Animal Behaviour 145 (2018) 51–57

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Barn owl nestlings vocally escalate when interrupted by a sibling: evidence from an interactive playback experiment

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ARTICLE INFO

Article history:
Received 7 June 2018
Initial acceptance 20 July 2018
Final acceptance 31 August 2018

MS. number: 18-00383R

Keywords:
auditory feedback
communication
interactive playback
overlapping
sibling negotiation
temporal dynamics
Tyto alba

To resolve conflicts of interest, animals can vocally signal their resource-holding potential and motivation to compete. This allows conspecifics to adjust their behaviour to each other without fighting physically. Making sure that competitors correctly assess each other's vocal information requires mechanisms to prevent signal interference. Alternating calls with those of an opponent (i.e. waiting until the opponent's call has ended before starting to vocalize) is widely observed in animals and could be partly acquired through learning. Regardless of whether competitors interrupt conspecifics as a signal of dominance or by accident, the information transferred by the interrupted individual is likely to be partly blurred. Interrupted individuals would hence benefit from counterattacking by calling more intensely, indicating to their competitors that calling simultaneously is counterproductive. We tested this 'social feedback' hypothesis in the barn owl, *Tyto alba*, in which young siblings negotiate vocally over which individual will have priority access to the next food item delivered. It has already been shown that nestlings actively avoid interrupting each other, but it remains untested whether nestlings give social feedback when interrupted. To test this, we developed an 'automated interactive playback' which broadcast calls that either interrupted or did not interrupt the calls of a singleton nestling. When a playback call interrupted a nestling, this individual immediately intensified vocal communication by quickly producing a long call and by producing more calls. As previously shown, this reaction tends to silence competitors and thereby increases the individual's likelihood of obtaining the next food item. Such social feedback could reinforce the evolutionary stability of vocal sibling negotiation as a nonaggressive way to share food.

To reduce the cost of conflict in animals, natural selection has favoured the evolution of communication about resource-holding potential and motivation to compete (Maynard Smith, 1982; Parker, 1974). The individuals that are unlikely to win a contest should momentarily refrain from competing until the likelihood of winning increases (Parker, 1974). Refraining from competing can be beneficial to save energy that can be invested later, once the probability of monopolizing resources increases (Johnstone & Roulin, 2003). Transmitting information about each other's motivation to compete and assessing the opponents' motivation is therefore crucial to determine the likelihood of monopolizing a resource and in turn how much energy should be allocated in a specific contest. Not being accurately informed about each other's motivation to compete due to signal interference should be detrimental for competitors (McGregor & Peake, 2000; Todt & Naguib, 2000) and thus should be avoided.

Call alternation (i.e. when an opponent starts a call after its counterpart has terminated its call) is widely accepted as a strategy to avoid communicative interference. The avoidance of call overlap has been well studied in the context of noncompetitive (e.g. Carter, Skowronski, Faure, & Fenton, 2008; Ghazanfar, Smith-Rohrberg, Pollen, & Hauser, 2002; McCauley & Cato, 2000; Miller, Iguina, & Hauser, 2005; Schulz, Whitehead, Gero, & Rendell, 2008; Soltis, Leong, & Savage, 2005; Versace, Endress, & Hauser, 2008) and competitive vocal interactions (e.g. Dreiss et al., 2013; Popp, 1989; Stokes & Williams, 1968; Wasserman, 1977; Wilson, Ratcliffe, & Mennill, 2016; Yang, Ma, & Slabbekoorn, 2014). When two calls overlap, the transfer of information through vocal signals of both

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https://doi.org/10.1016/j.anbehav.2018.09.003
0003-3472/

the interrupted and the interrupting individuals are likely to be blurred, while when the calls are produced one after the other, the transfer of information is optimized. However, in some contexts call overlap cannot be avoided. In altricial species, parents often allocate food to their offspring according to ostentatious signals produced by their progeny referred to as 'begging' (Godfray, 1995; Kilner & Johnstone, 1997; Wright & Leonard, 2002). In species in which parents stay a limited amount of time with their offspring to decide to which individual(s) to allocate food, nestmates call simultaneously to attract the attention of the feeding parent. In situations where young nestmates vocalize for much longer to decide which one will be prioritized during feeding, they tend to call one after the other by carefully avoiding overlapping nestmates' calls. For instance, in meerkats, *Suricata suricatta*, parents and helpers forage close to their offspring and hence can hear their begging calls. In this system, the pups are constantly begging without interrupting each other, which increases total feeding rate (Madden, Kunc, English, Manser, & Clutton-Brock, 2009). In species such as the European starling, *Sturnus vulgaris* (Chaiken, 1990) and the barn owl, *Tyto alba* (Roulin, Kolliker, & Richner, 2000), offspring also vocalize in the long absence of the parents which forage far from the nest. In this case, the vocalizations, produced at a relatively low rate, are directed to siblings rather than to parents and tend not to be produced simultaneously (Dreiss et al., 2013). Although call overlap is avoided and not used as a signal of dominance, it can still occur accidentally when individuals call during the same period of time (Helfer & Osiejuk, 2015).

