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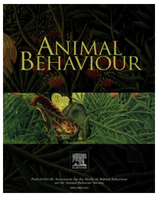

Social rules govern vocal competition in the barn owl

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To resolve the share of limited resources, animals often compete through exchange of signals about their relative motivation to compete. When two competitors are similarly motivated, the resolution of conflicts may be achieved in the course of an interactive process. In barn owls, *Tyto alba*, in which siblings vocally compete during the prolonged absence of parents over access to the next delivered food item, we investigated what governs the decision to leave or enter a contest, and at which level. Siblings alternated periods during which one of the two individuals vocalized more than the other. Individuals followed turn-taking rules to interrupt each other and momentarily dominate the vocal competition. These social rules were weakly sensitive to hunger level and age hierarchy. Hence, the investment in a conflict is determined not only by need and resource-holding potential, but also by social interactions. The use of turn-taking rules governing individual vocal investment has rarely been shown in a competitive context. We hypothesized that these rules would allow individuals to remain alert to one another's motivation while maintaining the cost of vocalizing at the lowest level.

Natural selection has favoured the evolution of behaviours and weapons to outcompete conspecifics, or of communication systems to resolve the share of resources (Maynard Smith, 1982; Parker, 1974). The term ‘negotiation’ is usually used for humans who bargain for resources and the process typically ends with a decision about which part of the resource each participant obtains (Nash, 1950). Evolutionary ecologists also use this concept to define situations in which animals communicate to reach an agreement about how a resource is shared or how to invest in a collaborative task (Johnstone & Hinde, 2006; Johnstone & Roulin, 2003; McNamara, Gasson, & Houston, 1999; Patricelli, Krakauer, & McElreath, 2011; Sirot, 2012). An individual that presents conspicuous ornaments or signals at higher levels than its opponents (e.g. produces louder begging calls in nestling birds) usually gains easier access to these limited resources (Godfray, 1991; Kilner, Noble, & Davies, 1999), but, for transient signals, this average signal level can vary over short periods of time, independently of variation in need or condition (Briffa, Elwood, & Dick, 1998; Greenfield, Tourtellot, & Snedden, 1997). The contest outcome is then the result of an interactive process settled during repeated interactions (Briffa et al., 1998; Enquist & Leimar, 1983; Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990; Payne & Pagel, 1996).

These variations in signal level during competitive interactions raise the possibility that animals assess the temporal dynamics of signal production and not only the absolute signalling level of conspecifics to adjust their behaviour (Patricelli, Uy, Walsh, & Borgia, 2002). Game theory has dominated the way evolutionary biologists envisage social interactions (Dobler & Kolliker, 2009; McNamara et al., 1999), and the dynamic process leading animals to behave in a certain way has hardly been investigated empirically (Briffa et al., 1998; Van Dyk, Taylor, & Evans, 2007). Much remains to be done to pinpoint the social factors that induce an individual to increase or decrease investment in signalling over short periods of time in the course of competitive interactions. Studying the short-term temporal dynamics of signalling should provide key elements in our understanding of social decision making.

In the present study, we investigated in barn owl, *Tyto alba*, nestlings what governs the investment in a sibling vocal contest, which will ultimately determine which individual obtains the next food item delivered by a parent. While parents are hunting, nestlings vocally compete and the most vocal nestling in the absence of parents has a higher chance of being fed when a parent returns than its less voluble siblings (Dreiss, Lahlah, & Roulin, 2010; Roulin,

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2002). Each nestling invests in a sib–sib vocal contest according to its hunger level, hungrier individuals producing longer calls at higher rates on average (Johnstone & Roulin, 2003, Roulin, 2002; Ruppli, Dreiss, & Roulin, 2013), but also according to its siblings' vocalizations, withdrawing when its siblings produce longer calls at higher rates (Roulin, 2002; Ruppli et al., 2013). Such vocal competition during this so-called 'sibling negotiation' has been suggested in several taxa (Bulmer, Celis, & Gil, 2008; Madden, Kunc, English, Manser, & Clutton-Brock, 2009) and would limit the cost of food competition (Johnstone & Roulin, 2003), because individuals invest in competition according to their chance of winning.

As in most competition, the aim of each nestling should be to impose itself in the contest, hence to produce longer calls and to be 'vocally dominant' (i.e. to produce more calls) than its siblings, since it would be more likely to obtain the prey item and gain direct fitness benefits (Dreiss, Lahlah, et al., 2010). In the meantime, individuals should obtain information from competing siblings. Indeed, it is pointless to compete for a predictable outcome (i.e. when the between-siblings asymmetry in food need is very high, the hungriest individual is more likely to win the contest), especially because the prey is indivisible and competitors are kin, sharing indirect genetic benefits (Johnstone & Roulin, 2003). We predicted that, at each time point, individuals should minimize the cost of vocal competition by producing the lowest level of signal that allows them to obtain the prey, hence maximizing signal efficiency. Individuals are hence expected to apportion their investment in the competition dynamically and participants are predicted to be vigilant to their siblings (Dreiss, Calcagno, et al., 2013), as shown by their tendency to avoid calling simultaneously (Dreiss, Ruppli, Oberli, et al., 2013). Because individuals should assess the motivation level of competitors, they are predicted to use acoustic cues to allow one another to alternate (Hauser & Fowler, 1992; Versace, Endress, & Hauser, 2008) or even to incite competitors to resume calling in order to obtain information about sibling motivation. Because vocally dominant individuals are likely to be fed first, but vocalizing is likely to be costly (Bühler & Epple, 1980), nestlings should endeavour to optimize their investment in competition by producing signals just intense enough to dominate the current competitive interaction. We hence predicted that nestling barn owls should escalate signal production until their siblings stop calling, and from this moment they should reduce their vocal investment until they are challenged again by siblings.

