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.
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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).
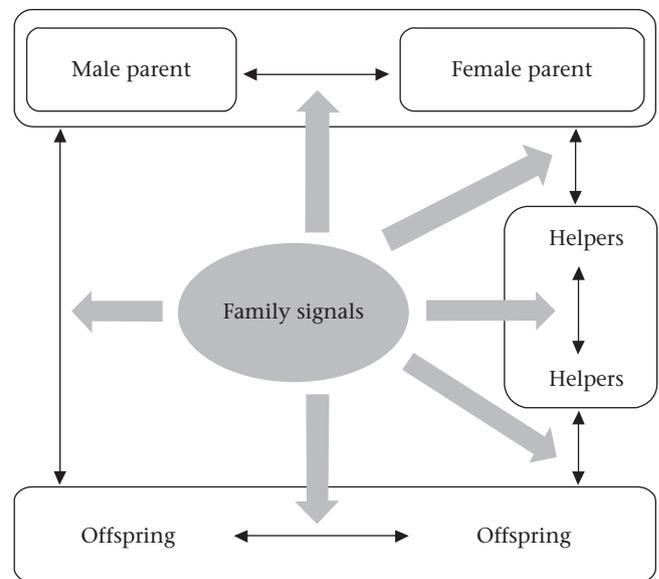
Figure 1. Traditionally, family signals have been studied solely in dyadic interactions among family members (i.e. male parent−female parent, parent−offspring and sib−sib interactions). However, given that family members share genes and probably similar physiological mechanisms underlying signal expression 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

Table 1
Clearest empirical evidence of animal signals that play a simultaneous role in various family conflicts

Species	Trait	Sender	Receiver	Family conflict	Response variable	Source
Insects						
Burying beetle	Chemical signals	Parents	Offspring	Parent–offspring	Begging	Smiseth et al. 2010
Nicrophorus vespilloides	(cuticular hydrocarbons)		Mates	Sexual	Male mate choice	Steiger et al. 2007
Honeybee *Apis mellifera*	Chemical signals (mandibular pheromone)	Queen	Worker	Worker–queen, Worker–larvae	Worker development and behaviour	Slessor et al. 2005
			Drones	Sexual?	Attraction	Gary 1962
Birds						
Herring gull *Larus argentatus*	Red spot	Parents	Offspring Mates?	Parent–offspring Sexual?	Begging	Tinbergen & Perdeck 1950
Yellow-legged gull *Larus cachinnans*	Red spot	Parents	Offspring Mates	Parent–offspring Sexual	Begging Mate parental care	Velando et al. 2013 Morales et al. 2009
Barn owl	Begging (parents absent)	Offspring	Parents	Parent–offspring	Parental care	Dreiss et al. 2010
Tyto alba			Siblings	Sibling	Begging (parents present)	Roulin et al. 2000; Dreiss et al. 2010
Great tit *Parus major*	Begging	Offspring	Parents	Parent–offspring	Parental care	Kölliker et al. 1998, 2000; Royle et al. 2012
			Siblings	Sibling	Social network structure	Royle et al. 2012
Mammals						
House mouse *Mus musculus*	Chemical signals (urine odour)	Parents	Offspring	Parent–offspring	Vocalizations	Santucci et al. 1994; Kapusta & Szentgyorgyi 2004
			Mates	Sexual	Female mate choice Male mate choice	Lin et al. 2005 Swaney et al. 2008
Banded mongoose *Mungos mungo*	Begging	Offspring	Helper 'escort'	Helper–offspring	Parental care	Bell 2007
			Siblings	Sibling	Begging	

in Mas & Kölliker 2008). Burying beetles are social insects that base their mating preferences on cuticular hydrocarbon profiles (Steiger et al. 2008). After mating, a male and a female beetle normally cooperate to raise their young on small vertebrate carcasses. They provide care by provisioning the larvae with predigested carrion and by defending the carcass from the frequent attacks by intruders (Scott 1998). The mechanism that allows a carcass owner to discriminate between its original mate and an intruder is based on the recognition of cuticular hydrocarbon profiles (Steiger et al. 2007). Moreover, it has been suggested that the conflict of interest between males and females over the duration of parental care is likely to be hormonally mediated (Scott 1998). Males, which are expected to benefit more than females from early desertion of the brood, are probably less likely to desert the brood when certain pheromones are present (Scott 1998). Remarkably, the cuticular hydrocarbons produced by *N. vespilloides* parents trigger larval begging and allow for larval kin discrimination (Smiseth et al. 2010). If the same hydrocarbon profiles were used in these different contexts, studies performed with this species would provide the first experimental evidence that a signal used in mate–mate interactions plays a role in the parent–offspring conflict over care (Table 1).

