

Vocal communication regulates sibling competition over food stock

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Received: 23 November 2015 / Revised: 24 March 2016 / Accepted: 29 March 2016 / Published online: 12 April 2016
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Abstract

Animals resolve conflicts over the share of resources by competing physically or signalling motivation with honest signals of need. In some species, young siblings vocally signal to each other their hunger level and the most vocal individual deters its siblings from competing for the non-divisible food item delivered at the next parental visit. This so-called sibling negotiation for forthcoming food has been studied only in this context. It therefore remains unclear whether siblings could also negotiate access to a pool of divisible resources, a situation that is similar to a group of individuals competing for an accessible food resource. To tackle this issue, we placed barn owl (*Tyto alba*) nestlings singly in artificial nests containing several mice, and we simulated the presence of a sibling calling at low or high rate using playback experiments. If nestling barn owls vocally negotiate over a divisible food stock, we propose the following two predictions. First, nestlings would vocally signal before eating from this stock of food, and second, numerous playback vocalizations would inhibit feeding. Accordingly, singleton nestlings vocalized just before consuming food stored in their artificial nest and they delayed the consumption of the food stock if hearing many playback

calls. The production of such food-associated vocalizations has been observed in foraging adults in various birds and mammals, but never in young animals and when resource is divisible and easily accessible. Our study raises the possibility that vocal communication could evolve in a variety of competitive contexts.

Significance statement

We present here the first experimental evidence that sibling barn owls use food-associated vocalizations to compete over the preys stored in the nest. Owlets emit calls just before consuming an available food item and broadcasting calls induces nestlings to temporarily refrain from eating from the food stock. This raises the possibility that vocal communication can mediate the share of a food stock accessible to all competitors.

Keywords Conflict · Food-associated call · Food stock · Negotiation · Sibling competition · Vocal communication · Barn owl · *Tyto alba*

Introduction

In species with parental care, the offspring of a brood are in conflict with their parents because they request more care than parents are willing to provide (Godfray 1991; Mock and Parker 1997). As a consequence, siblings raised together enter in competition and each individual tries to acquire a larger than equal share of the parental resources. Sibling competition is not restricted to species with parental care because mothers can abandon their clutch leaving the offspring competing for a pool of limited resources (Godfray and Parker 1992). In many species, this competition can lead siblings to aggress each other up to the point of siblicide (Mock and Parker 1997).

Communicated by M. Leonard

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The resolution of sibling conflict hence often promotes selfish rather than altruistic or cooperative behaviour. However, the cost of sibling competition being substantial (Mock and Parker 1997) and relatedness between individuals leading to a reduction of selfishness in some contexts (Hamilton 1964; Brown 1978), selection has also promoted the evolution of specific behaviours to reduce the level of sibling competition. This can involve active food sharing between siblings (Marti 1989; Roulin et al. 2012, 2016; Roulin and Dreiss 2012; Falk et al. 2014), refraining from adopting selfish behaviours, such as permitting subordinate siblings to feed in periods of food shortage (Anderson and Ricklefs 1995), sharing the cost of begging food from parents (Johnstone 2004; Mathevon and Charrier 2004) or avoiding begging competition (e.g. Madden et al. 2009). Siblings may also adjust their prospective investment in the competition by assessing each other's resource holding potential and motivation to compete (Parker 1974). Accordingly, in some birds, nestlings not only display begging signals to their parents about their need to acquire resources but also to their siblings in the absence of parents (barn owl *Tyto alba*, Roulin et al. 2000; spotless starling *Sturnus unicolor*, Bulmer et al. 2008; barn swallow *Hirundo rustica*, Romano et al. 2013). While parents are foraging, the most motivated individual indicates to its siblings its intention to compete over the food resources that parents will bring back to their nest. Being informed, their siblings momentarily retreat from the contest by reducing vocalizing towards siblings and reducing begging once parents return with a prey item, so that the motivated individual can obtain the resources without having to compete physically. This process, referred to as "sibling negotiation", would reduce the cost of sibling competition (Roulin et al. 2000; Bulmer et al. 2008). Although potentially of general applicability, tests of this hypothesis are so far restricted to the situation where siblings compete over the non-divisible food item next delivered by a parent. It therefore remains unclear whether offspring negotiate priority access to limited parental resources in other feeding contexts.

Current theory posits that the evolution of sibling negotiation is more likely to occur in species in which parental resources are not divisible, i.e. per nest visit, parents bring a single food item to be consumed by a single offspring (Johnstone and Roulin 2003). Under this condition, one individual monopolizes the single food bolus brought by a parent implying that only this individual is paid back for its effort invested in sibling competition. In that case, siblings have better inform each other about their motivation to compete once parents are back with food, so that individuals invest in the contest according to their likelihood of monopolizing the resource, i.e. retreat if this likelihood is low and compete if it is high. In the present study, we test the hypothesis that young animals also use vocal communication to compete for priority access to a pool of divisible resources. In various group-living species of birds and mammals, adults produce calls when

foraging, which deter competitors from approaching (e.g. Radford and Ridley 2008; Wright et al. 2014) or serve as social recruitment (review in Clay et al. 2012). Such communication is likely to emerge also among some broods and litters, primitive forms of group living, to regulate access to food resource. Such a non-aggressive way to partition divisible resources would allow animals to reduce the level of competition, thereby saving time and energy to be invested in other currencies.

