Original Article

Big brother is watching you: eavesdropping to resolve family conflicts

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Adult animals can eavesdrop on behavioral interactions between potential opponents to assess their competitive ability and motivation to contest resources without interacting directly with them. Surprisingly, eavesdropping is not yet considered as an important factor used to resolve conflicts between family members. In this study, we show that nestling barn owls (*Tyto alba*) competing for food eavesdrop on nestmates' vocal interactions to assess the dominance status and food needs of opponents. During a first training playback session, we broadcasted to singleton bystander nestlings a simulated vocal interaction between 2 prerecorded individuals, 1 relatively old (i.e., senior) and 1 younger nestling (i.e., junior). One playback individual, the "responder," called systematically just after the "initiator" playback individual, hence displaying a higher hunger level. To test whether nestlings have eavesdropped on this interaction, we broadcasted the same prerecorded individuals separately in a subsequent playback test session. Nestlings vocalized more rapidly after former initiators' than responders' calls and they produced more calls when the broadcasted individual was formerly a junior initiator. They chiefly challenged vocally juniors and initiators against whom the likelihood of winning a vocal contest is higher. Owlets, therefore, identified the age hierarchy between 2 competitors based on their vocalizations. They also memorized the dynamics of competitors' previous vocal interactions, and used this information to optimally adjust signaling level once interacting with only 1 of the competitor. We conclude that siblings eavesdrop on one another to resolve conflicts over parental resources. *Key words:* acoustic, communication, competition, memory, negotiation, sibling. *[Behav Ecol]*

INTRODUCTION

When animals are in conflict over limited resources such as food, territories, or mates, they assess each other's resource-holding potential and motivation to compete. This is crucial to optimally adjust investment in competition (Parker 1974). A relatively cheap way to assess a competitor is to eavesdrop on its behavioral interactions with other individuals because animals can gain information about the state of their surrounding competitors without paying the costs of taking part into those interactions (McGregor 1993; Whitfield 2002). Eavesdropping occurs in a broad range of animals in many communication channels and different competitive situations (Oliveira et al. 1998; Aquiloni and Gherardi 2010). Surprisingly, the potential role of eavesdropping in resolving contests between family members has been disregarded so far in the literature.

A family can be viewed as a communication network (Horn and Leonard 2005), where the offspring signal their need to parents (Kilner and Johnstone 1997; Mas and Kolliker 2008) and siblings (Roulin et al. 2000; Bulmer et al. 2008; Madden et al. 2009) and where parents signal their willingness to provide food (Magrath et al. 2007). Staggered births often establish an age hierarchy among the siblings and parental feeding events spread over long periods of time induce pronounced asymmetry in food requirements. Before competing over limited parental resources, each offspring should therefore assess the short-term variations in hunger level of their dominant and subordinate siblings. Evolutionary biologists implicitly assume that only direct confrontation between juvenile siblings allow them to optimally modulate their behavior to a prevailing competitive situation (Godfray 1995; Leonard and Horn 1998, 2001; Madden et al. 2009). Provided that young animals have the cognitive ability to recognize the identity of competitor siblings and then integrate and memorize the outcome of previous interactions between them, they could assess hunger level and position in the within-brood age hierarchy by eavesdropping on their competitive interactions.

The barn owl (*Tyto alba*) is suitable species in which to test whether nestlings eavesdrop on competitor siblings' vocal interactions to adjust the level of vocal signaling. Between the staggered parental feeding visits, siblings vocally negotiate which of them will have priority access to the next delivered indivisible food item (Roulin et al. 2000; Johnstone and Roulin, 2003; Dreiss et al. 2010b). Typically, hungry individuals vocalize more intensely than their siblings to induce the less hungry individuals to retreat from negotiating and ultimately from begging on the parents' arrival (Dreiss et al. 2010b). Thus, vocal negotiation while parents are away increases the likelihood of being fed (Roulin et al. 2000). Broods comprise up to 9 offspring that might differ in age by 3 weeks. As a consequence, an individual is expected to reduce the level of vocal negotiation when facing a highly motivated and dominant senior sibling for whom the probability of obtaining the next food item is higher (Roulin 2004a).

