

Nestling barn owls assess short-term variation in the amount of vocally competing siblings

Charlène A. Ruppli, Amélie N. Dreiss & Alexandre Roulin

Animal Cognition

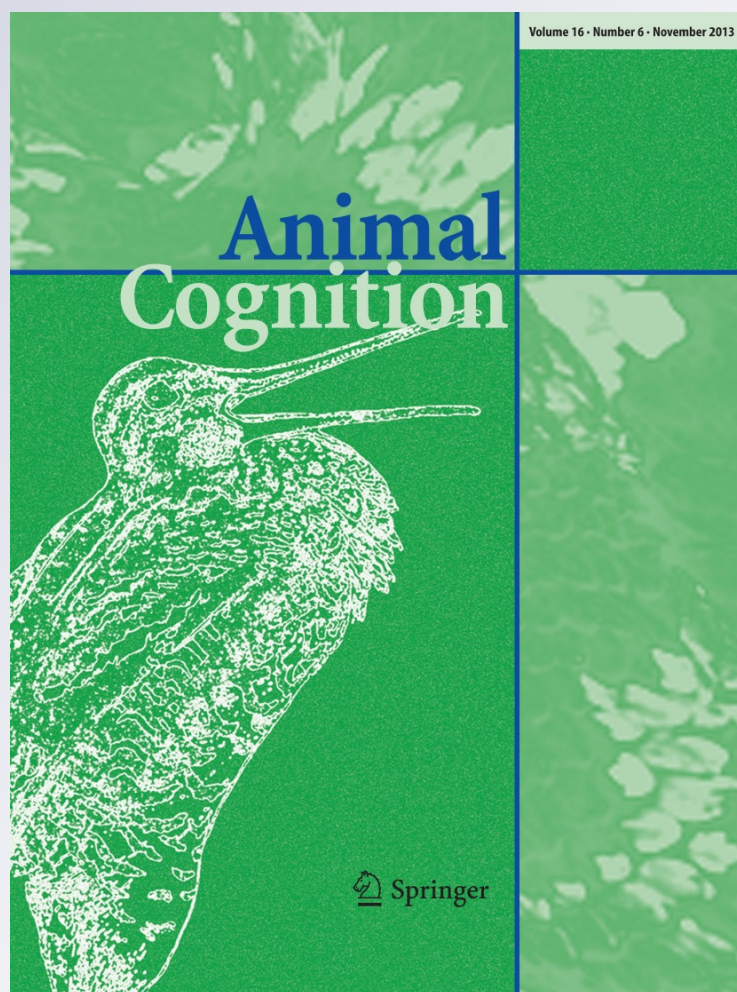
ISSN 1435-9448

Volume 16

Number 6

Anim Cogn (2013) 16:993-1000

DOI 10.1007/s10071-013-0634-y



Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Nestling barn owls assess short-term variation in the amount of vocally competing siblings

Charlène A. Ruppli · Amélie N. Dreiss ·
Alexandre Roulin

Received: 29 January 2013/Revised: 11 April 2013/Accepted: 12 April 2013/Published online: 19 April 2013
© Springer-Verlag Berlin Heidelberg 2013

Abstract Assessing the amount of rivals is crucial to optimally adjust investment into a contest. If laboratory animals show numerical abilities, little is known about the ecological implications particularly in young animals. The two to nine barn owl (*Tyto alba*) siblings vocally compete for priority of access to food resources before parents actually deliver them. In dyads, the individual that vocalizes at the highest rate in the absence of parents deters its siblings from competing for next delivered prey. We tested the novel hypothesis that to optimally adjust vocal investment, barn owl nestlings assess how many of their siblings are currently competing. To singleton owlets, we broadcasted a fixed global number of calls emitted by one, two or four pre-recorded unfamiliar nestlings. We could thus distinguish the independent effect on singletons' vocal behavior of the global number of calls produced by a brood from the number of competitors that produced these calls. Overall, nestlings retreated more from vocal contest when facing more competitors. However, in front of one highly motivated competitor, nestlings refrained from vocalizing to a larger extent than when competing against more but less motivated individuals. Therefore, young animals assess variation in the number of currently competing siblings based on individual-specific vocal cues.

Keywords Competition · Numerical ability · Sibling negotiation · Vocal communication

Charlène A. Ruppli and Amélie N. Dreiss contributed equally to this work.

C. A. Ruppli · A. N. Dreiss (✉) · A. Roulin
Department of Ecology and Evolution, University of Lausanne,
Building Biophore, 1015 Lausanne, Switzerland
e-mail: Amelie.Dreiss@unil.ch

Introduction

Animals compete for limited resources such as mates, territories or food. As the likelihood of winning a contest decreases with the number of rivals, their competitive ability and motivation to compete, animals are predicted not only to assess rivals' resource holding potential (Parker 1974; Enquist and Leimar 1983), but also assess how many of them are currently competing and to which extent. Such numeric competences may be selected in order to optimally adjust investment in competition (McComb et al. 1994; Wilson et al. 2001; Tanner 2006; Benson-Amram et al. 2011). Facing many individuals that are weakly motivated to compete over a limited amount of resources may represent a different challenge than to compete with few individuals that compete intensely over the same pool of limited resources. If several authors have shown that individuals are able to adjust investment in competition in relation to the number of competing individuals (McComb et al. 1994; Wilson et al. 2001), it is sometimes unclear whether individuals assess variation in the number of individuals that are currently competing per se or whether this adjustment is done in relation to the total number of stimuli produced by all these individuals while competing.