Barn owl (*Tyto alba*) is an ideal model to investigate whether nestlings could vocally negotiate a stock of food resources that can be divided among several individuals. Owl nestlings are seldom aggressive (Cramp and Simmons 1985) and highly vocal. Owllet vocalizations, which are simple hissing calls, honestly reflect hunger level (Ruppli et al. 2013a) and are used to beg for the food item brought by parents and to negotiate with siblings priority access to this item before the arrival of parents (Roulin et al. 2000; Dreiss et al. 2010b). These food items are non-divisible and given to a single offspring at each parental visit. However, because parents usually deliver the daily offspring food requirement in the first few hours of the night (Durant et al. 2013), food items can accumulate in the nest and be consumed at a later time at night or during daylight hours when parents are away and do not provide food any more (Roulin 2004b). At a certain time point of the night and when food provisioning is important, parents drop prey items in the nest directly without giving it to a nestling (AR pers. obs.), probably because the offspring are momentarily satiated. Here, our aim is to investigate whether barn owl siblings vocally negotiate when competing for access to this stock of several prey items. Contrary to the food brought by parents, this accumulated food stock is accessible and usually divisible because it often contains several prey items. Such a study has the potential to reveal that sibling negotiation is used in a much larger context than when competing over a single non-divisible prey item next delivered by a parent. It would raise the possibility that, even in animals without parental care, siblings can use negotiation when they compete for a pool of resources, for instance when insects abandon their eggs near a food source (e.g. Campbell and Runnion 2003). Although a negotiation system is less likely to evolve when resources are divisible (Johnstone and Roulin 2003), it can be favoured if it reduces the competition for food, which in the barn owls takes the form of frequent food theft (Roulin et al. 2016) and occasional beak pecking (AND pers. obs.).

We recorded the vocal and feeding behaviour of barn owl nestlings in an experimental nest (without any parent) containing several mice, and we played back owllet calls at a high or low rate. These playback treatments mimic a situation where a nestling has to share a stock of food with either a hungry or a satiated sibling calling at high and low call rate, respectively, and are hence referred to as "competitive" and "non-competitive",

respectively. Playbacks were emitted during 75 % of the time (45 min in a row per hour) to evaluate the impact of a temporal retreat from the vocal contest of the competitor sibling (i.e. when no calls were broadcast during 25 % of the time, i.e. 15 min per hour), which happens in natural broods when the vocal siblings have just been fed. We compared nestling vocal and feeding behaviours between the two playback treatments and between vocalization (45 min) and silence periods (15 min) in each playback treatment. We examined the following three predictions assuming that a function of vocalizing in the absence of parents is to deter siblings from competing for the food stock. First, assuming that vocalizations transfer functional information about hunger or motivation to siblings, we expect that nestlings vocalize before handling a prey to inform their intention to eat soon and hence to deter their siblings from stealing their prey item (Roulin et al. 2008). Second, we predict that vocalization signals would affect the behaviour of siblings, and hence, nestlings having free access to a stock of prey items would refrain from consuming food when hearing a hungry competitor. Food stock would thus be consumed slower in high than low call rate treatment. Third, we predicted that nestlings would eat more often during the periods of silence than when calls are broadcast, as silence periods indicate that nestmates have been fed and hence do not compete anymore over food resources (Roulin et al. 2000; Dreiss et al. 2010b). This effect should predominate when facing a competitive rather than a non-competitive playback, because nestlings are more likely to withdraw from a contest in front of high than low competitive siblings, as their likelihood of winning a contest is lower (Ruppli et al. 2013a). To verify that the vocalization and feeding patterns are not restricted to playback experiments, we further analysed vocal exchanges in pairs of nestlings that could interact physically and vocally in the presence of prey remains. As a control condition, we also report the vocalization pattern of singleton owlets feeding on a food stock.

Methods

The study was performed on a wild population of barn owls in Western Switzerland (46°49'N/06°56'E) where 236 nest boxes have been installed on barns. Age was estimated by measuring wing length (Roulin 2004a) and sex identified with molecular markers (Py et al. 2006). Food stock can accumulate to up to more than 40 prey items; the stock decreases during the day when parents do not provide food anymore (Fig. 1). At nestling capture before experiments, 53 % of the broods contained at least one rodent and 19 % six rodents or more.