To avoid being interrupted, individuals should leave enough time between two calls to give conspecifics the opportunity to vocalize (Camacho-Schlenker, Courvoisier, & Aubin, 2011) and, to avoid interrupting conspecifics, individuals should wait until an opponent has finished its call before starting to vocalize (Versace et al., 2008). Adhering to these specific alternation rules might not be innate but learned through 'social feedback' from conspecifics. Typically, human children speak simultaneously more often if they are neglected by their parents (Black & Logan, 1995). Similarly, in the European starling, when nestlings are raised in captivity without any contact with adults, they sing continuously without giving conspecifics the opportunity to call without being interrupted. This suggests that starlings learn to avoid interrupting conspecifics through social feedback from adults (Henry, Craig, Lemasson, & Hausberger, 2015). In line with this idea, common marmoset parents, *Callithrix jacchus*, stop vocalizing when an offspring interrupts their calls. By doing so, parents inform their offspring not to interrupt them again (Chow, Mitchell, & Miller, 2015). Once the rules to avoid vocalizing simultaneously to conspecifics are learned, social feedback should still be used if an individual persists in interrupting conspecifics.

In the present study, we examined the hypothesis that interrupting conspecifics is socially controlled with 'social feedback'. To this end, we considered the barn owl where young siblings vocally negotiate priority of access to the next prey item delivered by a parent (Roulin et al., 2000). Each nestling produces thousands of calls per night during the prolonged absence of the parents while these are foraging. In our population, each nestling consumes three to four prey items per night, usually voles. Since at each parental visit, occurring every 45 min on average, the delivered indivisible prey item is consumed by a single nestling, siblings differ strongly in food need. For this reason, the outcome of sibling competition is predictable, with the hungriest individual being most likely to monopolize the next food item, given its high motivation to compete (Johnstone & Roulin, 2003; Roulin, 2002). Nestlings therefore vocalize in the absence of parents to inform their siblings about their relative motivation to compete with the most vocal individual indicating to its siblings its intention to compete fiercely for access to the next food item. As a response, its less hungry siblings momentarily refrain from competing until the likelihood of successfully monopolizing a food item increases (Dreiss, Lahlah, & Roulin, 2010; Roulin, Dreiss, Fioravanti, & Bize, 2009; Ruppli, Dreiss, & Roulin, 2013). This communication system, referred to as 'sibling negotiation', is directed to siblings rather than to parents which hunt too far from the nest to hear their offspring (Roulin et al., 2000).

It has already been shown that siblings interrupt each other five times less often than expected by chance, which corresponds to only 2% of the calls produced by an individual in nonexperimental conditions. Moreover, nestlings actively avoid interrupting playback calls (Dreiss et al., 2013). The tendency to interrupt does not vary with nestling age, position in the within-brood age hierarchy (in this species there is a pronounced age hierarchy resulting from staggered hatching) and hunger level, suggesting that this behaviour is used neither as a signal to dominate siblings nor to transmit information about the motivation to compete. We thus believe that interrupting siblings is not done on purpose but occurs by chance (Dreiss et al., 2013). Interestingly, bystander nestlings engage in more intense vocal negotiation when listening to a playback in which they could hear a nestling interrupted by another individual (Dreiss et al., 2013). This reaction to interrupted calls could be social feedback to inform siblings to avoid calling simultaneously. Such social feedback could help maintain the very low rate of overlapping calls observed by Dreiss et al. (2013).

The response to being interrupted has not yet been tested because it requires a highly sensitive interactive playback that would be able to interrupt very short calls (owlet calls last 0.8 s on average). To this end, we developed an 'automated interactive playback' that detects negotiation calls produced by a nestling in real time. The playback then broadcasts a prerecorded call that either does or does not overlap the nestling's call. We predicted that when a nestling is interrupted by the interactive playback, it should vocalize more intensely than when not interrupted, to send social feedback. Intensifying vocal behaviour after having been interrupted would reduce the likelihood of the interrupter getting the next food item. The interrupter would thus be motivated to take more care not to interrupt its siblings again. This interpretation is based on the fact that by vocalizing more intensely, an individual induces its siblings to withdraw from a contest (Dreiss et al., 2010; Roulin et al., 2009; Ruppli et al., 2013). The production of social feedback could therefore reinforce the evolutionary stability of vocal sibling negotiation by reducing interference while communicating which would improve signal transmission (McGregor & Peake, 2000; Todt, 1981; Todt & Naguib, 2000).

METHODS

Experimental Procedure

The study was performed on 10 free-living broods of barn owls in western Switzerland (46°4′N, 6°5′E). Between 8 August and 9 September 2014, 23 male and 15 female nestlings aged 41 days on average (range 30–48 days) were brought to the laboratory for 3 full days (and hence 2 nights). During the first night of acclimation, siblings were placed together in a wooden nestbox similar to the one where they were raised. Upon arrival at the laboratory in the morning, they were fed ad libitum (67 g of mice per nestling; Durant & Handrich, 1998). At 08:00 the next morning, the uneaten food was removed and at 12:00, all nestlings were weighed and isolated in experimental wooden nestboxes to allow them to get used to their new environment and to avoid disturbance prior to the experiment. The interactive playback was performed from