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Barn owls do not interrupt their siblings

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Animals communicate with conspecifics to resolve conflicts over how resources are shared. Since signals reflect individuals' resource-holding potential and motivation to compete, it is crucial that opponents efficiently transmit and receive information to adjust investment optimally in competitive interactions. Acoustic communication is particularly flexible as it can be quickly modulated according to background noise and audience. Diverse mechanisms have evolved to minimize acoustic signal interference, one being the avoidance of signal overlap by adjusting the timing of call production to alternate calls with those of competitors. However, the occurrence and function of overlap avoidance in the resolution of competition among relatives have barely been studied. Using young barn owl siblings, *Tyto alba*, which vocally negotiate over who will have priority access to food provided by parents, we investigated the extent to which nestlings avoid calling simultaneously and the function of this behaviour. We found that nestlings overlapped both their live siblings' calls and experimentally broadcast calls at least five times less often than expected at random. Furthermore, a focal nestling engaged more intensely in vocal negotiation when competing with nestmates that called simultaneously compared to those that did not overlap their respective calls. This suggests that barn owl nestlings avoid calling simultaneously, as overlapped calls are less efficient at deterring siblings from competing. Overlap avoidance reduces signal interference and, as a consequence, would improve the efficiency of communication among kin.

Animals are often in conflict over limited resources. To avoid the cost of physical competition, animals communicate with one another to indicate their motivation and competitive ability to contest resources (Parker 1974; Maynard Smith 1982). Provided that communication entails costs, and hence reliably reflects signallers' motivation to compete, the individuals that invest more effort in signalling have priority access to resources. Individuals facing competitors that display high motivation are more likely to give up a contest for which the outcome is predictable (Parker 1974). This phenomenon is reinforced when competitors are kin (Hamilton 1964), since a less motivated individual derives benefits by giving up a contest not only because it avoids competing for an unlikely winning outcome, but also because the contested resources are consumed by a genetically related individual, thus providing inclusive fitness benefits. To advertise their motivation to compete, body condition or social status, conspecifics have not only to produce signals efficiently, but also to perceive the signals of opponents. The avoidance of signal interference is thus an important component of animal communication (Schwartz 1993; Brumm & Slabbekoorn 2005).

Animals can communicate using various channels. Acoustic communication is particularly interesting because individuals can modulate vocal signalling rapidly in relation to environmental and social cues (e.g. Remage-Healey & Bass 2006), and they have the possibility to adopt a large range of signalling strategies (e.g. Todt & Naguib 2000). As acoustic communication can be obscured by background noise and conspecific interference, various mechanisms have evolved to ensure that signals of different individuals can be discriminated by conspecifics. For instance, the human auditory system has the ability to discriminate between different speakers in a crowd even when the sounds are produced simultaneously, the so-called cocktail party problem (Aubin & Jouventin 1998; Bee & Micheyl 2008). Among species of insects, frogs and birds that vocalize in large groups or in noisy environments, individuals shift their call features to avoid overlapping in frequency, so that their vocalizations can be distinguished from one another (Narins & Zelick 1988; Römer & Bailey 1998; Slabbekoorn & Peet 2003). Production of acoustic signals in groups can also be set by temporal organization rules (Ficken et al. 1974; Gerhardt 1994) and alternating acoustic signals, referred to as antiphonal calling, has been documented in groups of bats (Carter et al. 2008) and in

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numerous birds (Stokes & Williams 1968). Some primates can even detect and wait for silent windows to vocalize (Versace et al. 2008). This temporal organization leads to an alternation of vocal signals, reducing the risk of individuals calling simultaneously.

A particular situation occurs when individuals communicating with one another belong to the same family. In some altricial species, siblings vocalize in the absence of parents to communicate their motivation to compete with one another (Roulin et al. 2000; Johnstone & Roulin 2003; Bulmer et al. 2008; Magrath et al. 2010). This form of communication, referred to as 'sibling negotiation', reduces the level of sibling competition, and is more likely to evolve in species in which nestmates are full rather than half siblings and when the cost of sibling competition is high rather than low (Johnstone & Roulin 2003). Such vocal exchanges are usually not heard by parents and therefore cannot be interpreted as a form of begging behaviour that evolved to convey honest information to parents (Roulin et al. 2000). In the barn owl, *Tyto alba*, the single food item brought by a parent is indivisible and only one offspring is fed per parental feeding visit. Therefore, each nestling should invest more effort in negotiation when its chance of outcompeting its siblings increases (Johnstone & Roulin 2003). Hence, it is essential that each nestling assesses the level of competitiveness and motivation of all surrounding siblings, to invest effort optimally in sibling competition. Hungrier individuals vocalize at a higher rate with longer calls to signal to nestmates their higher motivation to compete for the next food item to arrive (Roulin 2002; Dreiss et al. 2010b), which would reduce sibling begging towards parents and thus the cost of sibling competition (Johnstone & Roulin 2003). This intense vocal behaviour of hungry individuals induces siblings to reduce their vocalizations in the absence (sib–sib negotiation) and presence (begging) of parents and hence to withdraw momentarily from the contest over the next food item (Roulin 2002; Dreiss et al. 2010b). Thus, in the absence of parents, nestlings need to hear and be heard, to adjust investment optimally in sibling competition once parents arrive with food. During a single night nestlings can produce thousands of calls, implying that this communication system may be costly in terms of energy and time invested (e.g. in another system: Kilner 2001; Rodriguez-Gironés et al. 2001; Chappell & Bachman 2002). We hypothesized that, to maximize transmission of vocal signals between siblings, nestlings avoid calling simultaneously, otherwise they may have to call even more often to transfer the same amount of information. Although a previous study in the European starling, *Sturnus vulgaris*, observed that siblings would avoid overlapping their vocalizations when parents are away (Chaiken 1990), no experimental test has yet been performed.

