14 min of the 15 min preceding the first parental feeding visit of the night (so-called 'negotiation period'), and during the first parental feeding visit (so-called 'begging period')

		Junior	Senior	Paired *t* test		
				t	*df*	*P*
Negotiation	Nestling age (days)	33.0±11.2	39.8±11.2			
	Call rate (no. calls/min)	7.6±5.9	4.1±4.5	3.70	73	<0.001
	Call duration (s)	0.68±0.13	0.65±0.18	0.55	44	0.58
	Position relative to nest entrance (%)	34.2±40.1	40.4±41.4	0.70	69	0.48
Begging	Call rate (no. calls/min)	45.6±20.4	36.6±17.4	2.04	49	0.046

The variable 'Position relative to nest entrance' refers to the percentage of time a given individual was positioned closer to the nestbox entrance than its sibling. The sum of the two percentages (i.e. 34.2 + 40.4 = 74.6) does not equal 100 because the two individuals were positioned at an equal distance to the nestbox entrance 25.4% of the time. Means are quoted ± SD.

to distinguish them on video footage. We recorded the negotiation rate of each individual as the number of calls/min produced during the first 14 min of the 15 min preceding the first parental visit of the night; at this visit parents always brought a food item. Calls could be easily assigned to one of the two individuals as nestlings open their bill while calling, and calls can be distinguished by ear. There was no sign that during these 14 min nestlings noticed the presence of a parent in the surroundings of the nestbox, given that they suddenly behave differently once a parent signals its presence by calling or making some noise near the nestbox. As explained in Roulin et al. (2009), we also measured the mean duration of calls produced by each nestling in 45 nests (we added data of 21 nests compared to Roulin et al. 2009). Roulin et al. (2009) examined the temporal dynamics of sib–sib vocal interactions and thus used recordings for which precise analysis could be done on calls for a long period of time. For the present paper, our aim was to have a measure of mean call duration for each nestling. For this reason, we could use more videotapes, as we added the recordings on which at least 90% of the calls produced before the first arrival of a parent were measurable. As an index of jostling for position, we recorded the proportion of time that each nestling was closer to the nestbox entrance than its nestmate during the first 14 min of the 15 min preceding the first parental visit of the night. This could be done in 70 nests. The sum of the percentages of the junior and senior siblings does not necessarily equal 100 because the two individuals can sometimes be positioned at an equal distance to the