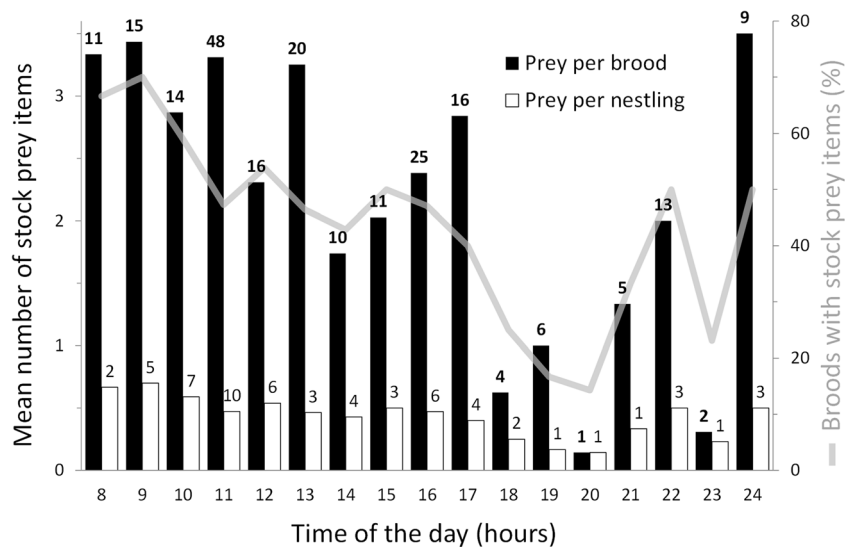
Playback experiment

Nestlings were brought to the laboratory in the afternoon and placed in a similar wooden nest box as the nest of birth (100 × 60 × 50 cm), except that they were twice as high to allow video recording and that the opening to the outside was smaller to prevent nestling escape. Nestlings stayed at the laboratory for three nights and they were brought back to their nest box on the fourth day. We video recorded the nestlings using an infrared-sensitive camera placed on the ceiling (TVCCD-150SET, Monacor International GmbH & Co. KG, Bremen, Germany) to assess the time when nestlings started and stopped to consume a food item and we recorded calls with a microphone placed on the ceiling (MC930, Beyerdynamic GmbH & Co. KG, Heilbronn, Germany) using Cubase (Steinberg Media Technologies GmbH, Hamburg, Germany) set at 44.1 kHz sampling rate and 16-bit resolution. Feeding behaviour was analysed on soundless video footage, blindly to nestling vocalization and playback broadcast. Owllet calls were detected automatically and analysed for their duration and rate, as these two features reflect hunger level (Ruppli et al. 2013a), using Matlab (MathWorks, Natick, MA, USA). Comparison of recordings with playback soundtrack permitted to exclude playback calls. Visual scanning of recordings were done to verify the accuracy of the method (Dreiss et al. 2013a; for an acoustic description of calls, see Dreiss et al. 2014).

The experiment was carried out between 16 July and 9 September 2013 on 11 female and 16 male nestlings from eight broods containing 2–6 individuals (mean ± SE 3.8 ± 0.5). They were aged 23–44 days (32 ± 1, fledging takes place at 55 days of age). At that age, they are old enough to be thermo-independent and able to eat food without maternal help. At the arrival in the laboratory, we placed all siblings in the same nest box for acclimation. In the evening at 18:00, we provided six laboratory mice (10–14 g each) per owlet, an amount that covers their daily need (67 g a day between 20 and 60 days of age, Durant and Handrich 1998). The second day, at 0800, we placed one nestling per nest box, and any remaining food item was removed to standardize hunger level until 1800 when the experiment started. At that time, six mice were placed in the box of each nestling and we started to emit a playback sequence (either the competitive or non-competitive treatment, chosen randomly) until 0800 on the next day, using a loudspeaker placed in a corner of the box slightly above nestling head (nEar05 eXperience, ESI Audiotechnik GmbH, Leonberg, Germany). The intensity of broadcast calls was adjusted by ear to the intensity of vocalizations observed in nature. Mice were removed at that time. At 1800, we placed again six mice and we broadcast the other playback treatment until 0800 in the next morning.

To build the playback sequences, we used calls of six owlets that did not consume any food in the preceding 28 h

Fig. 1 Mean number of stock prey items each hour per brood (black bars, left axis) and per nestling (white bars, left axis) and percentage of broods with stock prey items (grey line, right axis). Maximum number of prey items found is indicated above the bars. Data are from 5 years (2007, 2010–2012, 2015), 158 broods from 1 to 60 days after hatching of the first egg and 517 observations



(aged 25–35 days, four males and two females); these owlets were recorded at night in the absence of parents in 2008 (see Ruppli et al. 2013a). For each focal nestling, we built two unique playback sequences (one competitive and non-competitive) using 20 different calls emitted by a single owlet. Playback calls lasted 0.8 s (i.e. the mean duration of calls in parent absence Ruppli et al. 2013a) and their intensity was standardized using the Audacity software v.2.0.5 (<http://audacity.sourceforge.net>, a procedure that does not affect other acoustic parameters). We randomized the time interval between calls with the rule that playback emitted 16 calls/min for the competitive treatment and 4 calls/min for the non-competitive treatment. The broadcast vocalizations are different from begging events in which nestlings beg simultaneously at ca. 40 calls/min (Dreiss et al. 2010b). The calling rates were set based on the values of 68 pairs of individuals recorded in 2008 in parent absence. The 5th and 10th percentiles of individual call rates were 3 and 5 calls/min respectively, whereas the 75th and 90th percentiles were 15 and 19 calls/min, respectively (AND unpubl. results). Nestlings produce up to 45 calls per minute. For each individual, we broadcast 14 times in a row the same 45-min playback sequence, each sequence followed by 15 min of silence. Owlets react in a similar way in front of unfamiliar playback calls and live nestlings' calls (they avoid overlapping playback calls, Dreiss et al. 2013b; they refrain from calling in front of a highly vocal playback, Ruppli et al. 2013a; they insert their calls between playback calls in the same way they do with live nestlings, Dreiss et al. 2015) and are not physiologically stressed in nest boxes placed in the laboratory (Dreiss et al. 2010a).

