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Essay

Signals in family conflicts

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Although the role of animal signals in the resolution of family conflicts has been thoroughly studied, it has been typically analysed in isolated two-player interactions. For instance, parents are usually considered as the sole receivers of offspring begging signals or mates the receivers of sexual displays. However, this view does not wholly encompass the dynamic and complex nature of the family scenario. In this essay, we review for the first time the clearest evidence of animal signals found to play a role in more than one family context (e.g. mate–mate, parent–offspring and sib–sib interactions). We then argue that these signals might have coevolved in multiple family contexts because the whole network of related individuals shares genes and similar physiological mechanisms underlying signal expression and perception abilities. Finally, we propose candidate traits that we would expect to function in multiple family contexts and we consider questions that could be addressed in further studies to understand better the evolution of family signals.

In animal societies, including humans, information exchange helps researchers understand the interactions among group members (reviewed in Carazo & Font 2010; Seyfarth et al. 2010; Ruxton & Schaefer 2011). Learning how individuals use social information for their common and private interests is one of the keys to answering outstanding questions in evolutionary biology, such as the origin of sociality (Danchin & Wagner 1997) and cooperation (Axelrod & Hamilton 1981). The information that individuals gather from others modulates fitness-related decisions such as where to live, what to eat and with whom to interact (Danchin et al. 2004). For instance, information on opponents' condition determines dominance hierarchies during conflicts (e.g. Huntingford & deLeaniz 1997) and may mitigate the costs of agonistic interactions (Logue et al. 2010). On the other hand, because individuals need to receive information from conspecifics, they simultaneously make themselves vulnerable to manipulation that may cause them to deviate from their optimum behaviour (Rice & Holland 1997). Hence, both information exchange and manipulation can influence the outcome of social interactions and conflict resolution in societies (Kilner & Hinde 2008).

Interactions among family members are some of the most common and basic social behaviours exhibited by animals. Family members constitute a small society with overlapping but not identical genetic interests, which have been identified as three main forms of evolutionary conflict. Each offspring is more closely related to itself than to its parents and siblings. Therefore, optimal parental investment levels for offspring are greater than for parents ('parent–offspring conflict'; Trivers 1974). Individual offspring in turn value their own wellbeing more highly than that of their siblings and thus should try to take a disproportionate share of food ('sibling conflict'; O'Connor 1978). Finally, each parent would profit if the other provided more care ('sexual conflict'; Lessells 1999). Given that all family members coincide in time and space to adjust their decision rules over the same resource (i.e. parental care), all possible conflicts can take place at the same time and thus they should be analysed simultaneously, as previously proposed by Parker et al. (2002). However, as a model of social relationships, intrafamily interactions (parent–offspring, sibling and mate–mate interactions) have been traditionally studied as isolated events, either theoretically or empirically (but see Parker 1985; Hinde &

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Kilner 2007). This prevailing approach has proven highly productive in many respects, but has also fostered a limited and overly simplistic view of the complex and dynamic nature of the family arena.

Analysing intrafamily interactions simultaneously may result in a more complete view of the mechanisms that underlie conflict resolution, such as the use of signals among family members (Godfray & Johnstone 2000). As in other social contexts, signals may serve to exchange information between individuals. For instance, sexual displays can inform mates about the direct or indirect genetic benefits they would accrue by increasing current parental investment (Burley 1986), and offspring begging signals may convey information to parents about offspring need or quality and thus about the benefits of giving extra food (Godfray 1991; Mock et al. 2011). However, sexual displays are usually thought to have evolved solely in the context of sexual selection and begging signals in the parent–offspring conflict. Yet, could these signals be involved in other family contexts as well? To answer this question, we first need to know whether there is evidence that signalling behaviours affect all family members. In fact, signals are built on the multitude of sensory capacities and neuroendocrine responses previously present in the organism and already established through strong selection (West-Eberhard 1984), and these pre-existing sensory biases are probably the same in mates and offspring and may lead to similar responses (see, for instance, studies on human facial neoteny: Jones et al. 1995; on females imitating begging behaviour of chicks in birds: Tinbergen 1959).

It is widely accepted that most animal communication has evolved in the context of a network environment (i.e. several signallers and receivers within communication range of each other; McGregor 2005). For instance, it has long been recognized that so-called 'sexual signals' can function in many social contexts other than intrasexual or intersexual competition for mates (West-Eberhard 1983). Still, this broadly accepted complexity of signalling dynamics has rarely been applied to the particular case of the family, where, as in broader social networks, related individuals (but also unrelated ones; e.g. the mates) communicate within transmission range of each other's signals (Fig. 1). Whether signals expressed by family members can be used in multiple family conflicts remains an open question in most species studied to date.