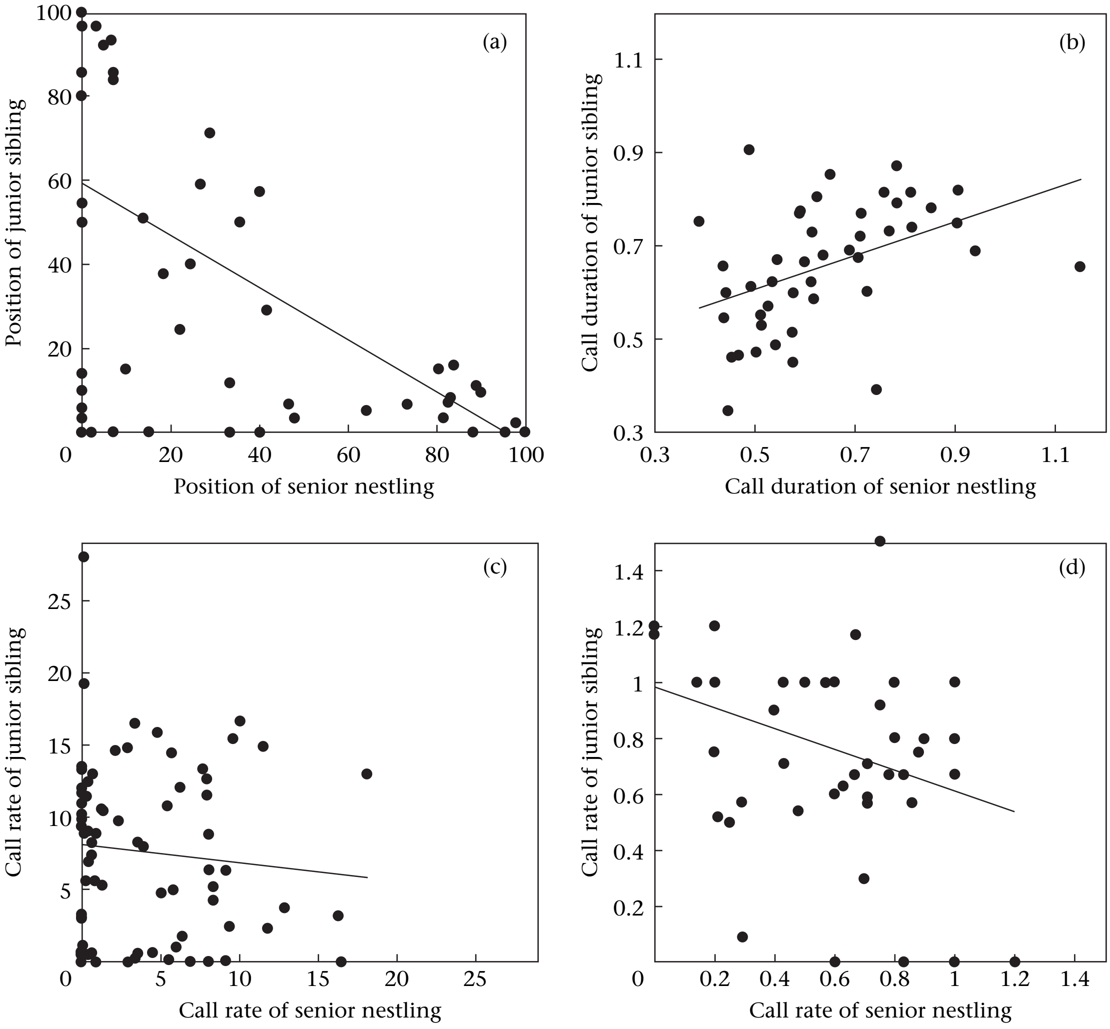
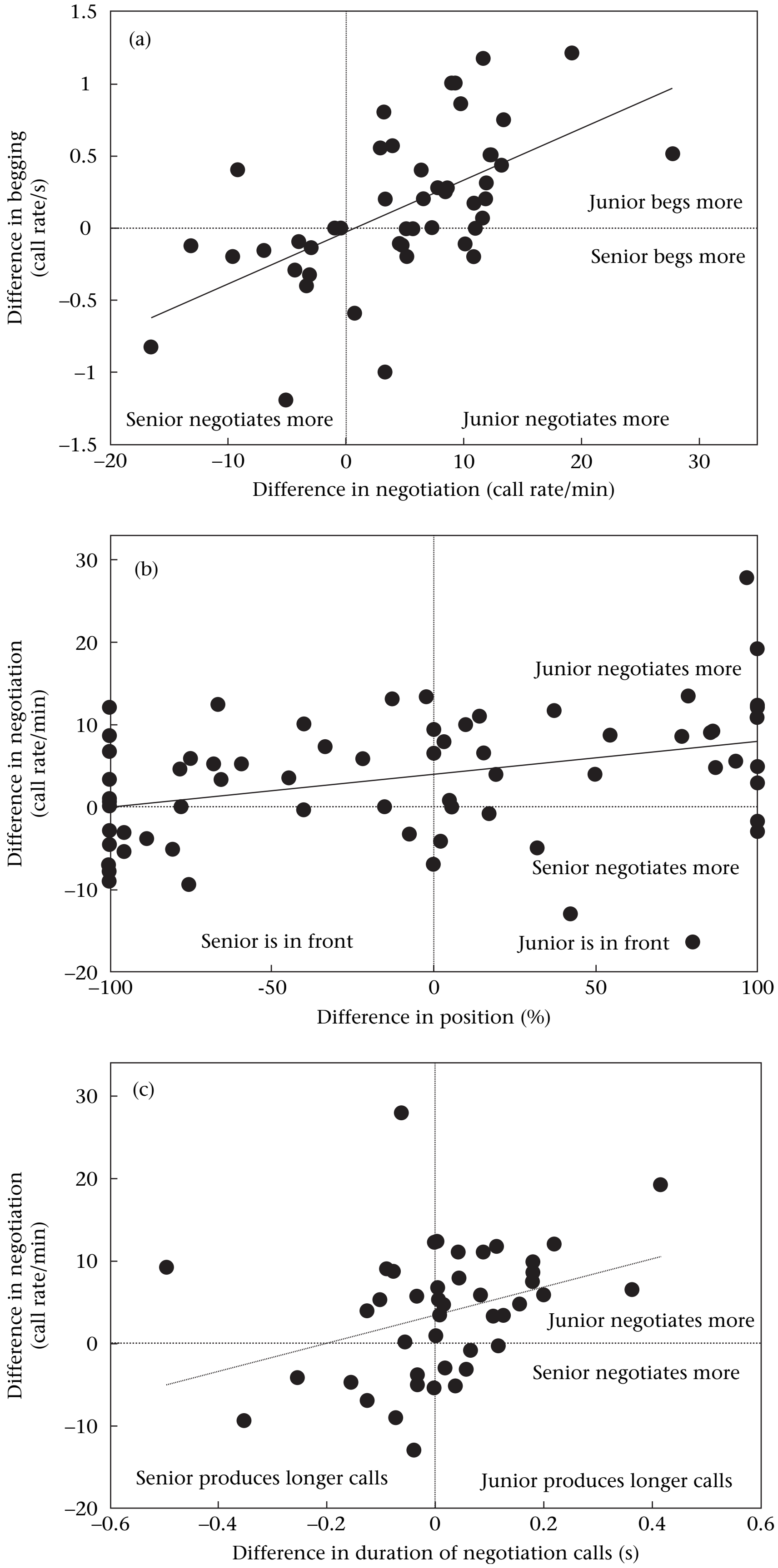