Vocalizations of owlets in pairs and alone

To determine whether nestlings vocalize before handling a prey in presence of a live sibling or alone, we analysed vocal

behaviour of pairs of nestlings and of singleton nestlings in the presence of prey remains. The experiment was carried out between 27 May and 5 August 2012 on 34 female and 37 male nestlings from 20 broods of 2–9 young (mean \pm SE: 5.2 ± 0.3). They were aged 21–40 days (31 ± 1). Upon arrival at the laboratory, each individual was recorded during three sessions of 23 h each, from 1400 to 1300 the next day, once alone and twice with a sibling. This experiment was designed to study diel behavioural patterns of nestlings without external disturbance. At the beginning of each session, we put five laboratory mice (24 g each) per owlet. During each 23-h treatment, individuals were left undisturbed in a nest box where they could interact physically and vocally while consuming the prey remains. During this time lapse, we filmed nestling behaviour and recorded vocalizations with a single microphone. Although we could not determine the identity of the individual that produced each call, we could measure calling rate before, during and after a nestling consumed a food item. Video and acoustic analyses were performed with the same methods as above.

Statistical analyses

Effect of playback treatment

We analysed “feeding duration per prey” and “total weight of all prey items eaten during the night” (both log transformed for normalization) with linear mixed models. For the dependent variable “feeding time” (i.e. number of minutes elapsed between the beginning of a playback and consumption of a mouse), we performed generalized linear mixed models with a zero-inflated overdispersed Poisson distribution (Joe and Zhu 2005). The independent terms were as follows: playback treatment, experimental night (first or second night), nestling sex

and age, and order at which prey items were consumed (except for the analysis of total weight of all prey items eaten for which we considered the average per night and not per prey item). As we had more than one measure per individual and at least two individuals per nest of birth in our playback experiments, we controlled for the non-independence of the data by incorporating nestling identity nested in the nestling brood as a random factor in all models.

We compared the number of calls and feedings occurring during the 15-min-long silence periods and during the 45-min-long playback periods with chi-square tests.

Calling behaviour before, during and after having eaten a food item

To investigate whether nestlings called at different levels before, during and after a feeding event, we computed the mean number of calls produced at each “timing”: in the period from 20 to 10 min before starting to consume a food item, in the following 10 min (i.e. the 10 min before food consumption), while eating the food item, between the end of consuming this item and 10 min later and finally during the next 10 min. We did not consider vocal data between two feeding events separated by less than 40 min.

For the *Playback experiment*, call duration was analysed with linear mixed model and number of calls was analysed with generalized linear mixed models with zero-inflated Poisson distribution. Nestling identity nested in nestling brood was set as random factor.

For *Vocalizations of owlets in pairs and alone*, call duration (log transformed) was analysed with linear mixed model and number of calls was analysed with generalized linear mixed models with Poisson distribution. We averaged vocal parameters per “timing” and experimental box. Pair or nestling identity (for owlet pairs and singleton owlets, respectively) nested in the brood and experimental night were set as random factors. To assess the difference between each “timing” category, we computed *t* statistic as the factor estimate divided by its standard error.

We used the software SAS v9.1 (SAS Institute Inc., Cary, NC). We presented full models without selection. We checked the distribution of residuals of mixed models and scaled Pearson’s statistics of generalized mixed models. *P* values are estimated in type three tests of fixed effects. Estimates are given \pm SE.

Results

Effect of playback treatments on feeding behaviour

Nestlings consumed food items every 2 h on average (2:07 \pm 0:06). They consumed the prey items earlier in the night when facing the non-competitive playback treatment (few playback calls) compared to the night when facing the competitive treatment (many playback calls; Table 1). In pairwise comparison within nestling, prey items were consumed 29 min later per prey on average during the competitive treatment (Fig. 2). The total weight of prey items consumed per night (mean \pm SE: 58.3 \pm 1.8 g; range: 13–78 g) was not significantly related to the playback treatment (linear mixed model: $F_{1,25}=0.84$, $P=0.37$, competitive vs. non-competitive: -0.13 ± 0.14), experimental night ($F_{1,25}=1.24$, $P=0.28$, first vs. second night 0.16 ± 0.15), nestling sex ($F_{1,25}=3.45$, $P=0.08$, male vs. female -0.41 ± 0.22) and nesting age ($F_{1,25}=0.08$, $P=0.78$, 0.01 ± 0.02).

Per hour, we broadcast calls during the first 45 min, and hence, if feeding events occur randomly, 75 % of the prey items would have been consumed during the playback and 25 % during the silence periods. This was, however, not the case, because owls tended to avoid eating when hearing the competitive playback (only 62 % of the prey items were consumed during the playback and 38 % during the silence, chi-square test: $\chi^2_1=9.08$, $P=0.003$), but not when hearing the non-competitive playback (71 vs. 29 %; $\chi^2_1=0.94$, $P=0.33$).