In this essay, we aim to expand early ideas on the role of signals in multiple family contexts (Parker et al. 2002). First, we review the clearest evidence that signalling behaviours affect all family members. Then we analyse the informative or manipulative function of these signals as a mechanism for multiple conflict resolution. To conclude, we argue that family signals and the processes leading to signal expression are only partly captured by a single family conflict and can be best understood in the light of complex interactions among family members.

SIGNALS THAT WORK IN MULTIPLE FAMILY CONTEXTS

Offspring Begging Signals

The main mechanisms proposed for the resolution of parent–offspring conflict (honest signalling and scramble competition mechanisms) assume that begging displays are directed at parents. A common prediction of these models is that the probability of receiving food from parents is proportional to the strength of begging stimuli (Mock & Parker 1997; Royle et al. 2002), which has been amply verified in various taxa (e.g. in insects: Smiseth & Moore 2002; in birds: Leonard et al. 2003). However, very few studies have broadened this traditional perspective of a dyadic signalling system (from one nestling to the parent) and explored the extent to which offspring adjust signalling levels to each other (Horn & Leonard 2005).

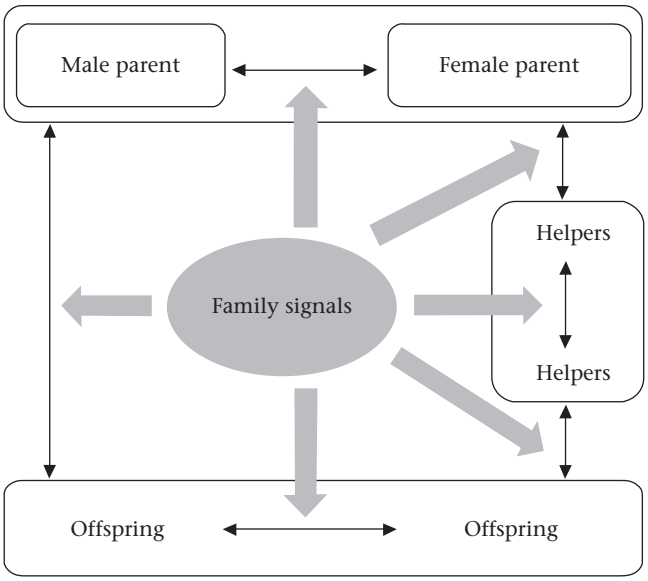

Figure 1. Traditionally, family signals have been studied solely in dyadic interactions among family members (i.e. male parent–female parent, parent–offspring and sib–sib interactions). However, given that family members share genes and probably similar physiological mechanisms underlying signal expression and perception abilities, signals can simultaneously affect the interactions among all family members. The family can thus be viewed as a network of related individuals that communicate within transmission range of each other's signals. Modified from Parker et al. 2002 with permission from the Royal Society.

Studies in the barn owl, *Tyto alba*, suggest that siblings exchange begging signals in the absence of parents to inform each other about their need and to 'negotiate' the levels at which they will beg when parents arrive at the nest ('sibling negotiation hypothesis'; Roulin et al. 2000). Thus, begging signals in the barn owl play a simultaneous role in the parent–offspring and sibling conflicts (Table 1). The idea that begging displays have multiple receivers may explain why offspring sometimes beg in the absence of parents, a behaviour that would otherwise be interpreted as costly and nonadaptive. Sibling negotiation calls also seem to be characteristic of the spotless starling, *Sturnus unicolor*, although in this case parent-absent begging calls are acoustically distinct from begging signals directed at parents (Bulmer et al. 2008).

Similarly, the begging behaviour of great tit, *Parus major*, nestlings not only affects parental feeding rates (Kölliker et al. 1998, 2000), but also the social network structure of nestlings (i.e. the brood mean strength of associations among nestlings; Royle et al. 2012) (Table 1).

Also in mammals, banded mongoose, *Mungos mungo*, offspring increase their begging rates when the background level of begging by littermates is experimentally lowered (Bell 2007). Additionally, helpers ('escorts') are influenced by the total begging signal produced by a litter (Bell 2007). Therefore, in this communally breeding system begging signals function in both the helper–offspring and sibling conflicts (Table 1).

Parental Signals

As already mentioned, the role of 'sexual displays' is often considered solely in mate–mate interactions, either before or after pairing. However, studies on the burying beetle, *Nicrophorus vespilloides*, reveal that these signals can also be involved in the parent–offspring conflict. This is one of the rare cases in the Coleoptera with biparental care and food provisioning to individual offspring, two important sources of intrafamily conflict (reviewed