Figure 1. Pairwise correlations between the behaviours of junior and senior sibling barn owls (a, b, c) before the arrival of a parent and (d) in the presence of a parent delivering a prey item. Data were collected in two-chick broods at the beginning of the night; behaviours in the absence of parents were recorded during the first 14 min of the 15 min preceding the first parental feeding visit of the night. (a) Mean percentage of time each individual was closer to the nestbox entrance than its sibling. (b) Mean duration of negotiation calls (s). (c) Number of negotiation calls/min. (d) Number of begging calls/s. Regression lines are drawn for illustrative purposes.


(a)
Difference in begging (call rate/s)
Difference in negotiation (call rate/min)
1.5
1
0.5
0
−0.5
−1
−1.5
−20
−10
0
10
20
30
Junior begs more
Senior begs more
Senior negotiates more
Junior negotiates more
(b)
Difference in negotiation (call rate/min)
Difference in position (%)
30
20
10
0
−10
−20
−100
-50
0
50
100
Junior negotiates more
Senior negotiates more
Senior is in front
Junior is in front
(c)
Difference in negotiation (call rate/min)
Difference in duration of negotiation calls (s)
30
20
10
0
−10
−20
−0.6
−0.4
−0.2
0
0.2
0.4
0.6
Junior negotiates more
Senior negotiates more
Senior produces longer calls
Junior produces longer calls

nestbox entrance. In 50 nests, we recorded begging as the number of calls produced between a parent entering the nestbox and giving its prey to one of the two offspring. We divided this number by the amount of time during which the calls had been produced (on average 9.1 ± 1.2 s). We knew the identity of the individual consuming the first delivered prey item of the night in 64 nests. Sample sizes varied for the different behavioural components (i.e. rate of negotiation calls, call duration, rate of begging calls and nest position) because the two siblings were not always visible on video footage. Results were similar (same final models with similar P values; not shown) when we analysed the nests for which we estimated all behavioural components in the two siblings.

The study was carried out with the authorization of the ‘Service Vétérinaire du canton de Vaud’ (for ethical details, see Roulin & Bersier 2007).