To study eavesdropping between siblings that vocally interact, we performed playback experiments to examine whether

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barn owl nestlings listen to competing siblings and use this information to adjust vocalization levels when they subsequently interact with each of them separately. Preliminary experiments on vocal exchanges between siblings found that hungry individuals produce more calls and produce them more rapidly after their opponent (see Methods). In this experiment, we first played a prerecorded vocal exchange between 2 unfamiliar individuals, 1 senior (the oldest) and 1 junior (the youngest), to singleton nestlings alone in a nest. In this simulated vocal exchange (so-called training playback), 1 playback individual, the "responder," vocalized systematically just after the "initiator," hence displaying a higher motivation to compete for food resource than the initiator. After having broadcasted this vocal exchange, we tested the vocal response of singleton nestlings when listening only to the calls of the initiator or only of the responder. Initiators being less motivated to compete than responders and juniors being less competitive than their senior siblings, the theoretical likelihood of obtaining the impending prey item is higher for nestlings competing with junior or with initiators than with other individuals. If owlets eavesdrop on vocal dyadic interactions, we thus expect that they invest more in vocalization when listening only to a former initiator than former responder, and when facing a junior competitor rather than a senior competitor.

METHODS

General procedure

We performed the study in 2009 between June 21 and September 23 in western Switzerland (46°4′N, 6°5′E) on a population of wild barn owls breeding in nest-boxes. Fifty-four owlets, including 19 males and 35 females, from 16 broods were brought to the laboratory at around 13:00 h. They were aged between 26 and 45 days (mean ± SE: 36 ± 1), and were on average 19 days prefledging age (which takes place at ca. 55 days). Individuals were brought back to their nest after 3 nights of captivity. The owlets were already thermo-independent and their parents were naturally sleeping outside their nest-box. In the barn owl, incubation starts as soon as the first egg has been laid and since eggs are laid every 2.5 days, the 2–9 siblings can significantly differ in age. Nestling age was estimated shortly after hatching by measuring the length of the left flattened wing from a bird's wrist to the tip of the longest primary (Roulin 2004b). Nestling sex was determined using molecular markers (Py et al. 2006).

Nestlings were housed individually in an experimental nest-box similar to the one in which they were reared in naturally ($62 \times 56 \times 37$ cm^3), but separated into 2 equal parts by a thin wooden wall pierced with holes. In these conditions, they behave as in nature (Roulin et al. 2009) and are not physiologically stressed (Dreiss et al. 2010a). One owlet was placed at 1 side of a box, whereas the other side contained a loudspeaker (near05 experience, ESI Audiotechnik GmbH, Leonberg, Germany). We recorded each individual with a microphone (MC930, Beyerdynamic GmbH & Co KG, Heilbronn, Germany) oriented toward it and fixed on the inside roof of the box. The playback experiment was carried out on the third and last night of captivity starting at midnight. By that time, all nestlings had been food deprived from the preceding morning at 8:00 h.

The playback experiment was based on an experiment carried out in 2008, in which we found that calling rapidly after a sibling can signal hunger level and hence the motivation to compete over parental food resources. In the 2008 experiment, we recorded naturally occurring vocal interactions in 78 pairs of siblings from 41 nests. Nestlings were taken from the

wild and put into similar nest-boxes as those used in 2009, but with 1 nestling placed in each part of the boxes. We recorded their vocal interactions from 19:00 to 23:30 h on 1 night when both individuals were experimentally food deprived, and on another night when both individuals were experimentally food satiated (order of recordings was reversed for half the birds). The latency for a chick to call after its sibling ended a call was shorter for hungry individuals, after controlling for seniority (oldest or youngest sibling of the pair) and number of calls per minute which increases with hunger level (mean calling latency per minute was shorter in food-deprived than food-satiated individuals [8.20 ± 0.07 s vs. 8.46 ± 0.16 s]; effect of food treatment: $F_{1,17659} = 14.50$, $P = 0.0001$ in a mixed model with individual nested in sibling pair as random factors, seniority and number of call per minute as independent terms).