Despite the straightforward benefits individuals should derive from counting competitors, little is known about the extent to which wild animals use numerical competences in socio-ecologically relevant contexts. Literature on non-human animals' numerical competences shows that animals as various as insects (Dacke and Srinivasan 2008; Gross et al. 2009), fish (Agrillo et al. 2011), amphibians (Uller et al. 2003), birds (Rayburn-Reeves et al. 2010) and mammals (Brannon and Terrace 1998; Kilian et al. 2003; Vonk and Beran 2012) can distinguish between small numerosities—often up to four. These studies are

performed in the laboratory and often with individuals trained to discriminate among artificial objects. The capacity to perceive a change in number may help individuals to maximize fitness at different life stages and different contexts such as inter-group competition (McComb et al. 1994; Wilson et al. 2001), brood parasitism (Lyon 2003), predation (Bisazza et al. 2010) or foraging (Hunt et al. 2008; Krusche et al. 2010). Only a few experiments such as choice procedures in some fish and insects (Carazo et al. 2009; Gómez-Laplaza and Gerlai 2011) and playback experiments in wild birds and mammals (e.g., McComb et al. 1994; Seddon and Tobias 2003; Kitchen 2004) report that animals perceive a change in the total amount of visual or vocal stimuli, that is correlated with the number of conspecifics, and accordingly dose effort in mating or competing decisions.

To our knowledge, the ecological importance of numerical ability has not been evaluated in the context of family interactions and sibling competition. In altricial species, offspring commonly compete to attract parental attention and obtain a larger than equal share of parental resources (MacNair and Parker 1979). In a family, the intensity of scramble competition and begging solicitations signal offspring need and determine, in part, how food resources are shared among the progeny (McRae et al. 1993; Kilner and Johnstone 1997). Studies in animals typically showed that nestlings adjust begging behavior not only in relation to their own need but also to the competitive ability (Price et al. 1996; Cotton et al. 1999; Roulin 2004), postural or vocal signals (Smith and Montgomerie 1991; Leonard and Horn 1998; Madden et al. 2009; Marques et al. 2011) and location of their siblings in the nest (Kölliker et al. 1998; Ostreiher 2001). In contrast, nothing is known about whether young animals are able to assess the amount of siblings that are currently competing to adjust their investment into the competition over parental resources. Although change in brood size influences the way altricial animals beg for food from their parents (Soler and Aviles 2010), it is not known whether individuals adjust their behavior in relation to brood size per se or to the global amount of stimuli by the brood. Given that some nestlings can be momentarily sated, only part of the progeny is expected to compete over food. This raises the possibility that to optimally adjust vocal investment young animals assess siblings' signaling level not only to evaluate their motivation to compete, but also to determine how many of them are currently competing. The competitive environment experienced by an individual may be indeed different if begging solicitations are produced by one sibling that is very motivated to compete for parental resources or by several mildly motivated siblings. The aim of our study is therefore to experimentally partition the relative role of these two factors, number and motivation of

competitors, in how nestling birds adjust begging behavior in relation to brood size.

We thus investigated whether barn owl nestlings (*Tyto alba*) adjust effort invested in the contest for parental resources to the number and motivation of nestmates that are momentarily vocally competing. In this nocturnal species, the two to nine young not only beg toward parents to solicit food, but also vocally communicate with their siblings in the prolonged absence of parents between feeding events (Roulin 2002; Johnstone and Roulin 2003). Because a single offspring is fed per parental visit, only one individual is paid back for the effort invested in sibling competition. Hence, this sib–sib communication system, referred to as “sibling negotiation” (Roulin 2002; Johnstone and Roulin 2003), allows nestlings to inform each other about their willingness to compete once parents are back with an indivisible small mammal. This system allows each individual to optimally adjust investment in sibling competition according to its chance of obtaining the next delivered prey item (Roulin 2002). Typically, when facing a nestling which vocalizes intensely in the absence of parents, siblings retreat from the contest by reducing their level of vocal negotiation and begging for the prey item delivered once parents are back. Negotiating at a high level therefore gives priority access to the impending food resource and this at lower costs compared to a situation where negotiation would not take place (Roulin 2002; Johnstone and Roulin 2003).

We repeatedly showed that barn owl nestlings invest in vocal negotiation according to the level at which their siblings vocalize, hence to their chance of winning the contest (Roulin 2002; Dreiss et al. 2010b). Nestling barn owls accordingly decrease their vocal negotiation when brood size increases both in natural conditions (Roulin 2002) and when experimentally manipulated (Roulin et al. 2000). It is, however, unclear whether owlets also assess the number of nestmates that are currently negotiating or only the global competitive level through the number of calls produced by the entire brood. Assessing the number of vocal competitors would certainly be adaptive since the likelihood of obtaining the next indivisible prey item decreases with the amount of hungry rivals. The number of siblings takes part in negotiation, and thus, the ambient competitive level varies across feeding events along with the hunger level and the motivation to compete of each nestling. If the competitive environment experienced by an individual is different when vocal solicitations are produced by one sibling that is very motivated to compete for parental resources or by several mildly motivated siblings, nestlings should invest in competition accordingly. To singleton nestlings, we broadcasted pre-recorded negotiation calls of one, two or four unfamiliar nestlings at different rates. We predict that singleton owlets adjust their

vocalization behavior in relation to both the rate at which negotiation calls are broadcasted per se and to the number of individuals contributing to the overall signal.