In birds, there is another suggestive example. However, in this case, a signal expressed by the parents was first proposed to function in the parent–offspring conflict and thereafter (more than 50 years later) in the sexual conflict over care. In his pioneering work, Tinbergen suggested that the red spot on the bill of herring gull, *Larus argentatus*, parents stimulates innate begging responses in newly hatched chicks (Tinbergen & Perdeck 1950), a classic example in behavioural studies. Notably, in the closely related yellow-legged gull, *Larus cachinnans*, the red spot plays a role in the sexual conflict over care, since mates of spot-enlarged parents increase food provisioning to offspring relative to controls (Morales et al. 2009). Moreover, in this species chicks beg more intensely when presented with an adult head dummy with an enlarged red spot (Velando et al. 2013). Overall, these results indicate that the gull's red spot functions simultaneously in the sexual and the parent–offspring conflicts (Table 1).

In mammals, the urine of house mice, *Mus musculus domesticus*, contains signalling proteins that affect mating preferences in both sexes (Lin et al. 2005; Swaney et al. 2008). Moreover, the odour of urine produced by the male and female parents influences the rate of ultrasonic vocalizations in pups (Santucci et al. 1994; Kapusta & Szentgyorgyi 2004). These high-frequency signals are produced by pups when they are placed outside the nest and they induce retrieving behaviours in mothers (reviewed in Kölliker & Richner 2001). As in the examples in insects and birds given above, urine pheromones in mammals represent candidate signals with a function in both the sexual and the parent–offspring conflicts (Table 1).

Complex Family: Chemical Signals in Eusocial Insects

Social insects have been proposed as the best experimental systems for understanding the ancestral conditions for the evolution of family signals (Mas & Kölliker 2008). In particular, our understanding of chemical signals in a family network is best provided through eusocial insects, whose organization in colonies is determined primarily by pheromones that are actively produced by the queen, the workers at various tasks and life stages and by the brood (Slessor et al. 2005). Kin selection predicts a conflict between the queen and her worker daughters over reproduction. Also, although workers and female larvae are usually more genetically related than parents and offspring (owing to the haplodiploid reproductive system), there is potential conflict over care between them. Each larva obtains greater inclusive fitness by developing as a queen than as a worker (Ratnieks et al. 2006). In the honeybee, *Apis mellifera*, it is known that components of the queen mandibular pheromone attract drones, stimulate workers to form the retinue, to rear brood and to forage for food, and, more importantly, they suppress the development of workers' ovaries and thus their reproductive capacity (reviewed in Slessor et al. 2005). The latter shows that queen mandibular signals have a profound influence in the worker–queen conflict over reproduction, but also indirectly in the worker–larvae conflict (Table 1). In this haplodiploid system, males only transfer genes to the female (diploid) offspring and thus

prefer a female (queen)-biased sex ratio in their offspring, while the queen prefers an unbiased sex ratio (Baer 2003). Although probable, the role of pheromones in queen–male conflict over paternity and sex ratio remains uncertain.

WHY ARE SIGNALS USED IN SIMULTANEOUS FAMILY CONTEXTS?

One probable answer is that similar mechanisms underlie communication among family members. In a family, the final outcome of conflicts may be 'negotiated' according to the information obtained from the opponents' signals or behaviour (McNamara et al. 1999; Lessells & McNamara 2012). The flexibility of negotiation among family members is partly determined by the quality of the information on offer (Hinde & Kilner 2007), and the information is likely to be accessible to all family members and not only used in dyadic interactions (McGregor 2005). Likewise, sensory biases can be present in all family members and thus manipulative signals may affect multiple family contexts. Both information exchange and manipulation are likely to influence the behavioural rules followed by individuals that are in conflict (Beekman et al. 2003).