Playback experiments

In 2009, we first broadcasted a training playback of a vocal exchange between 2 prerecorded individuals to 54 singleton nestlings. The aim of this training playback is to allow singleton nestlings to eavesdrop on 2 nestlings that interact vocally. The 2 broadcasted individuals differed in age, the mean age difference being 10.3 ± 0.6 days (range: 2–19). A training playback lasted approximately 26 min and comprised 144 pairs of 2 calls from an "initiator" individual always calling 1.40 ± 0.01 s before the other individual, denoted "responder." Pairs of 2 calls were separated by a silence of 7.00 ± 0.01 s (Figure 1). The 144 pairs of calls consisted in 4 blocks of the same 36 pairs of calls. In this way, in each training playback the 2 individuals had different roles—being either the initiator or the responder—but also in seniority—being either a junior or a senior individual.

After having broadcasted one of these training playback sequences to a singleton nestling, we sequentially broadcasted the initiator's and the responder's calls to each owlet in a random order. These 2 testing soundtracks lasted approximately 6 min and comprised the same 36 different calls from each playback individual that were placed at intervals of 10.03 ± 0.02 s in a random order, with each call played only once along the soundtrack (Figure 1).

Each of the 54 experimental nestlings heard a unique combination of playback sequences, that is, either different initiator–responder pairs or the broadcasted individuals were played back in a different order in the first and second testing playbacks (Figure 1). The experimental nestlings that listened to the 4 categories of playbacks as listed in the Figure 1 showed no significant difference in age and sex (Anova: $F_{3,50} = 2.55$, $P = 0.07$ and $F_{3,50} = 0.64$, $P = 0.59$, respectively).

Construction of playback soundtracks

To build the playback soundtracks, we used natural calls we had recorded in 2008 from pairs of siblings starved for the preceding 24 h and that could vocally interact. We selected calls from seven 26- to 45-days-old individuals (5 males and 2 females) collected from 7 different broods. Each playback individual was assigned an equal number of times to the role of "initiator" and "responder" during playbacks. The 2 youngest individuals used to generate playbacks were only assigned the role of junior in playbacks, the 2 oldest individuals assigned only the role of senior, and the 3 other individuals were alternatively assigned to the "junior" and "senior" roles. We isolated 36 calls of about 0.8 s (mean ± SE: 0.796 ± 0.001 s) from each nestling, which corresponded to the average call duration computed from the experimentally food-deprived pairs of nestlings recorded in 2008 (mean
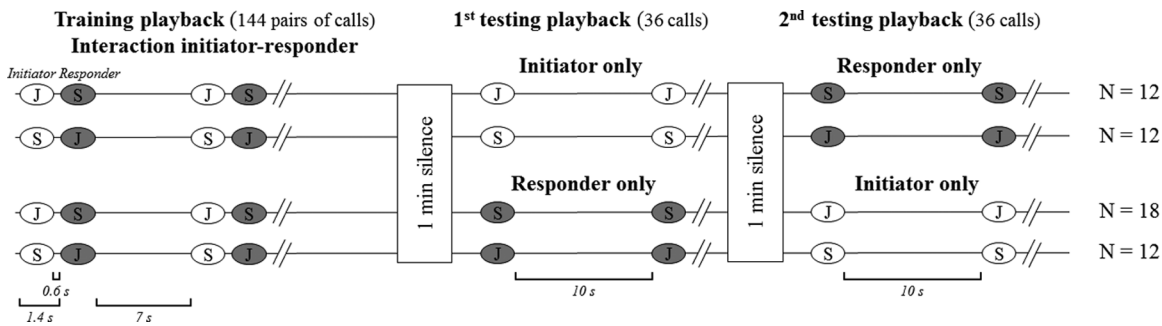
Figure 1

Design of the 4 possible playback combinations broadcasted to singleton nestlings and number of singleton nestlings for each combination. J stands for junior and S for senior barn owl nestlings. In the initiator–responder training playback sequence, the initiator systematically called before the responder during approximately 26 min. In the first and second testing playback sequences, only the initiator or the responder individuals were broadcasted during 6 min each. *N* stands for the number of lively nestlings that heard each type of combination of sequence.

± SE: 0.81±0.01 s, based on 154 503 recorded calls). We standardized the maximum amplitude of all calls using the Audacity software (http://audacity.sourceforge.net); this manipulation does not affect the other acoustic features of the calls. The chosen call latency between initiator and responder for the playback corresponds to the first percentile of calling latency of the food-deprived pairs of nestlings recorded in 2008. The chosen call rate corresponds to the mean call rate of 2 food-deprived siblings that freely interact vocally (mean ± SE: 11.96±0.05 calls/min, *n* = 68 pairs of siblings recorded in 2008).