Methods

Data collection

The study was performed in western Switzerland (46°49'N/06°56'E) on a population of wild barn owls. We carried out the experiment once nestlings were old enough to be thermo-independent and could consume food without maternal help. We estimated nestlings' age shortly after hatching by measuring the length of the left flattened wing from the bird's wrist to the tip of the longest primary (Roulin 2004).

Between May and September 2011 at ca. 1200 hours, we brought to the laboratory 57 male and 64 female nestlings aged 33 ± 4 days (mean \pm SD, range 20–41), issued from 31 broods (mean brood size in the field \pm SD = 6 ± 1 nestlings). We hosted them during two nights, before bringing them back to their original nest at ca. 1200 hours. We kept each individual in a wooden nest-box similar to the one in which it was reared in the field. Each nest-box was separated into two equal parts, with one nestling on the left side and a loudspeaker (near05experience, ESI Audiotechnik GmbH, Leonberg, Germany) on the right side. Nest-boxes were acoustically isolated with mineral foam on the sides and the roof, and at the time of recordings, they were closed. To facilitate ventilation, we connected nest-boxes to the outside with a plastic pipe. The acoustic isolation was efficient since calls were not audible by a human observer standing in the room.

Owlets were acclimated to the laboratory conditions during the first 24 h, and nestlings were not physiologically stressed, as shown by the absence of a rise in baseline corticosterone level compared to the situation prevailing under natural, undisturbed conditions (Dreiss et al. 2010a). On their arrival, we offered laboratory mice to the owlets as well as on each morning at ca. 0900 hours with ca. 50 g of laboratory mice, which is slightly inferior to their daily food requirement of about 67 g, in order to stimulate them to vocally compete at night during our playback experiments which started at 2345 hours on the second night.

Design of playback sequences

To build playback sequences, we selected 24 natural calls per individual in 21 barn owl nestlings (13 males and 8 females aged 32 ± 6 days (SD)) issued from 19 broods. These individuals were recorded during free vocal dyadic interactions between pairs of starved siblings in 2008

hosted in the same laboratory conditions as in 2011, except that the sibling replaced the loudspeaker. All calls lasted ca. 0.8 s, which corresponds to the mean and median length of calls observed in the free dyadic interactions recorded in 2008 (mean \pm SEM = 0.811 ± 0.0007 s, median = 0.800 s, range 0.220–2.310 s, $n = 61,332$ calls from 98 owlets). We standardized call intensity using free Audacity software v.1.3 Beta (<http://audacity.sourceforge.net>), a procedure that does not affect call frequencies and duration. Based on these standardized calls, individuals could be statistically discriminated, which supported potential for individual recognition by experimental nestlings to which we broadcasted them (Dreiss et al. 2012).

To each of the 121 singleton nestlings, we broadcasted 9 playback sequences lasting 4 min each and separated by 6 min of silence. We chose these timings because preliminary studies showed that owlets adjust their vocal behavior mostly according to the 2 preceding minutes of a vocal exchange with a counterpart. The 9 sequences corresponded to the combinations of three different call rates: 6, 12 or 24 calls per minute, emitted by one, two or four individuals. Although broods contain up to nine nestlings in our study population, only a few individuals call in any single minute (pers. obs.). We hence chose to test nestlings' ability to discriminate the number of vocal siblings within this natural range. Testing small numerosities (≤ 4) and a large ratio of difference between the tested numbers is a first step in the study of numerical ability in barn owls since no preliminary experiment has been reported so far. These three call rates correspond to the natural range we observed in free vocal interactions that took place between starved owlets in 2008, during minutes when owlets produced at least one call (mean \pm SEM = 7.86 ± 0.06 calls/min, median = 7.00, range 1–34, $n = 61,332$ calls from 98 owlets). In the sequences where we broadcasted two or four playback individuals, we allocated the same number of pre-recorded calls for each playback individual. For example, for playbacks of four individuals for which call rate was set to 24 calls/min, we inserted 24 calls of each of the four playback individuals in the 4-min-long playback sequence (Table 1).

Table 1 Experimental playback design to study whether barn owl nestlings are able to assess how many siblings are currently vocalizing

Number of broadcasted donor nestlings	Call rate from each donor nestling (calls/min)		
1 nestling	6	12	24
2 nestlings	3	6	12
4 nestlings	1.5	3	6
Overall playback call rate (calls/min)	6	12	24

To avoid pseudo-replication, we broadcasted to each singleton nestling a unique combination of calls (Kroodsma et al. 2001). Using an automatic Matlab program (version R2008b MathWorks, Natick, MA, U.S.A.), we inserted calls in a random order along the 4-min-long playback sequences and separated these calls with randomly chosen time intervals. Nevertheless, we set the minimal pause between two consecutive calls to 1 s; intervals of less than 1 s between two consecutive calls emitted by two individuals corresponded to only 0.08 % of all individual pauses ($n = 250,924$ pauses from 98 owlets) observed in the recordings of free dyadic interactions in 2008. We randomized the order of the 9 sequences across the 121 nestlings. In each sequence, we also randomly inserted the calls and identity of each playback individual.