In the barn owl example (Table 1), informative negotiation of resources among siblings has been proposed as a possible solution of intrabrood conflict. The hungrier nestlings invest relatively more effort in displaying to their rivals, since they are more motivated to contest the next item delivered when parents arrive. In contrast, the less hungry nestlings are expected to invest less in displaying to rivals in order to reduce begging costs (Roulin et al. 2000). Hence, offspring may gain by advertising their need to one another with costly begging displays, because this deters the less needy siblings from competing intensely when a parent arrives at the nest. Owl parents in turn adjust their provisioning rate to offspring begging level (Dreiss et al. 2010). Hence, reliable information offered by begging displays probably underlies multiple family contexts.

Begging intensity in great tits (Table 1) also conveys reliable information about offspring hunger levels (Kölliker et al. 1998). Begging intensity is more evenly distributed within broods when female parents provide more food than male parents, which suggests that parents are not equally responsive to variation in the information conveyed, that is, hunger levels (Royle et al. 2012). Moreover, begging behaviour relates to offspring gregariousness, which in turn predicts family fitness (Royle et al. 2012). Thus, begging signals probably contribute to shaping cooperative behaviour among family members, enhancing group performance. Similarly, in the communally breeding banded mongoose (Table 1), information exchange by means of begging signals may facilitate cooperation among family members. Each pup forms an exclusive relationship with a single helper, 'its escort', but escorts are affected by begging of the whole brood, favouring cooperation among littermates (Bell 2007). Since all brood mates benefit from having companions, cooperative begging signals potentially offset underlying genetic conflicts (Bell 2007).

Also, reliable information conveyed by the red spot on the bill may affect negotiation rules within a family of yellow-legged gulls (Table 1). Red spot expression is costly for parents to produce and reflects their current antioxidant status (Pérez et al. 2008). Thus, mates can use this information to evaluate the direct or indirect benefits of their own investment, according to the differential allocation theory (Burley 1986). It is unknown whether the information conveyed by the red spot can also affect parent–offspring negotiation rules on the amount of resources allocated to them. It seems likely, since offspring show a begging preference for larger red spots (Velando et al. 2013), presumably expressed by high-quality caregivers. Alternatively, parents could be exploiting a sensory bias in chicks towards red objects. Begging signals triggered by the adult's red spot are costly to produce and inform parents about the chick's hunger and condition (Noguera et al. 2010). Hence, the red spot expression in the parents might impose a cost to chicks that prevents begging exaggeration and, in this case, parents would always 'win' the conflict (Godfray 1991).

Chemical signals may also offer reliable information to other family members. In the honeybee (Table 1), it has been argued that the queen pheromones would flexibly affect the outcome of worker–queen conflict over reproduction if they were honest signals of queen fertility and, hence, would inform workers about the genetic benefits they would gain by self-restraint (Keller & Nonacs 1993). Yet, as in the example in gulls given above, it is unresolved whether parental signals (queen pheromones in the case of the honeybee) are informative or manipulative. If the signals are manipulative in the honeybee, the queen would have control and always win the conflict with workers, irrespective of her fertility.

CONCLUSIONS AND PROSPECTS

The examples shown in Table 1 reveal that a given signal can function simultaneously in various family contexts and that family members are not confined to dyadic interactions, but rather they form a dynamic communication network. This perspective suggests new questions that need to be addressed to understand fully the evolution of signals in the family arena.

First, signals used in intrafamily interactions act as reciprocal environmental influences on the phenotype of other family members, and thus they may exert indirect genetic effects on them (Moore et al. 1997; Kölliker et al. 2012). For instance, the early social environment of offspring shapes the strategy not only that they later adopt as parents but also that they transmit to their own offspring (Meunier & Kölliker 2012). When fitness-related traits of family members influence each other and are heritable, the consequence is a correlational selection among these traits (i.e. social epistasis; Wolf & Brodie 1998). Thus, if 'sexual' signals influence mate and offspring behaviour, an interesting aspect is that offspring preferences may also play a role in runaway selection (i.e. linkage disequilibrium between sexual trait and preferences). Therefore, they could increase directional selection on sexual traits when genetic covariance is positive or limit their expression when covariance is negative (West-Eberhard 1983).