Acoustic analyses

We used Matlab v.7.7 (MathWorks, Natick, MA) to assign calls to playback or nestlings and to measure the timing and duration of the calls. In particular, we measured the latency of the responses by the nestlings to playback calls, that is, the time taken for each owlet to start to call after a playback call. The calling latency could be negative when an owlet's call overlapped the broadcasted call. The analyzed calling latency is the average of the owlet calls' latency.

Statistical analyses

Statistical analyses were performed with the software SAS v.9.1 (SAS Institute Inc., Cary, NC). We performed 2 mixed models to analyze the vocal response of nestlings when hearing the initiator and the responder during the first and second testing playback sequences. One mixed model included owlet's calling latency as dependent variable and the other model included the number of calls. As independent factors, we fitted: 1) the role of the broadcasted individual (i.e., initiator or responder) in the training playback sequence; 2) the seniority of the broadcasted individual (the older individual of the 2 broadcasted owlets was denoted "senior" and the younger individual "junior"); and, 3) the order in which the playback was received (i.e., whether it was played back first or second).

Because the same playback individual was broadcasted to more than 1 nestling, for all models we controlled for the identity of the 2 broadcasted individuals as a random factor. We included as random factor the brood identity of nestlings because we often used more than 1 nestling per brood. Because absolute age of the broadcasted individuals did not explain variation in calling behavior of the focal live nestlings, we removed this fourth independent variable from the analyses. In all analyses, absolute age, age rank in their natural nest, and sex of the 54 focal nestlings did not affect the way they behaved vocally when hearing the playbacks. Therefore, for clarity we did not

include these variables in the models presented in the article. Assumptions for the models used (homoscedastic and normal distributions of variables and residuals) were verified in each test. We performed backward model selection. Final models only contained significant effects ($P < 0.05$) and main effects involved in significant interactions. We verified that final models selected always presented the smallest Akaike information criterion (AIC) compared with initial and intermediate models.

Ethical note

The experiments were approved by the veterinary services of Canton de Vaud (Form No. 2109.1). We always left 1 or 2 nestlings in the natural nest and we had already observed that parents do not adjust feeding rate to short-term variations in food need (Roulin et al. 2000). Therefore, temporally removing several nestlings from a nest never induced parents to abandon their nest. Keeping owlets at the university did not negatively affect their body condition because mean body mass and survival at fledgling did not significantly differ between nestlings brought to the university and nestlings left in their nest (Wilcoxon test on body mass at fledgling stage of recorded and nonrecorded siblings in 2009: $Z = 1.9$, $P = 0.051$ [recorded: 350±5 g; nonrecorded: 329±6 g] and on mortality: $Z = 1.7$, $P = 0.08$ [recorded: 2%; nonrecorded: 10%]), whereas body mass at capture did not differ between the 2 groups ($Z = 1.2$, $P = 0.22$). In the laboratory, nestlings were not physiologically stressed, as shown by the absence of a rise in baseline corticosterone level compared with the situation prevailing under natural, undisturbed conditions (Dreiss et al. 2010a).

RESULTS

As expected, nestlings vocalized more rapidly just after the initiator produced a call compared with the responder, regardless of seniority ($F_{1,34} = 5.27$, $P = 0.027$, Table 1, Figure 2). No other main effects or interactions were significantly related to nestling's calling latency. Furthermore, the number of calls produced by singleton nestlings was significantly related to the statistical interaction between competitor individuals' role in training playback and their seniority ($F_{1,82} = 8.58$, $P = 0.004$, Table 1). To investigate this interaction, we have conducted additional analyses. When responding to an initiator alone, nestlings produced twice as many calls when listening to a junior, as opposed to a senior ($4.0±0.7$ calls per minute vs. $1.9±0.5$, $F_{1,51} = 4.92$, $P = 0.031$ in a mixed model with brood identity of nestlings and identity of the playback individual as random factor) (Figure 3), but were similarly vocal when

Table 1

Vocal response of bystander barn owl nestlings listening to a playback of an individual (during the so-called test session, Figure 1) that was previously heard interacting with another individual (during the so-called training session, Figure 1)