Hence, over the whole night, nestlings facing a competitive playback treatment ate as many prey items as when facing a non-competitive treatment. However, they delayed the time when they consumed food in the

Table 1 Rapidity to consume prey items stored in the nest in 27 barn owl singleton nestlings

	Estimate \pm SE	<i>F</i>	<i>P</i>
Playback treatment (competitive vs. non-competitive)	0.18 \pm 0.06	8.4	<i>0.004</i>
Experimental night (first vs. second)	0.28 \pm 0.06	20.9	<i><0.0001</i>
Prey order	0.45 \pm 0.02	684.1	<i><0.0001</i>
Nestling sex	0.15 \pm 0.18	0.7	0.40
Nestling age	0.01 \pm 0.02	0.7	0.41

Results of a generalized linear mixed model with as dependent variable the time lapse between the start of experiment (18 h) and the time when owls started to consume a prey item ($df=238$), with the nestling identity nested in brood identity as random factor (estimate 0.18 ± 0.06). The factor “Prey order” indicates the order at which prey items were consumed; 1 = first prey item consumed, 2 = second prey item consumed, and so on. Significant terms are written in italic

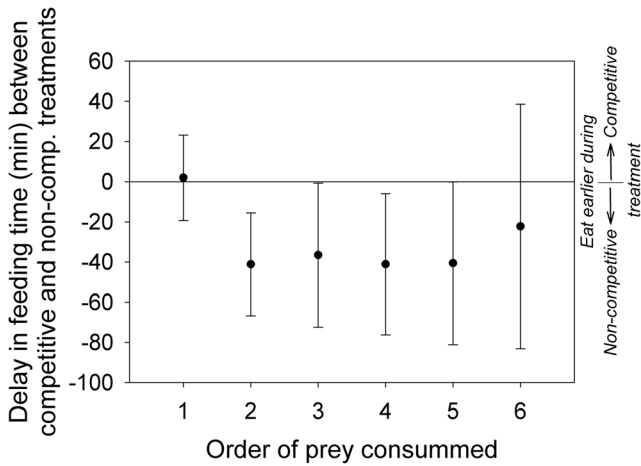


Fig. 2 Difference in owlets' time of feeding (min) between the competitive treatment (high playback call rate) and non-competitive treatment (low playback call rate), for each prey consumed (differences are calculated within nestling, average difference values are given \pm SE). We distinguish prey items by the order at which they were consumed (first to sixth)

competitive treatment, because they were more likely to wait for the playback to stop before eating (Fig. 3). As shown in Fig. 3, this preference to eat during periods of silence was more pronounced at the beginning of the night. During the first 5 h of the experiment, nestlings ate significantly fewer prey items when hearing a competitive playback than a non-competitive playback (Wilcoxon signed rank test: $S = -57$, $P = 0.039$, $N = 27$ nestlings) and compensated by eating significantly more items during the silence periods (Wilcoxon signed rank test: $S = 42$, $P = 0.021$, $N = 27$ nestlings).

Nestlings took less time to consume the first prey items of the night compared to the last items (mean \pm SE: first mouse 1 min 52 \pm 22 s; sixth mouse 3 min

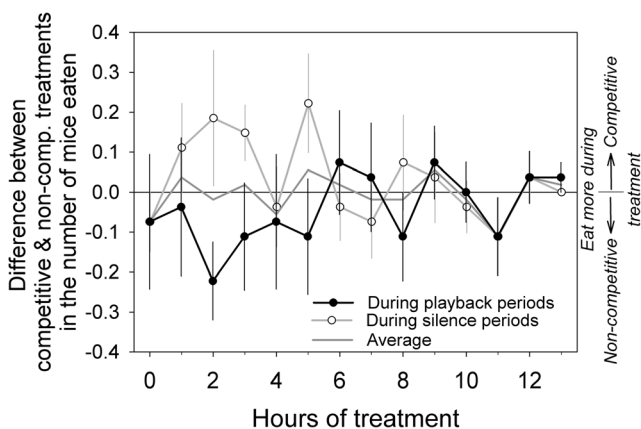


Fig. 3 Difference in the mean number of mice eaten in nestlings facing a competitive treatment and a non-competitive treatment, during each 45 min of playback periods (black), during the following silences of 15 min (white), and on average over the two periods (grey). Differences are calculated within nestling, average difference values are given \pm SE

45 \pm 50 s; range 10 s–18 min 13 s; prey order effect: $F_{1,237} = 10.53$, $P = 0.0013$, 0.11 \pm 0.03) and older nestlings took less time to eat an item than their younger nestmates (age effect: $F_{1,237} = 8.10$, $P = 0.0048$, -0.08 \pm 0.03); in the same model, the playback treatment (competitive vs. non-competitive: $F_{1,227} = 0.01$, $P = 0.96$, -0.01 \pm 0.10), experimental night (i.e. first or second; $F_{1,237} = 1.92$, $P = 0.17$, -0.15 \pm 0.11) and nestling sex ($F_{1,237} = 0.62$, $P = 0.43$, male vs. female: 0.21 \pm 0.27) did not explain any significant part of the variation in the time taken to consume prey items.

Effect of playback treatments on nestling vocalization

In the competitive treatment, nestlings vocalized more often during the 15-min periods of silence than during the 45 min of playback than expected at random ($\chi^2_1 = 22.54$, $P < 0.0001$), which was not the case in the non-competitive treatment ($\chi^2_1 = 0.40$, $P = 0.53$; Fig. 4). Therefore, nestlings vocalised more often during the periods of silence in the competitive than non-competitive treatment (Wilcoxon signed rank test: $S = 67$, $P = 0.026$), whereas nestling call rate was not significantly different between the two playback treatments when calls were broadcast ($S = 49$, $P = 0.17$). In contrast, the mean duration of calls did not differ significantly between the time periods (difference between competitive and non-competitive treatment, during silence: $S = -4$, $P = 0.86$; during playback: $S = -22$, $P = 0.45$).