Nevertheless, we should first explore whether sexually selected traits that affect offspring behaviour in Table 1 are rare cases or examples of an overlooked process. We consider that a promising starting point for further research is to study the role of parental signals during parent–offspring interactions in species in which sexual imprinting has already been demonstrated (such as many species of fowl, ducks, geese, pigeons and doves, gulls, parrots and songbirds). In many animals, early exposure of young animals to parental signals has a dramatic influence on sexual preferences when they reach adulthood (e.g. Lorenz 1935; Kendrick et al. 1998; Penn & Potts 1998; Jacob et al. 2002; Kozak et al. 2011). Hence, adults base their preferences on the scents, sounds, colours or other stimuli to which they were inevitably exposed as offspring very early in their development. This indicates that parental signals strongly influence, with a delay, offspring behaviour. But do they influence offspring during parent–offspring interactions as well? Apart from studies in mammals, which suggest that offspring have the ability to recognize and select their mother's scent during development (Yamazaki et al. 2000; reviewed in Brennan & Kendrick 2006), this question remains practically unexplored. Another group of candidate traits are those expressed in species with prolonged and intensive parental care. For instance, in many seabirds offspring are continuously exposed to conspicuous colours

on the parent's bill, gape, eye rings and feet, some of which are known to play a role in sexual selection (Torres & Velando 2003; 2005) and to reflect current parental nutritional quality (Kristiansen et al. 2006; Velando et al. 2006; Leclaire et al. 2011). These examples may also help to solve questions on the evolution of female ornamentation. After mating, one explanation for the presence of ornaments in the pair bond is that they evolve because they stimulate the partner to increase parental investment (Servedio et al. 2013). However, this possibility has been little explored in females (reviewed in Ratikainen & Kokko 2010). An additional explanation that would be interesting to test is whether offspring can be receivers of maternal signals and, in general, of parental signals in species with intense biparental care.

Second, given that signals are accessible to all family members, parental care strategies are probably influenced by the interaction between signals expressed by different members. For instance, parental provisioning behaviour in yellow-legged gulls depends on both the expression of the red spot on the mate's bill and offspring begging signals (Morales et al. 2009). Thus, parental decision rules are complex because they integrate the information conveyed by different types of signals in simultaneous family conflicts. Further empirical studies that simultaneously manipulate two different signals (e.g. signals used in mate attraction and offspring signals) are required to know how their joint effect influences the behavioural strategies of all family members.

Third, to understand the type of signals that function in multiple conflicts we also need to determine whether parental allocation is controlled primarily by parents or by their offspring. Depending on who controls parental investment, a given signal is likely either to manipulate or to inform other family members, or both. If parents control food provisioning, we may expect honest offspring signals to evolve to convey reliable information about hunger or condition (Parker et al. 2002). But if parents lack full control of food allocation, offspring may be expected to use begging signals to manipulate parental provisioning (Parker et al. 2002), but at the same time to negotiate with their siblings over who has priority in the following feeding attempt (Johnstone & Roulin 2003).

Lastly, another issue that remains practically unexplored is whether parental signals can influence the decision rules of helpers in cooperatively breeding vertebrates, as demonstrated in insect colonies. If there are direct benefits of helping (e.g. increased survival, mating success, ability to rear offspring or chances of successful dispersal; Clutton-Brock 2002), nonbreeding individuals could compete to become helpers. Signals could thus be used to form dominance hierarchies among relatives (and also among nonrelatives) that establish an order of participation in cooperative breeding tasks and access to resources. Exploring the role of signals during the formation of dominance hierarchies in social organisms and its effects in the whole family will contribute to explaining how cooperative breeding is maintained.

We have emphasized that parental investment reflects the simultaneous resolution of multiple family conflicts, as previously proposed by Parker (1985) and Parker et al. (2002). Here we provide a more detailed development of this idea with a special focus on signals and the processes leading to their expression. Whatever their origin, signals are not isolated from other actors and signals in the family scenario. They might have coevolved in multiple contexts within the network of related individuals, because they share genes and similar physiological mechanisms underlying signal expression and perception abilities. Given that selection can act on multiple traits simultaneously, the evolutionary response to selection for parental provisioning should depend on the genetic covariances between the signalling behaviours of all family members (Kölliker et al. 2005). Signals may be selected through the sum of adaptive responses of family members, although their expression may also be constrained by maladaptive responses owing to shared sensory capacities. Future coadaptation models should consider mate–mate as well as parent–offspring interactions to explore how parental care can be coadapted because of the combined effects of these multiple signalling behaviours on fitness.