	Nestling's calling latency			Nestling's call number		
	F	df	P	F	df	P
Testing playback order (first vs. second)	0.91	1,37	0.35	0.61	1,81	0.44
Role in training playback (initiator vs. responder)	**5.27**	**1,34**	**0.027**	**0.06**	**1,82**	**0.81**
Seniority (junior vs. senior)	0.63	1,37	0.43	**0.06**	**1,82**	**0.81**
Playback order × role in training playback	0.01	1,34	0.94	3.26	1,79	0.07
Playback order × seniority	0.01	1,34	0.91	2.38	1,79	0.13
Role in training playback × seniority	1.94	1,34	0.17	**8.58**	**1,82**	**0.004**

Results of final models are written in bold and nonsignificant results eliminated from the initial full models in plain.
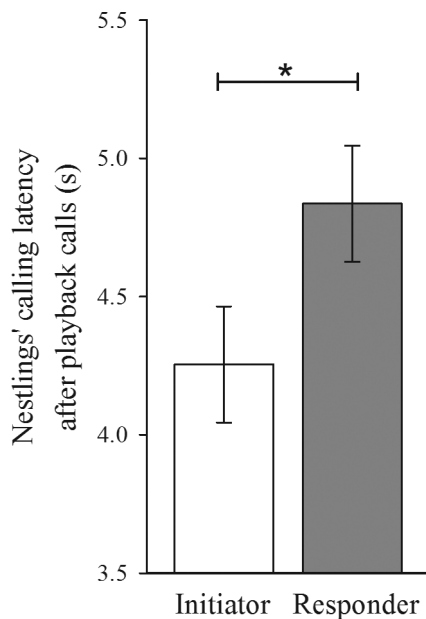
Figure 2

Nestlings' latency (mean ± SE) to call after the calls of initiator and responder barn owl nestlings separately broadcasted during the first and second testing playbacks. Nestlings called more rapidly after individuals that were the initiator rather the responder during the training playback sequence. The symbol * is for $P < 0.05$ in a mixed model (see Table 1).

Figure 3

Eavesdropping behavior of barn owl nestlings. After nestlings heard a vocal dyadic interaction between an initiator and a responder nestling during training playback, we tested the number of calls (±SE) they produced when listening only to the same initiator or responder. Nestlings produced significantly more calls when listening to a junior initiator than to a senior initiator or to a junior responder during testing playbacks. The symbol * is for $P < 0.05$ in a mixed model (see Table 1).

DISCUSSION

Our results show that owlets do eavesdrop on competitive interactions between other owlets. We found that owlets adjusted their vocal behavior according to the perceived motivation and competitiveness of nest mates in a previous interaction. This suggests that owlets are able to: 1) gather information on the competitive role played by 2 vocally interacting nestmates (i.e., which of the 2 brood mates was calling before the other) as well as their relative seniority (i.e., which of the 2 brood mates is the older); and, 2) remember this information for at least a few minutes before using it to adjust their vocal behavior. To our knowledge, this is the first evidence that bird nestlings have such cognitive abilities, which could be used to resolve conflicts over the share of resources.

In many species, individual acoustic features underlie distinct signatures about its identity, such as sex, familiarity, sexual maturity, or dominance status (Davies and Halliday 1978; Tomaszycki et al. 2001; Blumstein and Munos 2005), and some studies show that receivers can discriminate individuals on the basis of these signals (Godard 1991; Hare 1998; Gherardi et al. 2005). Young animals have also shown to have the capacity to distinguish each other's familiarity and relatedness (Beecher and Beecher 1983; Palestis and Burger 1999; Maletinska et al. 2002). However, to our knowledge, the capacity for young nonhumans animals to discriminate individual siblings from one another has only been experimentally demonstrated in Greylag Geese (*Anser anser*) (Scheiber et al. 2011). The adjustment of owlet behavior after a vocal interaction supposes that they discriminate among callers using acoustic cues. This discrimination may be the result of individual recognition or of the ability to classify callers according to their relative age. We showed, indeed, that nestlings behaved differently according to the seniority of the 2 playback individuals.