Acoustic analyses

We placed a microphone (MC930, Beyerdynamic GmbH & Co KG, Heilbronn, Germany) inside nest-boxes against the roof underside and in direction to the nestling. By comparing broadcasted sound tracks to recorded sound tracks, we could easily discriminate calls produced by the owlet from those emitted by the loudspeaker using a semi-automatic program in Matlab v. R2008b. For each of the nine 4-min-long sequences, the Matlab program recorded the number of calls produced by the nestling and calculated the mean duration of its calls in seconds. Among the 121 tested nestlings, 36 of them did not vocalize at all throughout the nine playback sequences, a frequently observed situation in the wild (pers. obs.). Depending on the time at which nestlings ate the provided prey (which was not controlled), some nestlings could be more hungry than others. Moreover, the silent individuals did not differ from the vocal individuals in gender ($\chi^2 = 0.19$, $df = 1$, $P = 0.67$), but were on average 2 days older (ANOVA: $F_{1,117} = 4.42$, $P = 0.038$). As older nestlings are more competitive, they could invest less in vocalization and still outcompete their younger siblings (Roulin 2004). Also, old nestlings naturally lose body mass before fledging implying that their appetite decreases with age. It is hence expected that they produce fewer calls at the same given level of hunger. Because numerical discrimination ability could only be tested on vocal individuals, we analyzed the response of the 83 nestlings that produced at least one call (mean \pm SEM = 70 ± 11 calls, range 1–412 produced by 38 males and 45 females aged 33 ± 4 days (SD)).

Statistical procedure

For each of the nine 4-min-long playback sequences, we computed the number of calls and mean call duration of nestlings. We ran a generalized linear mixed model with

Poisson error distribution to analyze the number of calls produced by nestlings and a linear mixed model to analyze the mean call duration. We fitted the identity of nestlings nested in brood of origin as a random intercept to control for the 9 repeated measurements per individual and the fact that several tested nestlings came from the same nest. Fixed effects comprised the number of broadcasted calls (6, 12 or 24 calls/min) and the number of playback individuals that emitted these calls (one, two or four). We also added the order at which we broadcasted the playback sequence (1–9) as a continuous covariate to control for the effect of time-dependent vocal behavior, since owlets become more motivated to call with time as they become hungrier. For each nestling and acoustic variable, we had a maximum of nine data points corresponding to the total number of calls and to the mean call duration computed over the nine 4-min-long playback sequences corresponding to the 9 combinations of call rates (i.e., 6, 12 or 24 calls/min) and number of playback individuals (i.e., one, two or four). Because not all nestlings called when hearing a given playback sequence, we had a larger number of observations to test variation in nestling's call number ($n = 747$) than in nestling's call duration ($n = 417$). In a preliminary analysis, we included sex and age of nestlings as covariates, but they proved to have non-significant effect on vocal output and were hence removed from the final analyses. In the case of significant interaction between the terms "playback call rate" and "number of playback individuals," for each of the three call rates we ran similar mixed models to examine the influence of the number of individuals broadcasted on the vocal behavior of nestlings.

Analyses were performed with SAS V9.2 (SAS Institute Inc., Cary, NC, USA). Residuals of linear mixed models were checked for normality.

Results

Experimental nestlings vocalized less often when calls were broadcasted at a higher rate (term "Playback (PB) call rate" in Table 2 and Fig. 1a). They also modulated the number of calls they produced in relation to the number of playback individuals used to generate the playback sequences (term "Number of PB individuals"), but in a way that depended on the rate at which calls were broadcasted (interaction "PB call rate \times Number of PB individuals"). Nestlings vocalized significantly more often when we broadcasted a single individual compared to multiple individuals, that is, two and four, both when we played back 6 calls/min (Fig. 1a; similar GLMM as in Table 2, $F_{1,163} = 7.8$, $P = 0.0006$) and 12 calls/min (similar model: $F_{1,163} = 4.0$, $P = 0.02$). When we broadcasted 24 calls/min, nestlings vocalized more often when

Table 2 Number and mean duration of calls produced by barn owl nestlings hearing one, two or four playback individuals calling at various rates (i.e., 6, 12 or 24 calls/min)

Dependent variable	Number of calls			Call duration		
	<i>F</i>	<i>df</i>	<i>P</i> value	<i>F</i>	<i>df</i>	<i>P</i> value
Sequence order	29.6	1,655	<0.0001	19.0	1,331	<0.0001
Playback (PB) call rate	237.6	2,655	<0.0001	0.2	2,329	0.80
Number of PB individuals	8.3	2,655	0.0003	6.6	2,331	0.002
PB call rate × Number of PB individuals	9.2	4,655	<0.0001	1.3	4,325	0.28

A generalized linear mixed model with Poisson error distribution was used to test variation in the number of calls singletons emitted in response to the playbacks and a linear mixed model to test variation in the mean duration of the calls produced by singleton nestlings. Both models comprised the identity of nestlings nested in brood where they were raised in the field as random intercept. The analyses were based on 83 nestlings issued from 33 broods. Because each owlet experienced nine playbacks broadcasted in a random order, we controlled statistically for the order at which each playback was broadcasted (term “sequence order”)

hearing calls produced by two rather than one or four playback individuals (Fig. 1a; similar model: $F_{1,163} = 11.7$, $P < 0.0001$).

Independently of the rate at which we broadcasted calls, nestlings emitted shorter vocalizations when they heard four rather one or two playback individuals (Fig. 1b and Table 2).

The significant effect of the variable “sequence order” indicates that with time nestlings produced more and longer calls (Table 2).