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References

Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, **211**, 1390–1396.

Baer, B. 2003. Bumblebees as model organisms to study male sexual selection in social insects. *Behavioral Ecology and Sociobiology*, **54**, 521–533.

Beekman, M., Komdeur, J. & Ratnieks, F. L. W. 2003. Reproductive conflicts in social animals: who has power? *Trends in Ecology & Evolution*, **18**, 277–282.

Bell, M. B. V. 2007. Cooperative begging in banded mongoose pups. *Current Biology*, **17**, 717–721.

Brennan, P. A. & Kendrick, K. M. 2006. Mammalian social odours: attraction and individual recognition. *Philosophical Transactions of the Royal Society B*, **361**, 2061–2078.

Bulmer, E., Celis, P. & Gil, D. 2008. Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*). *Behavioral Ecology*, **19**, 279–284.

Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.

Carazo, P. & Font, E. 2010. Putting information back into biological communication. *Journal of Evolutionary Biology*, **23**, 661–669.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualisms in cooperative vertebrates. *Science*, **296**, 69–72.

Danchin, E. & Wagner, R. H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, **12**, 342–347.

Danchin, E., Giraldeau, L. A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487–491.

Dreiss, A., Lahlah, N. & Roulin, A. 2010. How siblings adjust sib-sib communication and begging signals to each other. *Animal Behaviour*, **80**, 1049–1055.

Gary, N. E. 1962. Chemical mating attractants in the queen honey bee. *Science*, **136**, 773–774.

Godfray, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature*, **352**, 328–330.

Godfray, H. C. J. & Johnstone, R. A. 2000. Begging and bleating: the evolution of parent-offspring signalling. *Philosophical Transactions of the Royal Society B*, **355**, 1581–1591.

Hinde, C. A. & Kilner, R. M. 2007. Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B*, **274**, 53–60.

Horn, A. G. & Leonard, M. L. 2005. Nesting begging as a communication network. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 170–190. Cambridge: Cambridge University Press.

Huntingford, F. A. & deLeaniz, C. G. 1997. Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. *Journal of Fish Biology*, **51**, 1009–1014.

Jacob, S., McClintock, M. K., Zelano, B. & Ober, C. 2002. Paternally inherited HLA alleles are associated with women's choice of male odor. *Nature Genetics*, **30**, 175–179.

Johnstone, R. A. & Roulin, A. 2003. Sibling negotiation. *Behavioral Ecology*, **14**, 780–786.

Jones, D., Brace, C. L., Jankowiak, W., Laland, K. N. & Musselman, L. E. 1995. Sexual selection, physical attractiveness, and facial neoteny: cross-cultural evidence and implications. *Current Anthropology*, **36**, 723–748.

Kapusta, J. & Szentgyorgyi, H. 2004. Ultrasonic responses of CBA pups to the odour of genetically different mice. *Behaviour*, **141**, 157–167.

Keller, L. & Nonacs, P. 1993. The role of queen pheromones in social insects: queen control or queen signal. *Animal Behaviour*, **45**, 787–794.

Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A. & Skinner, J. D. 1998. Mothers determine sexual preferences. *Nature*, **395**, 229–230.

Kilner, R. M. & Hinde, C. A. 2008. Information warfare and parent-offspring conflict. *Advances in the Study of Behavior*, **38**, 283–336.

Kölliker, M. & Richner, H. 2001. Parent-offspring conflict and the genetics of offspring solicitation and parental response. *Animal Behaviour*, **62**, 395–407.

Kölliker, M., Richner, H., Werner, I. & Heeb, P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Animal Behaviour*, **55**, 215–222.

Kölliker, M., Brinkhof, M. W. G., Heeb, P., Fitze, P. S. & Richner, H. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proceedings of the Royal Society B*, **267**, 2127–2132.

Kölliker, M., Brodie, E. D., III & Moore, A. J. 2005. The coadaptation of parental supply and offspring demand. *The American Naturalist*, **166**, 506–516.

Kölliker, M., Royle, N. J. & Smiseth, P. T. 2012. Parent–offspring co-adaptation. In: *The Evolution of Parental Care* (Ed. by N. J. Royle, P. T. Smiseth & M. Kölliker), pp. 285–299. Oxford: Oxford University Press.