To test these hypotheses, we examined the temporal dynamics of vocal exchanges and investigated what induces an individual to momentarily increase or decrease investment in a vocal contest, i.e. the variation in call features over time, and finally to enter and abandon a vocal competition, i.e. the turn-taking rules. Our aim was to understand how animals dynamically modulate signals to one another in relation to short-term social interactions. We thus investigated how animals presenting similar levels of motivation to compete decide to invest in signalling at each time point of a contest in relation to the behaviour of their opponent. Using an automatic analysis of acoustic sonograms, we studied isolated pairs of siblings, alternately food-satiated or food-deprived, in random order, and comprising an older (the 'senior') and a younger individual (the 'junior'). The two individuals had the same food treatment in order to reduce the level of asymmetry in food need between them as much as possible. This design should allow us to study social turn-taking rules, which is difficult to do if the asymmetry in food need between two siblings is pronounced, since in that case only one individual is usually vocalizing (Roulin, 2002). To subsequently test the decision rules found in natural exchanges, we broadcast natural sequences of calls produced by a single nestling and analysed the individual response. Finally, to disentangle which acoustic factors induce a nestling to enter a vocal contest, we compiled playbacks of barn owl calls for which duration and production rate varied.

METHODS

We studied a wild population of barn owls breeding in nestboxes (62×56 cm and 37 cm high) located on barn walls in Switzerland (46°4′N, 6°5′E). In 2008 clutches of four to eight eggs were laid between 23 April and 6 August, in 2009 2–10 eggs between 12 May and 16 August and in 2011 four to nine eggs between 14 March and 22 July. Eggs are laid on average every 2.5 days and incubation starts after the first egg has been laid generating a pronounced age hierarchy among siblings. Throughout the night each barn owl nestling produces between 1000 and 5000 hissing calls towards its siblings to compete for priority in access to the next indivisible mouse delivered by a parent (Roulin, 2002).

Recording Vocal Interactions Between Pairs of Siblings

In 2008, when nestlings were 22–45 days old (mean ± SE: 35 ± 5), we brought 156 nestlings from 41 nests to the university; we always left one or more nestlings in the natural nest to make sure that parents did not abandon their brood. In the laboratory, we randomly matched siblings in 78 pairs and housed each pair in a soundproof wooden nestbox, identical in size to the ones in which they were reared under natural conditions. The box was divided in half by a thin wooden wall pierced with five holes at the top, so that siblings could hear each other without visually or physically interacting. The senior individual was 5 days older than its junior sibling on average (range in age difference 1–15 days). We examined the effect of seniority rather than absolute age, because previous studies showed that seniority has a stronger effect on vocalization than absolute age (Dreiss, Ruppli, Faller, & Roulin, 2013; Dreiss, Ruppli, & Roulin, 2014). Nestlings were kept in these boxes for 2 days and 3 nights and then returned to their original nest in the field. After a first night of acclimation, each pair of siblings was recorded twice from 1900 to 2340 hours, one night in a food-deprived state (no food given during the preceding 28 h) and another night in a food-satiated state (from 0000 to 1600 hours on the recording day we offered 130 g of laboratory mice, which exceeds their daily food requirement of 67 g on average), with the order of the two treatments being randomly assigned across pairs. Individuals that were starved on the first night were randomly chosen, since their mean body mass at the start of the experiment was similar to the mean body mass of individuals receiving food the first night (Student's t test: $t_{202} = 0.63$, $P = 0.53$). To avoid unnecessary disturbance we handled nestlings only once per day at 1600 hours and opened nestboxes again at midnight to add food. In 10 of the food-deprived pairs (6% of nestlings) and 24 of the food-satiated pairs (15% of nestlings), one of the two individuals did not vocalize during the 4.5 h recording period. This is also sometimes observed in natural conditions, as 15% of nestlings do not negotiate during the 15 min preceding the first prey delivery (reanalysis of data set in Dreiss, Lahlah, et al., 2010). Because our aim was to study vocal interactions between two individuals, we performed statistical analyses on the remaining 68 pairs of food-deprived siblings and 54 pairs of food-satiated siblings. Siblings of the same pair always received the same food treatment, because the conflict over obtaining food is resolved very rapidly when nestlings present different levels of need, the nestling facing a more hungry sibling producing very few calls (11 times less than its sibling on average, data from Roulin, Kolliker, & Richner, 2000). When in a similar food state, the most vocal nestling only produced four times more calls than its sibling (data from Roulin et al., 2000).