Discussion

In the present paper, we experimentally tested the hypothesis that young animals still dependent on their parents have the ability to discriminate the number of siblings that are currently competing over the same pool of parental resources, so as to dose effort invested in sibling competition. As a model system, we considered the barn owl in which nestlings vocally negotiate among them priority for access to the impending indivisible food item next delivered by a parent. The individual that produces many and long calls deters siblings from vocally negotiating and ultimately begging food from parents (Roulin 2002; Johnstone and Roulin 2003; Dreiss et al. 2010b). An individual escalates vocal negotiation when its chance of winning the contest is higher, that is, when it faces a less motivated sibling, that emits few and/or short calls (Dreiss et al. 2010b). We thus predicted that owlets assess both the number and motivation of siblings that are currently competing from their calls. Accordingly, we found that owlets refrained from vocalizing when hearing more calls per se, that is, broadcasted at 6, 12 and 24 calls per minute. Most importantly, in each case, singleton nestlings also differentially modulated the number and/or duration of their vocalizations according to whether the broadcasted calls were emitted by one, two or four playback individuals. Since we broadcasted the different

playback sequences in a random order with several minutes of silence separating two sequences, owlets most likely assessed the absolute number of calls and individuals broadcasted in each sequence rather than compared the relative numbers of two adjacent sequences. Hence, we can interpret our results with confidence as experimental evidence that barn owl nestlings are able to discriminate variation in the number of nestmates that are competing at different levels and use this information to adjust their vocal behavior. This discrimination between quantities of competitors suggests a simple form of numerical competence in owlets. Our study presents the first report of numerical abilities in a nocturnal species and in the context of sibling competition. This is an important conclusion because at night nestlings can assess variation in the number of competing siblings mainly by assessing vocal cues.

In various species, discriminating two quantities is easier when the ratio between the two quantities is high and when the quantities are small (e.g., Bisazza et al. 2010). Here, we have tested a relatively small number of playback individuals (1–4). Even if we tested high call rates (6, 12 and 24 calls/min), nestlings might evaluate the number of calls during a short time lapse (e.g., 10 s) and hence distinguish small numbers of calls (1, 2 and 4 calls/10 s). It hence remains open to question whether nestlings discriminate larger numerosities. Our results suggest that nestling barn owls are at least able to discriminate small numerosities with a large ratio difference between them (1 vs. 2 or 2 vs. 4). Non-verbal numerical competence is supposed to be based on two possible cognitive mechanisms. Under the “object file system,” individuals would evaluate the number of object by precisely tracking and remembering each individual objects (e.g., Feigenson et al. 2002), while under “analog magnitude system,” individuals would be able to roughly compare two quantities only if the difference between these two quantities is sufficiently large (e.g., Meck and Church 1983; Xu and Spelke 2000; Agrillo et al. 2010). The two cognitive mechanisms might

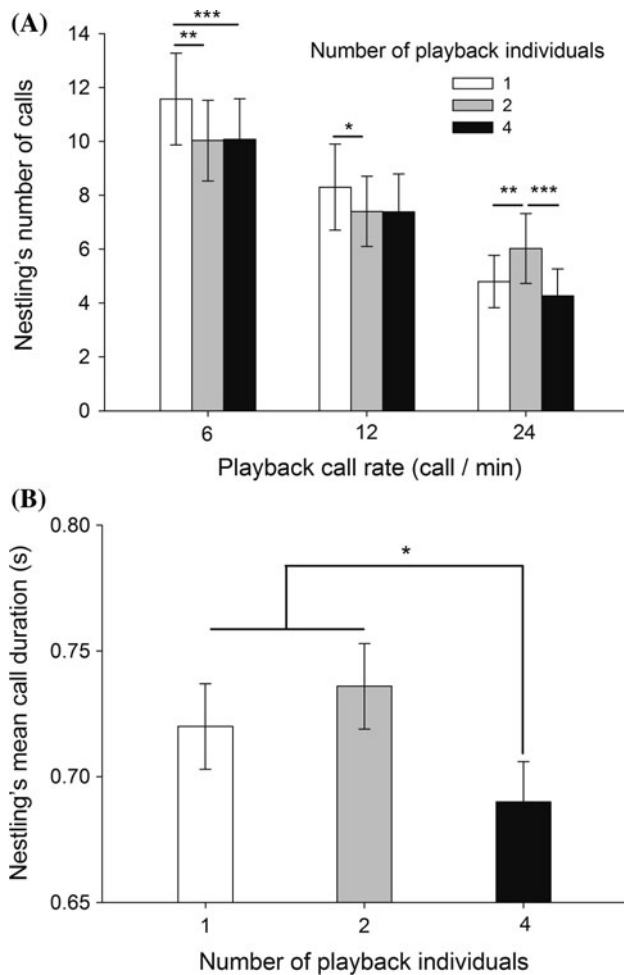


Fig. 1 Number (a) and mean duration (b) of calls (\pm SEM) of barn owl nestlings hearing one, two or four playback individuals calling at various rates (i.e., 6, 12 or 24 calls/min). Averages are computed over the raw data of 83 nestlings from 33 broods. Levels of significance ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$) reported above the bars are derived from mixed models examining the effect of the number of broadcasted nestlings on the nestling's call number and mean duration. Separate analyses were performed to examine the effect of the number of playback individuals for each playback call rate. The order at which calls of one, two or four individuals were broadcasted to each nestling was entered in the model as factor and nestling identity nested in brood was included as random intercept to control for the repeated measurements per nestling and per brood

exist to evaluate the number of acoustic events (Hauser et al. 2002), but we can only speculate on which mechanism is used by barn owls. Nestlings may plausibly use the two different systems simultaneously: the analog system to estimate overall call rate and a file system to track the number of callers. By this means, individuals would independently estimate call rate and number of callers and integrate both stimuli to produce their vocal response.