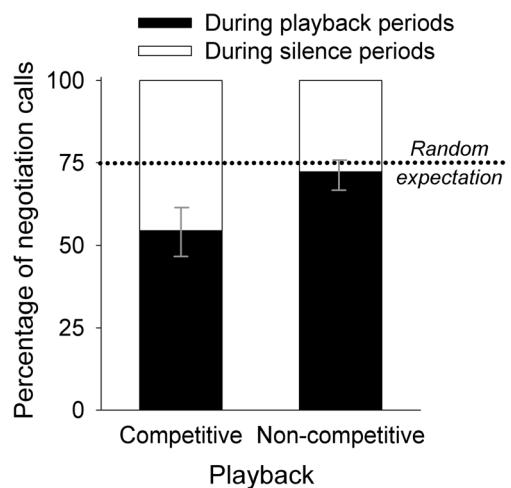


Fig. 4 Percentage of calls produced by singleton barn owl nestlings (\pm SE) facing a competitive (16 calls emitted per minute) and non-competitive playback (four calls emitted per minute) during the 45 min of playback emission and the next 15 min of silence. Random expectation (25 % of the calls should be produced during the silence period and 75 % during the playback period) is indicated with the broken line

Calling behaviour before, during and after having eaten a food item

Playback experiment

Nestlings increased their call rate during the 10 min before eating a prey item (Table 2a; Fig. 5a). Mean call duration did not vary significantly around feedings (Table 2a).

Vocalizations of owlets in pairs and alone

Call rate was also highest during the 10 min before eating a prey item in pairs of live siblings (Table 2c, Fig. 5b). Call rate changed with timing in isolated owlets, but was not significantly different during the 10–0 min and 20–10 min before eating (Table 2d, Fig. 5b). No change was detected in mean call duration (Table 2c and d).

Discussion

We present here the first experimental evidence that altricial young use vocal communication to compete for a divisible and accessible food stock. Nestlings emitted calls mainly during the 10 min preceding the consumption of food stored in the nest. Furthermore, broadcasting owlet calls in the absence of parents induced nestmates to temporarily refrain from eating the available food stock. This indicates that vocalizations alone inhibit siblings from eating even when no sign of physical competition is present. Calling before handling a food item would thus permit to ensure priority over the food stock and possibly reduce further competition in the form of food stealing and beak peaking by siblings. High vocalization rate just before eating was also found in pairs of siblings in the presence of a food stock, but not in isolated owlets, confirming the presence of a vocal communication between live siblings before feeding from an accessible stock. During competitive treatments, nestlings ate preferentially during the periods of silence, when the playback momentarily stopped.

Table 2 Call rate and mean duration of calls before, during and after having eaten a prey item stored in the nest in (a) singleton nestlings facing a playback (b) pairs of owlets without playback and (c) singleton owlets without playback

	Rate of nestling calls			Mean duration of nestling calls		
	Estimate ± SE	<i>F</i>	<i>P</i>	Estimate ± SE	<i>F</i>	<i>P</i>
a. Playback experiment						
Timing		<i>2.83</i>	<i>0.024</i>		0.33	0.86
–20 vs. –10	–0.55 ± 0.32			0.07 ± 0.07		
0 vs. –10	–1.12 ± 0.36			0.02 ± 0.09		
10 vs. –10	–0.69 ± 0.33			0.03 ± 0.07		
20 vs. –10	–0.50 ± 0.31			0.02 ± 0.07		
Playback treatment (competitive vs. non-competitive)	0.00 ± 0.20	0.01	0.98	–0.05 ± 0.05	0.80	0.37
Prey order	0.16 ± 0.07	<i>5.49</i>	<i>0.019</i>	0.01 ± 0.02	0.37	0.54
Experimental night (first vs. second)	0.27 ± 0.23	1.30	0.25	–0.01 ± 0.05	0.07	0.79
b. Vocalizations of owlets in pairs						
Timing		<i>30.04</i>	<i><0.0001</i>		1.44	0.22
–20 vs. –10	–0.30 ± 0.07			0.04 ± 0.02		
0 vs. –10	–0.63 ± 0.08			0.02 ± 0.02		
10 vs. –10	–0.47 ± 0.07			0.01 ± 0.02		
20 vs. –10	–0.70 ± 0.08			0.03 ± 0.02		
c. Vocalizations of owlets alone						
Timing		<i>7.50</i>	<i><0.0001</i>		1.13	0.35
–20 vs. –10	–0.15 ± 0.21			0.12 ± 0.08		
0 vs. –10	–2.21 ± 0.64			–0.04 ± 0.10		
10 vs. –10	–1.44 ± 0.43			0.09 ± 0.10		
20 vs. –10	–1.20 ± 0.35			0.06 ± 0.09		