Statistical Procedure

To analyse the likelihood of obtaining the first prey item of the night, we performed a generalized mixed model (glimmix, SAS Institute, Cary, NC, U.S.A.) with the identity of the nestling that obtained the prey item as the dependent binary variable (junior or senior). We included four covariates: differences between junior and senior in negotiation and begging call rates, call duration and position in the nestbox in the absence of parents. The difference in begging rate between junior and senior was analysed with a mixed model (SAS Institute, three covariates: differences between junior and senior in negotiation call rate, call duration and position). We used the same method for the analysis of the difference between junior and senior in negotiation call rate (two covariates: differences between junior and senior in call duration and position). We performed backward model selection using $P = 0.05$ as the threshold value for elimination. We verified that the final models selected had a smaller Akaike information criterion (AIC) than initial and intermediate models. Final models only contained significant effects and we present the statistical results of the initial model for the nonsignificant covariates eliminated during model selection. In all analyses, including mean sibling age and their age difference did not modify our conclusions; hence, we removed these variables to simplify the models. Note that this does not necessarily imply that within-brood age hierarchy does not play a role in how each individual adjusts its behaviour (senior nestlings can dominate their younger siblings whatever the age difference between them). Begging rate was normalized by a log transformation. For all models, residuals were normally distributed.

RESULTS

Behavioural Interactions Between Seniors and Juniors

Senior individuals consumed the first prey item of the night in 30 cases and juniors in 34 cases (binomial test: $P > 0.71$). Juniors produced on average more calls than seniors both in the absence and in the presence of parents (Table 1). This result confirms previous findings showing that, independently of age, juniors call more frequently than their senior sibling (Roulin 2004). In the absence of parents, the two individuals did not differ in the proportion of time they were closer to the nestbox entrance than their sibling or in mean call duration (Table 1). We carried out pairwise Pearson correlations to investigate whether the different behaviours were correlated between juniors and seniors. Nest positions of siblings were negatively correlated, which logically arises from the fact that the longer a nestling is in front, the longer its sibling is behind ($r_{68} = -0.65$, $P < 0.0001$; Fig. 1a). In the absence of parents, mean durations of calls produced by junior and senior siblings were positively correlated ($r_{43} = 0.43$, $P = 0.003$; Fig. 1b) but call rates were not ($r_{72} = 0.10$, $P = 0.41$; Fig. 1c). In the presence of parents, begging rates of junior and senior siblings were negatively correlated ($r_{48} = 0.32$, $P = 0.024$; Fig. 1d).

Adjustment of Vocal Signalling and Within-brood Food Allocation

The generalized mixed model showed that nestlings had a higher probability of obtaining the prey item both when they begged for food at a higher rate than their sibling (final model: $F_{1,37} = 12.61$, $P = 0.001$) and when they had produced longer negotiation calls in the absence of parents (final model: $F_{1,37} = 8.88$, $P = 0.005$). In contrast, negotiating at a higher rate (initial model: $F_{1,35} = 0.41$, $P = 0.53$) or being at the front more often (initial model: $F_{1,35} = 0.40$, $P = 0.53$) beforehand in the absence of parents did not explain which of the two siblings obtained the first prey item of the night.

Because the difference in begging rate between the two siblings was a key factor that determined which individual obtained the first prey item of the night, we investigated how siblings adjusted begging level to each other. The difference in begging call rate between senior and junior siblings was positively related to the difference in negotiation rate in the absence of parents (final model: $F_{1,48} = 24.15$, $P < 0.0001$; Fig. 2a), but not to the difference in the mean duration of their negotiation calls nor to their position in the absence of parents (initial model: $F_{1,36} = 0.56$, $P = 0.46$ versus $F_{1,36} = 0.21$, $P = 0.65$). Further analyses showed that the begging rates of both junior and senior siblings were related to their difference in negotiation rate ($F_{1,48} = 21.30$, $P < 0.0001$ and $F_{1,48} = 7.74$, $P = 0.008$, respectively). This result suggests that when the senior individual negotiates at a higher level than its junior sibling, it will beg at a higher rate while its sibling will reduce investment in begging.

As begging rate was sensitive to investment in negotiation rate, we investigated how siblings adjusted the latter component of signalling to each other. In the absence of parents, the difference between siblings in the rate of negotiating was positively related to the difference in their relative position in the nest and in the mean duration of their negotiation calls (final model: $F_{1,42} = 12.01$, $P = 0.001$ and $F_{1,42} = 5.31$, $P = 0.026$, respectively; Fig. 2b,c).