listening only to a junior as a senior responder (similar mixed model: $F_{1,51} = 2.92$, $P = 0.10$, Figure 2; see Table 1 for the full initial model including initiators and responders). Therefore, owlets vocalize differently according to the challenger role ("initiator" vs. "responder" hypothetically reflecting competitive effort) and seniority ("junior" vs. "senior" hypothetically reflecting competitive ability) previously witnessed during the training playback, even in our experimental situation where the broadcasted competitors were unfamiliar to the nestlings.
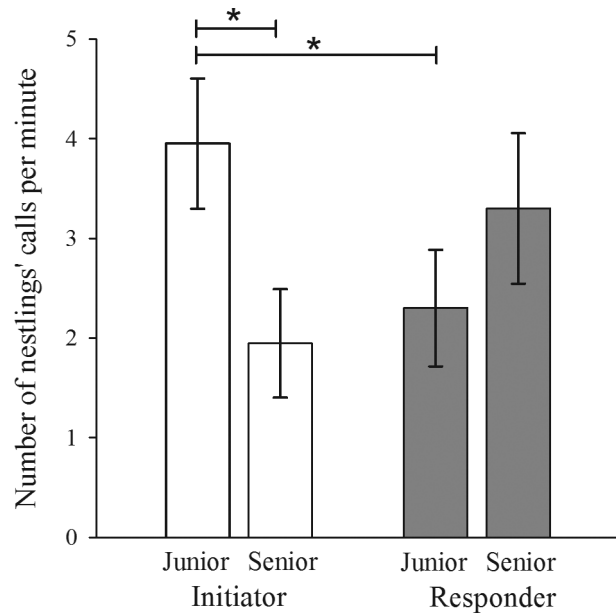
Interestingly, owlets adjusted their calling behavior in relation to the age hierarchy of the 2 witnessed individuals (i.e., which individual is the junior vs. senior) but not in relation to their absolute age. This is probably adaptive given that age hierarchy between siblings persists throughout the 55-day-long rearing period. In the dark nocturnal conditions of a relatively closed nest, barn owl siblings appear to mainly communicate vocally (Dreiss et al. 2010b), visual cues being faint. Calls of barn owl nestlings probably provide an age-specific signature that enables nestlings to discriminate their opponent according to their age, even when facing unfamiliar and hardly visible individuals. Age hierarchy is an important factor of sibling competition in many altricial species (Roulin 2004a; Drummond 2006). In a crowded nest, estimating the position of hungry vocal competitors in the within-brood age hierarchy would allow a focal individual to estimate its chance to win the contest for the next delivered prey.

Individual discrimination in the context of sibling negotiation would thus allow bystander nestlings to adjust their investment in sibling competition for food according to the level of competitiveness and motivation of their vocal siblings. The relative hunger state of siblings is worthwhile remembering if it does not fluctuate rapidly over time. In this study, we have shown that barn owl nestlings remember the state of 2 competitors for at least a few minutes. Two ecological factors that might influence the evolution of the social and cognitive ability to remember siblings' hunger state are parental feeding rate and the size of food items. In the barn owl, parents feed their brood on average every hour (Roulin 2002) with relatively large food items. Thus, siblings' hunger level does not oscillate quickly, as fed individuals are satiated for a while and hungry individuals can wait several minutes up to a few hours before being fed. Eavesdropping on the communicative network within a brood can thus reinforce the efficiency of exchange of valuable information during the vocal negotiation process among siblings.

Because barn owl nestlings have up to 8 competitors and because of relative low parental provisioning rate, it is possible that they could remember interactions between multiple individuals for longer periods of time. Furthermore, nestlings showed here that they discriminated between 2 individuals that only varied in their calling latency. In nature, hungry and satiated individuals show more contrasted vocal behaviors, as they also vary with respect to call duration and call rate (Roulin et al. 2009) and probably intensity of calls. Gaining information by eavesdropping a vocal interaction between individuals varying in hunger level must thus be easier in nature than in our experimental design. It is hence likely that barn owl nestling largely use eavesdropping in natural conditions.

To conclude, barn owl nestlings eavesdrop on each other's competitive interactions and are able to identify and remember the role of each opponent even before directly interacting with them. This ability enables them to adjust their vocal investment once interacting with these opponents. Therefore, young animals competing over parental resources can remember which of the 2 interacting siblings is highly motivated to compete (in this case responders) and has the higher resource-holding potential (ergo seniors) and use this information to adjust investment in sibling competition. Eavesdropping relatives' interactions therefore allows young animals to reduce the costs involved by the resolution of intrafamilial conflicts over parental resource.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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