“Timing” represents the period of call emission (20 to 10 min before eating a prey item, the 10 min before eating a prey item, during prey consumption, during the 10 min after having consumed this item, 10 to 20 min after having eaten a prey item) and “Prey order” the order at which prey items were consumed. Generalized linear mixed model for call rate ($df = (a) 946, (b) 332, (c) 72$) and linear mixed models for mean call duration ($df = (a) 55, (b) 332, (c) 72$) were performed with the nestling identity nested in brood identity as random factor. Significant terms are written in italic

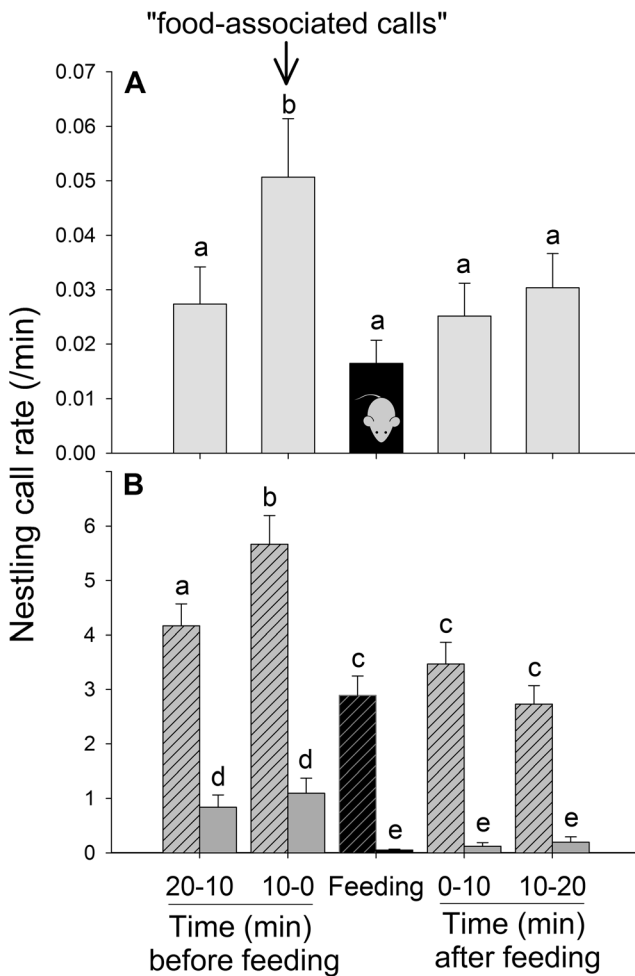


Fig. 5 Call rates (+SE) before, during and after having consumed a prey item taken from a stock of food in nestling barn owls. **a** Singleton nestling facing a playback, **(b)** pairs of live siblings (*striped bars*) and singleton nestlings without playback (*full bars*). The food-associated calls referred to the calls produced just before feeding. Five periods were defined: calls produced from 20 to 10 min before eating a prey item, the 10 min before the start of prey consumption, the feeding period, from the end of prey consumption to 10 min after having consumed this item, and from 10 to 20 min after having eaten a prey item. Means with *different letters* are significantly different in a GLMM ($P < 0.05$)

Hence, although nestlings postpone food consumption in front of a competitive playback, nestlings consumed a similar amount of prey items over the night during the two treatments, as they compensated by eating during silence in the competitive treatment. Further studies are needed to estimate to what extent and how long hungry owlets can repel siblings from eating. In our experiment, the repelling effect of the competitive playback on food consumption was higher at the beginning of the night (Fig. 3). At the end of the night, a change in hunger level, or more probably a habituation to the playback, might reduce its effect.

Comparable communication systems exist in adult primates (Caine et al. 1995; Boinski and Campbell 1996; Gros-Louis 2004) and birds (Radford and Ridley 2008), which

vocalize to announce ownership and thereby inhibit competitors to claim food. Sibling vocalizations around food stock could be compared to these "food-associated calls". To our knowledge, such signals have not been described in young animals before and in situations where the food is not hidden and easily accessible to all individuals. The presence of food-associated calls in front of food stock in barn owls indicates that animals can use vocal communication in many competitive contexts. Food calls emitted by adults could be related to producer-scronger games, where producers which find food are parasitized by scrongers (Vickery et al. 1991). To avoid being cheated, producers would vocally claim property of the recently discovered pool of resources. Communication leading an individual to momentarily abandon a resource to a conspecific is more likely to evolve and be maintained if individuals are genetically related and/or if this behaviour reduces the costs of competition (Hamilton 1964; Johnstone and Roulin 2003). Provided competition is costly and/or an animal group shares a certain degree of relatedness (because of limited dispersal for instance), such communication process might hence be favoured to limit aggression and reduce the stress induced by individuals that simultaneously compete for the same pool of food resources. In barn owls, our results suggest that siblings vocalize to signal their intention to consume part of a food stock, a behaviour that efficiently deters siblings from competing. For owlets, the benefits of withdrawing from the food contest in front of a highly motivated sibling, in terms of the indirect genetic benefits and reduction of competition level, should outweigh the cost of losing a direct benefit to obtain rapidly a food item. Producing "food-associated calls" before consuming a food stock could thus be a non-aggressive way to establish ownership over divisible resources among siblings. Because stealing a food item from a sibling is a frequent outcome in the barn owl (Roulin et al. 2012), nestlings can adopt a range of strategies to limit the risk of being robbed. When this risk is relatively high, nestlings can speed up the consumption of an entire item for instance by swallowing it instead of consuming it piece by piece (a phenomenon that was not observed in this study, but see Roulin et al. 2008), they can eat the item in a concealed place (Roulin et al. 2008) or they can possibly vocalize before eating (present study).