Laboratory choice experiments in newborn domestic chicks (*Gallus gallus*) previously demonstrated that even at very young ages, chicks can sequentially discriminate

between different quantities of artificial objects (Rugani et al. 2009). Together with their study, we provide here evidence for rudimentary numerical abilities in young birds, from multiple visual (Rugani et al. 2009) and vocal cues (present study). Numerical abilities in newborns have been studied in few species including humans (Izard et al. 2009) and guppies (*Poecilia reticulata*; Bisazza et al. 2010). The capacity to distinguish different numerosities improves in precision across development (Xu and Spelke 2000; Bisazza et al. 2010). As suggested by our experimental tests in 20-day-old barn owl nestlings, the ability to discriminate the number of vocal siblings could be innate or arise 1 or 2 weeks after hatching. Quantifying competing siblings would allow nestlings to adequately adjust their investment in food contest, and this ability appears adaptive in this system. The barn owl's ability to discriminate the quantity of other elements than siblings, such as objects, remains to be demonstrated. Indeed, numerical ability should be more developed when it is relevant in animal ecological conditions. For instance, capuchin monkeys (*Cebus apella*) are better able to distinguish difference in food than in token quantity (Addessi et al. 2008).

Without a game-theoretical approach, it is difficult to propose a priori predictions regarding how offspring should adjust effort in sibling competition according to variations in both the number and motivation of competitors. Here, we found that nestlings vocalized more often when hearing one rather than two or four broadcasted nestlings calling at a rate of 6 and 12 calls/min. When the playback call rate was set to 24 calls/min, the effect of number of competitors was not linear as nestlings emitted more calls when listening to two rather one or four nestlings. Furthermore, independently of the rate of broadcasted calls, nestlings produced longer calls when we broadcasted fewer individuals than four. The results showed that the playback call rate more strongly influenced nestling number of calls than did the number of playback individuals. The opposite was true for nestling response in term of call duration, as number of playback individuals had a stronger influence than the global playback call rate. Owlets globally invested more vocal effort when hearing fewer calls and fewer rivals. Assuming that producing many and long calls is costly (Roulin et al. 2009), by doing so, they save energy when the level of competition is too high. This energy could be reallocated once siblings are fed and hence once their own chance of obtaining the next delivered food item is higher (Roulin 2002). This is consistent with the "sibling negotiation hypothesis," which posits that when food is indivisible, young animals inform their siblings about their willingness to compete only if the expected chance of obtaining the impending indivisible food item is relatively high (Roulin 2002; Johnstone and Roulin 2003).

When we broadcasted calls from two or four individuals, we took care to allocate the same number of calls per individual in each playback sequence (Table 1). As a consequence, when we broadcasted calls from several individuals, each emitted in total very few calls indicating a low motivation to compete over the next delivered food item. When hearing 24 calls per minute produced by a single individual, owlets refrained from calling probably because the playback individual signaled a very high motivation to compete. Hence, there may be a threshold in opponents' motivation at which it becomes worth investing against more—but not too many—nestmates that are mildly motivated than against a single highly motivated sibling.

Our study mirror works performed in territorial songbirds and mammals showing that individuals retreat from vocalizing when facing two or three intruders compared to one (McComb et al. 1994; Seddon and Tobias 2003; Kitchen 2004; Benson-Amram et al. 2011). These studies suggest that animals predict the amount of competitors they will face on the basis of the number of intruders they hear. Jordan et al. (2005) indeed reported that rhesus monkeys associate the number of conspecifics they heard vocalizing with the video showing the same number of individuals. The same ability to associate visual and acoustic stimuli was shown by 7-month-old infants (Jordan and Brannon 2006), when hearing recordings containing 2 or 3 individuals. Further studies are needed in the barn owl to determine how accurately nestlings associate the amount of vocalizing siblings with number of visual or tactile stimuli.

If non-verbal numerical abilities have been described in various animals, it is debated whether individuals discriminate numbers or continuous variables that covary with discrete numbers, such as volume, area (e.g., for piece of food, Feigenson et al. 2002) or density (e.g., for number of individuals Bisazza et al. 2010). Indeed, the number of vocalizing individuals as manipulated in our experimental playbacks can covary with duration, number (McComb et al. 1994) or intensity (Kitchen 2004) of auditory stimuli. Our design is conservative, since the number of playback individuals varied independently of the number of broadcasted calls and of their duration and intensity, which were fixed. This design permits disentangling the effect of the number of competitors from the other vocal stimuli. The capacity of barn owl nestlings to discriminate the amount of competitors would hence be based on individual vocal signatures and variability in call features. Moreover, in a single playback sequence, the broadcasted individuals all emitted the same number of calls and, from a single loudspeaker, preventing nestlings to use siblings' position in the nest as a cue to discriminate them. Our design therefore mimics a very difficult situation for nestling barn owls to estimate the amount of competitors.

Acknowledgments We thank Isabelle Henry, Raphaële Flint, Sarah Bates, Paul Beziers for their assistance in the field and Christof Faller, Anaïs Edme, Heloïse Théro and Frédéric Oberli for their help in acoustic analyses. We thank Ken Cheng and two anonymous referees for their comments. The experiments were approved by the veterinary services of Canton de Vaud (license no. 2109.1). The study was financed by the Swiss National Science Foundation (SNF) to AR (Grant No. 31003A_120517) and the Foundation De Giacomi.