We tested this hypothesis of overlap avoidance in nestling barn owls experimentally, by studying unmanipulated vocal interactions between pairs of nestlings (i.e. dyads). Siblings differ in age owing to a pronounced hatching asynchrony, which results in asymmetries in the competitiveness of nestmates and different vocal behaviours (Roulin 2004). Given their stronger competitive abilities, seniors can usually outcompete their siblings while investing relatively less in vocalizations and they are less sensitive to the vocal behaviour of their junior siblings (Roulin 2004). We thus recorded naturally occurring vocal interactions between dyads of siblings that were either both food deprived or both food satiated, each dyad comprising one senior and one junior nestling. If overlap is an aggressive or competitive signal itself, it should be used more often by hungry individuals and more competitive individuals (here seniors). Alternatively, if nestlings avoid calling simultaneously to transfer information efficiently, they should avoid overlap whatever the competitive situation. We tested whether the degree to which an individual avoids calling simultaneously to its sibling varies with motivation, that is, its level of hunger, and with competitiveness, that is, between juniors and seniors, and with developmental stage (i.e. absolute age).

In such a design, each nestling produces calls at variable rhythms and hence the observation of siblings not calling simultaneously may simply result from the fact that siblings have different time-dependent activity patterns. Hence, to tackle the hypothesis that barn owl siblings actively avoid calling simultaneously, we analysed nestling response to playback experiments with variable call rate. In natural vocal interactions, the rhythm of nestlings' calls varies from loose clusters of rapid calls to relatively regular (see for instance Roulin et al. 2009). We thus analysed the vocal response of singleton nestlings (nestlings placed individually in an experimental box) to two different playback soundtracks, one with negotiation calls broadcast at random (unpredictable) time points, and another broadcast at a constant (predictable) rhythm. If barn owl siblings minimize acoustic signal interference, we predicted that individuals would call simultaneously to their siblings or the playback less often than expected at random, regardless of the rhythm at which calls are produced. To test the effect of competition on nestling propensity to avoid call overlap, we also varied playback call rate, call duration and number of calls. If overlap is a competitive signal, it should occur more often in competitive situations, when call rate and call duration are high (Roulin et al. 2009) and potentially when more individuals are calling. Conversely, nestlings are expected to avoid calling simultaneously in all situations if overlap avoidance efficiently allows information transfer.

Assuming that the adaptive function of not overlapping calls is to improve the efficiency of communication, we predicted that an individual will more efficiently deter its siblings from competing if it does not call simultaneously to them. To test this prediction we performed a third experiment. Singleton nestlings were broadcast pairs of calls produced by two individuals that were separated by a short pause (no overlap referred to as '0% overlap' treatment), overlapped on half of their duration ('50% overlap' treatment) or entirely ('100% overlap' treatment; Fig. 1). While broadcasting these

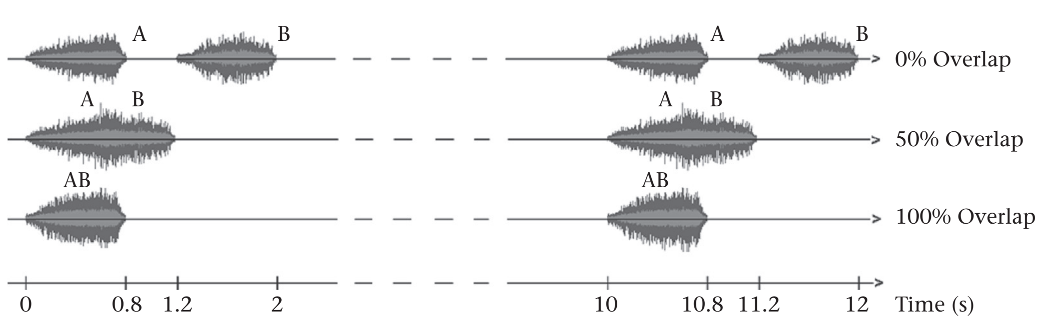

Figure 1. Diagram of the three playback treatments (experiment 3). Each treatment consisted of the repetition of a pair of calls from two different unfamiliar nestlings (A and B) every 10 s. '0% overlap': calls of A and B are separated by a pause of 0.4 s; '50% overlap': calls of A and B overlapped on 50% of their duration; and '100% overlap': calls of A and B are each overlapped on 100% of their duration. Treatments were randomly ordered across singleton nestlings.