Kozak, G. M., Head, M. L. & Boughman, J. W. 2011. Sexual imprinting on ecologically divergent traits leads to sexual isolation in sticklebacks. *Proceedings of the Royal Society B*, **278**, 2604–2610.

Kristiansen, K. O., Bustnes, J. O., Folstad, I. & Helberg, M. 2006. Carotenoid coloration in great black-backed gull *Larus marinus* reflects individual quality. *Journal of Avian Biology*, **37**, 6–12.

Leclaire, S., White, J., Arnoux, E., Faivre, B., Vetter, N., Hatch, S. A. & Danchin, E. 2011. Integument coloration signals reproductive success, heterozygosity, and antioxidant levels in chick-rearing black-legged kittiwakes. *Naturwissenschaften*, **98**, 773–782.

Leonard, M. L., Horn, A. G. & Parks, E. 2003. The role of posturing and calling in the begging display of nestling birds. *Behavioral Ecology and Sociobiology*, **54**, 188–193.

Lessells, C. M. 1999. Sexual conflict. In: *Levels of Selection in Evolution* (Ed. by L. Keller), pp. 75–99. Princeton, New Jersey: Princeton University Press.

Lessells, C. M. & McNamara, J. M. 2012. Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proceedings of the Royal Society B*, **279**, 1506–1514.

Lin, D. Y., Zhang, S. Z., Block, E. & Katz, L. C. 2005. Encoding social signals in the mouse main olfactory bulb. *Nature*, **434**, 470–477.

Logue, D. M., Abiola, I. O., Rains, D., Bailey, N. W., Zuk, M. & Cade, W. H. 2010. Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song. *Proceedings of the Royal Society B*, **277**, 2571–2575.

Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. *Journal of Ornithology*, **83**, 137–213.

McGregor, P. 2005. *Animal Communication Networks*. Cambridge: Cambridge University Press.

McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999. Incorporating rules for responding into evolutionary games. *Nature*, **401**, 368–371.

Mas, F. & Kölliker, M. 2008. Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution. *Animal Behaviour*, **76**, 1121–1131.

Meunier, J. & Kölliker, M. 2012. Parental antagonism and parent–offspring co-adaptation interact to shape family life. *Proceedings of the Royal Society B*, **279**, 3981–3988.

Mock, D. W., Dugas, M. B. & Strickler, S. A. 2011. Honest begging: expanding from signal of need. *Behavioral Ecology*, **22**, 909–917.

Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford: Oxford University Press.

Moore, A. J., Brodie, E. D. & Wolf, J. B. 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, **51**, 1352–1362.

Morales, J., Alonso-Alvarez, C., Pérez, C., Torres, R., Serafino, E. & Velando, A. 2009. Families on the spot: sexual signals influence parent–offspring interactions. *Proceedings of the Royal Society B*, **276**, 2477–2483.

Noguera, J. C., Morales, J., Pérez, C. & Velando, A. 2010. On the oxidative cost of begging: antioxidants enhance vocalizations in gull chicks. *Behavioral Ecology*, **21**, 479–484.

O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Animal Behaviour*, **26**, 79–96.

Parker, G. A. 1985. Models of parent–offspring conflict. V. Effects of the behaviour of the two parents. *Animal Behaviour*, **33**, 519–533.

Parker, G. A., Royle, N. J. & Hartley, I. R. 2002. Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society B*, **357**, 295–307.

Penn, D. & Potts, W. 1998. MHC-disassortative mating preferences reversed by cross-fostering. *Proceedings of the Royal Society B*, **265**, 1299–1306.

Pérez, C., Lores, M. & Velando, A. 2008. The availability of nonpigmentary antioxidant affects red coloration in gulls. *Behavioral Ecology*, **19**, 967–973.

Ratikainen, I. I. & Kokko, H. 2010. Differential allocation and compensation: who deserves the silver spoon? *Behavioral Ecology*, **21**, 195–200.

Ratnieks, F. L. W., Foster, K. R. & Wenseleers, T. 2006. Conflict resolution in insect societies. *Annual Review of Entomology*, **51**, 581–608.

Rice, W. R. & Holland, B. 1997. The enemies within: intergenomic conflict, inter-locus contest evolution (ICE) and the intraspecific red queen. *Behavioral Ecology and Sociobiology*, **41**, 1–10.