References

- Addressi E, Crescimbeni L, Visalberghi E (2008) Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). *Anim Cogn* 11(2):275–282. doi:10.1007/s10071-007-0111-6
- Agrillo C, Piffer L, Bisazza A (2010) Large number discrimination by Mosquitofish. *Plos One* 5(12). doi:10.1371/journal.pone.0015232
- Agrillo C, Piffer L, Bisazza A (2011) Number versus continuous quantity in numerosity judgments by fish. *Cognition* 119(2): 281–287. doi:10.1016/j.cognition.2010.10.022
- Benson-Amram S, Heinen VK, Dryer SL, Holekamp KE (2011) Numerical assessment and individual call discrimination by wild spotted hyaenas, *Crocuta crocuta*. *Anim Behav* 82(4):743–752. doi:10.1016/j.anbehav.2011.07.004
- Bisazza A, Piffer L, Serena G, Agrillo C (2010) Ontogeny of numerical abilities in fish. *Plos One* 5(11). doi:10.1371/journal.pone.0015516
- Brannon EM, Terrace HS (1998) Ordering of the numerosities 1 to 9 by monkeys. *Science* 282(5389):746–749. doi:10.1126/science.282.5389.746
- Carazo P, Font E, Forteza-Behrendt E, Desfilis E (2009) Quantity discrimination in *Tenebrio molitor*: evidence of numerosity discrimination in an invertebrate? *Anim Cogn* 12(3):463–470. doi:10.1007/s10071-008-0207-7
- Cotton PA, Wright J, Kacelnik A (1999) Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *Am Nat* 153(4):412–420
- Dacke M, Srinivasan MV (2008) Evidence for counting in insects. *Anim Cogn* 11(4):683–689. doi:10.1007/s10071-008-0159-y
- Dreiss AN, Henry I, Ruppli C, Almasi B, Roulin A (2010a) Darker eumelanic barn owls better withstand food depletion through resistance to food deprivation and lower appetite. *Oecologia* 164(1):65–71
- Dreiss AN, Lahlah N, Roulin A (2010b) How siblings adjust sib-sib communication and begging signals to each other. *Anim Behav* 80:1049–1055
- Dreiss AN, Ruppli CA, Faller C, Roulin A (2012) Big brother is watching you: eavesdropping to resolve family conflicts. *Behav Ecol*. doi:10.1093/beheco/ars210
- Enquist M, Leimar O (1983) Evolution of fighting behavior: decision rules and assessment of relative strength. *J Theor Biol* 102(3):387–410. doi:10.1016/0022-5193(83)90376-4
- Feigenson L, Carey S, Hauser M (2002) The representations underlying infants' choice of more: object files versus analog magnitudes. *Psychol Sci* 13(2):150–156. doi:10.1111/1467-9280.00427
- Gómez-Laplaza LM, Gerlai R (2011) Can angelfish (*Pterophyllum scalare*) count? Discrimination between different shoal sizes follows Weber's law. *Anim Cogn* 14(1):1–9. doi:10.1007/s10071-010-0337-6
- Gross HJ, Pahl M, Si A, Zhu H, Tautz J, Zhang S (2009) Number-based visual generalisation in the honeybee. *Plos One* 4(1). doi:10.1371/journal.pone.0004263
- Hauser MD, Dehaene S, Dehaene-Lambertz G, Patalano AL (2002) Spontaneous number discrimination of multi-format auditory