The production of food-associated calls in owlets during the 10 min before eating could be explained by proximate mechanisms, such as arousal (Clay et al. 2012) or a peak of hunger level just before eating. Calling before feeding on the food stock is unlikely to constitute recruitment calls attracting siblings to the food site as seen in some social animals (Brown et al. 1991; Caine et al. 1995), because owlet calls were repulsing rather than attracting to nestmates. The fact that playback calls affect owlets by refraining them from eating the food stock suggests that vocalizations have evolved or are maintained in part for this repelling function. In the total

absence of vocal competition (isolated nestlings without playback), call rate was higher during the 20 min before than the 20 min after eating, but did not increase significantly during the 10 min before eating. Hence, the presence of a vocal playback or of a live sibling favoured the production of food-associated calls. The average call rate of singleton nestlings (with or without playback) was much lower than in dyadic interactions, suggesting that vocal behaviour was also reduced in the absence of nestmates.

Competition over resources can involve a number of behaviours that entail substantial energetic costs and risk of injuries. To reduce these costs, animals can display signals that indicate to conspecifics their motivation to compete. Being informed about each other's intention, each individual of a group can then optimally adjust its competitive effort (Parker 1974; Maynard Smith 1982). In the barn owl, calls honestly reflect hunger level (Ruppli et al. 2013a) and are emitted when begging for food at parental arrival (Dreiss et al. 2010b). Calls are also used in the “sibling negotiation” process, in parental absence while waiting for them to bring food and hence in the absence of food stock (Roulin et al. 2000). Negotiation defines any situation that involves “Discussion aimed at reaching an agreement” (Oxford Dictionary). This terminology is generally used for humans who bargain a resource or a treaty. During an interactive process, each participant tries to obtain the largest portion of the pie as possible. Evolutionary ecologists also use this concept to define situations where animals performed a series of interactions to determine the share of a resource or the investment into a cooperative task (McNamara et al. 1999; Bell et al. 2010; Patricelli et al. 2011; Sirot 2012). These tactical adjustments during sequential stages can be made via exchange of transient signals such as vocalisations. Roulin et al. (2000) first used the term of “sibling negotiation” to describe the vocal interaction between siblings preceding a parental feeding event. In sibling negotiation, nestlings vocally interact in the absence of parents (Ruppli et al. 2013a; Dreiss et al. 2015), which influences the outcome of the pending competition (Dreiss et al. 2010b). Previous empirical work and theory concluded that sibling negotiation “is more likely to prove stable when the food provided by parents is non-divisible” (Johnstone and Roulin 2003). We here report data supporting the hypothesis that nestling birds also signal their intention to consume a portion of a divisible food stock (given that a food stock is composed of several prey items), a behaviour that deters their siblings from competing for it. In other words, nestlings would call more intensely just before handling and eating food items taken from a pile of stored food probably to claim their willingness to compete in the case siblings would

contest for the same items. This raises the possibility that animals can negotiate priority access to both divisible and non-divisible food resources, and even during their early development stages.

Conclusion

Our results suggest that sibling vocal communication has an important role, not only to determine which individual will receive the indivisible food item next delivered by a parent (Roulin et al. 2000) but also to determine how siblings share a pool of food items stored in their nest. This finding reveals an additional level of sophistication in the nestling barn owl communication system. More data are required to determine the relative influence of hunger level of a target nestling and of its siblings on how a food stock is shared among barn owl siblings. We also further need to evaluate the importance of this communication system in full broods. If food-associated calls reduce the competition, we expect that they occur more often when food is scarce and competitors are numerous. It would thus be interesting to examine whether the intensity, or some specific properties, of the communication process around food stock is related to the size or quality of the food stock (Hauser et al. 1993; Bugnyar et al. 2001; Clay et al. 2012). This communication could also be affected by the presence of competitors (Di Bitetti 2005), such as the number of hungry siblings, which is already known to modify sibling vocal negotiation (Ruppli et al. 2013b).

Acknowledgments We thank Paul Bézières, Pauline Ducouret, Estelle Ifrid and Baudouin des Monstiers for field assistance and Marty Leonard and two anonymous reviewers for constructive comments.

Compliance with ethical standards The experiment was carried out under the legal authorization of the Veterinary Service of Vaud canton (N°2109.1). It has been shown that reducing temporarily brood size does not decrease parental feeding rates (Roulin et al. 1999) and none of the experimental broods were abandoned. Keeping owlets at the laboratory does not negatively affect their body condition, since mean body mass and survival at fledging do not differ between experimental nestlings and those remaining in their natural nest (Dreiss et al. 2013b). Nestlings were fed with dead laboratory mice obtained from an animal house (Reptiles Farm, Servion, Switzerland).

This study was funded by Swiss National Science Foundation for funding (31003A-120517).

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Authors' contributions AD performed the playback experiment and FG analysed the vocalizations, LM and ML analysed the dyadic interactions. AND designed the experiments and supervised the project, AND and AR wrote the manuscript.

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