Roulin, A., Kölliker, M. & Richner, H. 2000. Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society B*, **267**, 459–463.

Royle, N. J., Hartley, I. R. & Parker, G. A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology & Evolution*, **17**, 434–440.

Royle, N. J., Pike, T. W., Heeb, P., Richner, H. & Kölliker, M. 2012. Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society B*, **279**, 4914–4992.

Ruxton, G. D. & Schaefer, H. M. 2011. Resolving current disagreements and ambiguities in the terminology of animal communication. *Journal of Evolutionary Biology*, **24**, 2574–2585.

Santucci, D., Masterson, D. & Elwood, R. W. 1994. Effects of age, sex, and odors from conspecific adult males on ultrasonic vocalizations of infant CS1 mice. *Behavioural Processes*, **32**, 285–295.

Scott, M. P. 1998. The ecology and behavior of burying beetles. *Annual Review of Entomology*, **34**, 367–373.

Servedio, M. R., Price, T. D. & Lande, R. 2013. Evolution of displays within the pair bond. *Proceedings of the Royal Society B*, **280**, 1757.

Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K. & Hammerschmidt, K. 2010. The central importance of information in studies of animal communication. *Animal Behaviour*, **80**, 3–8.

Slessor, K. N., Winston, M. L. & Le Conte, Y. 2005. Pheromone communication in the honeybee (*Apis mellifera* L.). *Journal of Chemical Ecology*, **31**, 2731–2745.

Smiseth, P. T. & Moore, A. J. 2002. Does resource availability affect offspring begging and parental provisioning in a partially begging species? *Animal Behaviour*, **63**, 577–585.

Smiseth, P. T., Andrews, C., Brown, E. & Prentice, P. M. 2010. Chemical stimuli from parents trigger larval begging in burying beetles. *Behavioral Ecology*, **21**, 526–531.

Steiger, S., Peschke, K., Francke, W. & Müller, J. K. 2007. The smell of parents: breeding status influences cuticular hydrocarbon pattern in the burying beetle *Nicrophorus vespilloides*. *Proceedings of the Royal Society B*, **274**, 2211–2220.

Steiger, S., Franz, R., Eggert, A.-K. & Müller, J. K. 2008. The Coolidge effect, individual recognition and selection for distinctive cuticular signatures in a burying beetle. *Proceedings of the Royal Society B*, **275**, 1831–1838.

Swaney, W. T., Curley, J. P., Champagne, F. A. & Keverne, E. B. 2008. The paternally expressed gene Peg3 regulates sexual experience-dependent preferences for estrous odors. *Behavioral Neuroscience*, **122**, 963–973.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour*, **15**, 1–70.

Tinbergen, N. & Perdeck, A. C. 1950. On the stimulus situation releasing the begging response in the newly hatched herring gull chick (*Larus argentatus argentatus* Pont.). *Behaviour*, **3**, 1–39.

Torres, R. & Velando, A. 2003. A dynamic trait affects continuous pair assessment in the blue-footed booby (*Sula nebouxii*). *Behavioral Ecology and Sociobiology*, **55**, 65–72.

Torres, R. & Velando, A. 2005. Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii*. *Animal Behaviour*, **69**, 59–65.

Trivers, R. 1974. Parent–offspring conflict. *American Zoologist*, **14**, 249–264.

Velando, A., Beamonte-Barrientos, R. & Torres, R. 2006. Pigment-based skin colour in the blue-footed booby: an honest signal of current condition used by females to adjust reproductive investment. *Oecologia*, **149**, 535–542.

Velando, A., Kim, S.-Y. & Noguera, J. C. 2013. Begging response of gull chicks to the red spot on the parental bill. *Animal Behaviour*, **85**, 1359–1366.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *The Quarterly Review of Biology*, **58**, 155–183.

West-Eberhard, M. J. 1984. Sexual selection, competitive communication and species-specific signals in insects. In: *Insect Communication* (Ed. by T. Lewis), pp. 283–324. New York: Academic Press.

Wolf, J. B. & Brodie, E. D. 1998. The coadaptation of parental and offspring characters. *Evolution*, **52**, 299–308.

Yamazaki, K., Beauchamp, G. K., Curran, M., Bard, J. & Boyse, E. A. 2000. Parent-progeny recognition as a function of MHC odortype identity. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 10500–10502.