- stimuli in cotton-top tamarins (*Saguinus oedipus*). *Cognition* 86(2):B23–B32. doi:[10.1016/s0010-0277\(02\)00158-0](https://doi.org/10.1016/s0010-0277(02)00158-0)
- Hunt S, Low J, Burns KC (2008) Adaptive numerical competency in a food-hoarding songbird. *P Roy Soc B-Biol Sci* 275(1649):2373–2379. doi:[10.1098/rspb.2008.0702](https://doi.org/10.1098/rspb.2008.0702)
- Izard V, Sann C, Spelke ES, Streri A (2009) Newborn infants perceive abstract numbers. *Proc Natl Acad Sci USA* 106(25):10382–10385. doi:[10.1073/pnas.0812142106](https://doi.org/10.1073/pnas.0812142106)
- Johnstone RA, Roulin A (2003) Sibling negotiation. *Behav Ecol* 14(6):780–786
- Jordan KE, Brannon EM (2006) The multisensory representation of number in infancy. *Proc Natl Acad Sci USA* 103(9):3486–3489. doi:[10.1073/pnas.0508107103](https://doi.org/10.1073/pnas.0508107103)
- Jordan KE, Brannon EM, Logothetis NK, Ghazanfar AA (2005) Monkeys match the number of voices they hear to the number of faces they see. *Curr Biol* 15(11):1034–1038. doi:[10.1016/j.cub.2005.04.056](https://doi.org/10.1016/j.cub.2005.04.056)
- Kilian A, Yaman S, von Fersen L, Güntürkün O (2003) A bottlenose dolphin discriminates visual stimuli differing in numerosity. *Learn Behav* 31(2):133–142
- Kilner R, Johnstone RA (1997) Begging the question: are offspring solicitation behaviours signals of needs. *Trends Ecol Evol* 12(1):11–15
- Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Anim Behav* 67:125–139. doi:[10.1016/j.anbehav.2003.03.007](https://doi.org/10.1016/j.anbehav.2003.03.007)
- Kölliker M, Richner H, Werner I, Heeb P (1998) Begging signals and biparental care: nestling choice between parental feeding locations. *Anim Behav* 55:215–222
- Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu WC (2001) Pseudoreplication in playback experiments, revisited a decade later. *Anim Behav* 61:1029–1033. doi:[10.1006/anbe.2000.1676](https://doi.org/10.1006/anbe.2000.1676)
- Krusche P, Uller C, Dicke U (2010) Quantity discrimination in salamanders. *J Exp Biol* 213(11):1822–1828. doi:[10.1242/jeb.039297](https://doi.org/10.1242/jeb.039297)
- Leonard ML, Horn AG (1998) Need and nestmates affect begging in tree swallows. *Behav Ecol Sociobiol* 42(6):431–436
- Lyon BE (2003) Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature* 422:495–499
- MacNair MR, Parker GA (1979) Models of parent-offspring conflict. III. Intra-brood conflict. *Anim Behav* 27:1202–1209
- Madden JR, Kunc HP, English S, Manser MB, Clutton-Brock TH (2009) Calling in the gap: competition or cooperation in littermates' begging behaviour? *P Roy Soc B-Biol Sci* 276(1660):1255–1262
- Marques PAM, Leonard ML, Horn AG, Contasti A (2011) How nestling tree swallows (*Tachycineta bicolor*) integrate their responses to hunger and signalling by nestmates. *Ethology* 117(2):163–170. doi:[10.1111/j.1439-0310.2010.01859.x](https://doi.org/10.1111/j.1439-0310.2010.01859.x)
- McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions. *Panthera leo*. *Anim Behav* 47(2):379–387. doi:[10.1006/anbe.1994.1052](https://doi.org/10.1006/anbe.1994.1052)
- McRae SB, Weatherhead PJ, Montgomerie R (1993) American robin nestlings compete by jockeying for position. *Behav Ecol and Sociobiol* 33(2):101–106
- Meck WH, Church RM (1983) A mode control model of counting and timing processes. *J Exp Psychol Anim B* 9(3):320–334. doi:[10.1037/0097-7403.9.3.320](https://doi.org/10.1037/0097-7403.9.3.320)
- Ostreiher R (2001) The importance of nestling location for obtaining food in open cup-nests. *Behav Ecol and Sociobiol* 49(5):340–347. doi:[10.1007/s002650000308](https://doi.org/10.1007/s002650000308)
- Parker GA (1974) Assessment strategy and evolution of fighting behavior. *J Theor Biol* 47:223–243
- Price K, Harvey H, Ydenberg R (1996) Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim Behav* 51:421–435
- Rayburn-Reeves RM, Miller HC, Zentall TR (2010) “Counting” by pigeons: discrimination of the number of biologically relevant sequential events. *Learn Behav* 38(2):169–176. doi:[10.3758/lb.38.2.169](https://doi.org/10.3758/lb.38.2.169)
- Roulin A (2002) The sibling negotiation hypothesis. In: Wright J, Leonard ML (eds) *The evolution of begging: competition, cooperation and communication*. Kluwer, Dordrecht, pp 107–127
- Roulin A (2004) Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the barn owl, *Tyto alba*. *Evol Ecol Res* 6(7):1083–1098
- Roulin A, Kölliker M, Richner H (2000) Barn owl (*Tyto alba*) siblings vocally negotiate resources. *P Roy Soc B-Biol Sci* 267(1442):459–463
- Roulin A, Dreiss AN, Fioravanti C, Bize P (2009) Vocal sib-sib interactions: how siblings adjust signalling level to each other. *Anim Behav* 77(3):717–725
- Rugani R, Fontanari L, Simoni E, Regolin L, Vallortigara G (2009) Arithmetic in newborn chicks. *P Roy Soc B-Biol Sci* 276(1666):2451–2460. doi:[10.1098/rspb.2009.0044](https://doi.org/10.1098/rspb.2009.0044)
- Seddon N, Tobias JA (2003) Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: evidence of numerical assessment? *J Avian Biol* 34(1):72–80
- Smith HG, Montgomerie R (1991) Nestling American Robins compete with siblings by begging. *Behav Ecol Sociobiol* 29(4):307–312
- Soler JJ, Aviles JM (2010) Sibling competition and conspicuousness of nestling gapes in altricial birds: a comparative study. *Plos One* 5 (5). doi:[10.1371/journal.pone.0010509](https://doi.org/10.1371/journal.pone.0010509)
- Tanner CJ (2006) Numerical assessment affects aggression and competitive ability: a team-fighting strategy for the ant *Formica xerophila*. *P Roy Soc B-Biol Sci* 273(1602):2737–2742. doi:[10.1098/rspb.2006.3626](https://doi.org/10.1098/rspb.2006.3626)
- Uller C, Jaeger R, Guidry G, Martin C (2003) Salamanders (*Plethodon cinereus*) go for more: rudiments of number in an amphibian. *Anim Cogn* 6(2):105–112. doi:[10.1007/s10071-003-0167-x](https://doi.org/10.1007/s10071-003-0167-x)
- Vonk J, Beran MJ (2012) Bears ‘count’ too: quantity estimation and comparison in black bears, *Ursus americanus*. *Anim Behav* 84(1):231–238. doi:[10.1016/j.anbehav.2012.05.001](https://doi.org/10.1016/j.anbehav.2012.05.001)
- Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Anim Behav* 61:1203–1216
- Xu F, Spelke ES (2000) Large number discrimination in 6-month-old infants. *Cognition* 74(1):B1–B11. doi:[10.1016/s0010-0277\(99\)00066-9](https://doi.org/10.1016/s0010-0277(99)00066-9)