DISCUSSION

Several studies have demonstrated that offspring adjust begging behaviour not only to their own level of need but also in relation to the number of siblings, siblings’ behaviour and their size. Most studies have considered begging posture, including proximity to the nest entrance, neck and legs stretching upwards, gaping, wings moving and latency to beg (Smith & Montgomerie 1991; Leonard &

Figure 2. Adjustment of negotiation and begging rates in relation to both vocal behaviour and jostling for position in nestling barn owls. (a) Difference in begging call rates in the presence of parents between junior and senior siblings in relation to their difference in negotiation call rates in the absence of parents. (b) Difference in negotiation call rates in the absence of parents between junior and senior siblings in relation to their difference in percentage of time each individual was closer to the nestbox entrance than its sibling. (c) Difference in negotiation call rates in the absence of parents between junior and senior siblings in relation to their difference in mean duration of negotiation calls. Data were collected in two-chick broods at the beginning of the night; behaviours in the absence of parents were recorded during the first 14 min of the 15 min preceding the first parental feeding visit of the night. Regression lines are drawn for illustrative purposes.

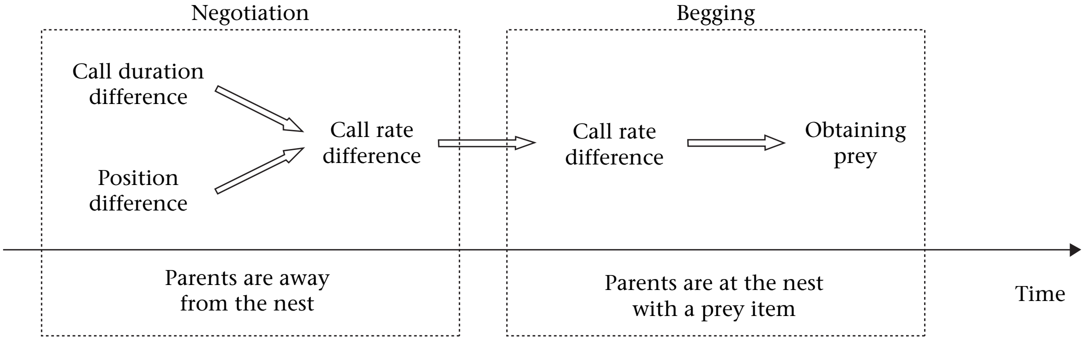


Figure 3. Synthesis of the hypothetical roles of the different behaviours leading to a nestling obtaining prey. In the absence of parents the individual that produces longer negotiation calls (i.e. 'Call duration difference' during the negotiation phase) and is positioned closer to the nestbox entrance (i.e. 'Position difference' during the negotiation phase) induces its siblings to negotiate at a lower rate (i.e. 'Call rate difference' during the negotiation phase). The individual that negotiates more than its sibling (i.e. 'Call rate difference' during the negotiation phase) induces its sibling to beg at a lower rate ('Call rate difference' during the begging phase), which positively influences its likelihood of obtaining a prey item from its parents (i.e. 'Obtaining prey').

Horn 1998; Cotton et al. 1999; Kedar et al. 2000; Rivers 2006), but rarely begging calls (Price et al. 1996; Bell 2007) and the temporal dynamics of how siblings adjust signalling level to each other. Therefore, it remains unclear how nestlings adjust begging calls, a trait that evolved to signal need, while begging posture may be primarily used in scramble competition (Kilner 1995; Lichtenstein & Sealy 1997; Ostreiher 2001; Rodriguez-Girones et al. 2001a; Leonard et al. 2003; Whittingham et al. 2003; Ploger & Medeiros 2004).

The present study, although correlative, suggests a mechanism of how barn owl siblings adjust negotiation behaviours (in the absence of parents) and begging (in their presence) to each other. In the prolonged absence of parents, the individual A that was positioned closer to the nestbox entrance and that produced longer negotiation calls seemed to induce its sibling B to reduce its vocalization rate, which in turn induced individual A to beg at a high rate once parents were back. Thus, both relative investment in jostling for position and call duration would determine relative investment in the rate of vocal negotiation, which would influence relative investment in begging for food, the crucial factor that determines which of the two individuals is fed first (Fig. 3). It remains unclear why the duration of negotiation calls produced in the absence of parents predicted the likelihood of being fed, as this parameter was not correlated with the rate of begging calls. It may be that the duration of negotiation calls is associated with behaviour in the presence of parents (jostling for position for instance) that influenced food provisioning by parents in the same way as begging. This could explain why call duration is related to getting food without being related to begging.

Our correlative results suggest that the different nestling behaviours expressed in the absence and presence of parents have different functions. The relative costs of the studied behaviours have not been tested formally, but it is probable that they present different constraints. In the absence of parents, the frequency of calling appears to be more sensitive to hunger level (Roulin 2001) than call duration (Roulin et al. 2009), suggesting that increasing the production of negotiation calls may be more costly than increasing the duration of each call. In a single night each nestling produces on average 1786 calls in the absence of parents, up to 37 calls in 1 min, and hence during the rearing period more than 70 000 calls may be produced per nestling (Roulin 2002). This extensive call production should thus have a substantial energetic cost, although production of single calls is thought to be energetically cheap in birds (Bachman & Chappell 1998; Oberweger & Goller 2001; Ward et al. 2003; but see Rodriguez-Girones et al. 2001b; Kilner 2001). Sibling barn owls challenge each other by modulating call duration in the very short term: when one individual produces longer calls, its sibling challenges this message by increasing the duration of its own calls (see Figures 1 and 2 in Roulin et al. 2009) leading to fine adjustment of call duration between siblings over time. This sib–sib vocal interaction system explains why the mean durations of calls produced by siblings are strongly positively correlated (Fig. 1b). These vocal challenges may allow siblings to identify which individual is the hungriest and thereby to adjust calling rate more precisely, an activity that is probably more costly. The individual that constantly produces longer calls appears to induce its sibling to reduce investment in negotiation rate (Fig. 2c) but not in call duration, given that siblings seem constantly to challenge each other with the duration of negotiation calls to ensure that signals are reliable (Roulin et al. 2009). We hypothesize that the least costly components of signalling influence the way siblings adjust the more costly components: producing long calls would be less costly than producing more negotiation calls, which would be less costly than producing more begging calls. Being placed where parents predictably deliver food (i.e. the nestbox entrance) before the arrival of a parent does not directly determine which of the two siblings is fed first but indicates to siblings the motivation to compete for food once parents are back. The position where parents deliver food is predictable and hence nestlings may position themselves close to the nestbox entrance instead of producing more or longer negotiation calls. This may again reduce the cost of signalling. It therefore seems that considering sib–sib signalling interactions in the absence of parents should provide useful insights into the resolution of parent–offspring conflicts.

Our observations provide novel insights into the underlying mechanisms by which offspring can control within-brood food allocation. Although within-brood food allocation is principally related to begging, this does not necessarily mean that parents actively control this allocation. Even if parents can choose to which individual they allocate food by assessing begging levels, the rate at which each nestling begs could be the result of complex sib–sib physical and signalling interactions taking place in the prolonged absence of parents. Previous studies in passerines showed that nestlings escalate begging behaviour after their siblings begged more intensely (Smith & Montgomerie 1991, Price & Ydenberg 1995, Leonard & Horn 1998). However, in passerines these adjustments appear to be extremely quick because parents deliver food very rapidly, implying that nestlings beg for short periods of time. It was thus unclear how siblings can be so rapid in their adjustment. Our study provides some new information by showing that complex vocal and physical behaviour taking place in the absence of parents may be necessary for siblings to adjust begging behaviour to each other correctly once parents are back at the nest with food. Relative sibling investment in begging behaviour depends on the effort put into sib–sib vocal communication occurring in the prolonged absence of parents, which itself depends on investment in physical competition and on the intensity of vocalization calls as measured by call duration. Thus, our results open new perspectives for understanding the role of vocal and physical interactions between siblings in begging behaviour and more generally parent–offspring interactions.

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