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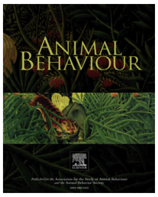

Essay

Begging and ectoparasite attraction

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Honesty of offspring begging behaviours is the keystone to understanding the evolution of parent–offspring communication. Three main begging costs have been traditionally advocated that ensure the reliability of offspring signalling: energy expenditure, loss of inclusive fitness and attraction of predators. Here, we propose that ectoparasites may eavesdrop on begging signals, especially acoustic signals, for host detection, a never considered but potentially generalized cost of begging that will constrain the evolution of exaggerated begging displays. Ectoparasitic insects possess a diversity of auditory systems for intraspecific communication that may be used to detect begging calls of host offspring. The use of auditory cues for host detection offers some advantages to ectoparasites, particularly in environments in which long-distance detection of hosts is necessary. There are well-known examples of interspecific eavesdropping on host auditory signals by parasites that include parasitoid flies attracted to calling crickets and cicadas, and frog-biting midges and mosquitoes attracted to frog calls. Eavesdropping on begging signals may have evolved in those parasites searching for hosts that display begging behaviours, which include not only birds but also mammals and some reptiles and insects with parental care of juveniles. Considering begging costs due to detection by ectoparasites may help us understand the reliability, and therefore the evolution, of signals of need and parent–offspring communication.

Begging behaviour, the mechanism by which offspring solicit food and other care from their parents, represents a classic example of a conflict of interest between parents and offspring (Trivers, 1974). Through begging, offspring try to manipulate their parents to receive the maximum possible amount of care, while the parents are compelled to make carefully informed decisions to adjust their parental effort and to allocate food within the brood in order to maximize fitness (Wright & Leonard, 2002). Consequently, the parent–offspring conflict of interest arises because the fitness gain of the caring parent and that of the signalling offspring do not coincide (Godfray, 1995; Trivers, 1974). In the face of this conflicting genetic interest, mechanisms ensuring reliability of signals of need are necessary for the evolution of adaptive parental responses and efficient parent–offspring communication (Godfray, 1995; Mock, Dugas, & Strickler, 2011; Wright & Leonard, 2002). Most mechanisms proposed to explain reliability of begging-related signals include the existence of costs that limit the exaggeration of begging displays (e.g. Godfray, 1991, 1995; Godfray & Johnstone, 2000; Grafen, 1990; Mock et al., 2011; Zahavi & Zahavi, 1997).

Three main costs of offspring begging have been traditionally recognized: energy expenditure (Chappell & Bachman, 2002), loss of inclusive fitness (Price, Ydenberg, & Daust, 2002) and attraction of predators (Haskell, 2002). Although evidence supporting the assumption of costly begging behaviour has accumulated (Magrath, Haff, Horn, & Leonard, 2010; Martín-Gálvez, Pérez-Contreras, Soler, & Soler, 2011; Moreno-Rueda, 2007; Roulin, 2001), no clear consensus exists on whether or not these costs are sufficient or needed to guarantee reliability of begging signals (Higham, 2014; Mock et al., 2011; Searcy & Nowicki, 2005; Számadó, 2011). While some studies have suggested negligible energetic costs of begging in terms of oxygen consumption (McCarty, 1996; Schleich & Busch, 2004), others have detected reduced growth (e.g. Kilner, 2001; Rodríguez-Gironés, Zúñiga, & Redondo, 2001; but see Leonard, Horn, & Porter, 2003) and immune response (e.g. Moreno-Rueda & Redondo, 2011) or increased oxidative stress (Moreno-Rueda, Redondo, Trenzado, Sanz, & Zúñiga, 2012; Noguera, Morales, Pérez, & Velando, 2010). A loss of inclusive fitness may be an important cost of begging, and there is evidence for this cost (Briskie, Naugler, & Leech, 1994; Moreno-Rueda, 2007). Finally,

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there are only a handful of studies showing that begging can attract predators (Haff & Magrath, 2011; Haskell, 1994; Ibáñez-Álamo, Arco, & Soler, 2012; Leech & Leonard, 1997; McDonald, Wilson, & Evans, 2009).

Here, we postulate that, in a similar way as has been suggested for predators, ectoparasites may eavesdrop on begging signals to locate their hosts, a potential cost of begging not hitherto suggested. Begging behaviour usually comprises acoustic and different nonacoustic signals including gaping, posturing or correlated cues such as CO_2 production (Wright & Leonard, 2002), which may all be involved in attraction of ectoparasites. However, we mainly focus on acoustic signals as these are likely to be the most conspicuous begging signals available to most parasites, while at the same time acoustic signals are more specific to begging than nonacoustic signals or correlated cues. Similarly, eavesdropping on acoustic begging signals by parasites may be widespread in young birds and mammals and some reptiles and insects that display parental care of juveniles. However, we support our argumentation mainly with examples derived from avian begging behaviour because this has been the most studied system regarding parent–offspring communication and the evolution of begging (Wright & Leonard, 2002).

The possibility that ectoparasites are attracted by nestling begging calls may help the interpretation of previous apparently contradictory or unexpected results. For example, experimental parasitism of great tit, *Parus major*, nests with fleas resulted unexpectedly in higher prevalence of infestation by *Protocalliphora* blow flies (Heeb, Kölliker, & Richner, 2000). This was hypothetically attributed to stronger olfactory cues in flea-infested nests due to increased level of need and thus begging-related physiological activity (Heeb et al., 2000). However, an alternative more parsimonious explanation is that blow flies directly eavesdropped on the increased acoustic intensity of the signal (Tripet & Richner, 1997) due to the experimental flea infestation. Similarly, female blue tits, *Cyanistes caeruleus*, increased provisioning rates when their blood parasite load was experimentally reduced, which led to fewer blow flies in their nests (Tomás, Merino, Moreno, Morales, & Martínez-de la Puente, 2007). Although this result may be related to improved antiparasitic abilities of healthier females, it may also be the consequence of a reduced intensity of nestling begging calls in experimental nests (increased provisioning rates decrease begging intensity: e.g. Granadeiro, Bolton, Silva, Nunes, & Furness, 2000), thereby reducing acoustic detection by blow flies. Although alternative explanations are possible, if attraction of ectoparasites is an additional cost of begging, it will interact with other previously proposed costs. This is because increased parasitism will increase energy consumption, reduce inclusive fitness and increase predation risk by increasing provisioning rates and thereby risk of predator detection.

In this essay, we first identify evidence suggesting that ectoparasites can use begging calls to locate hosts. We consider that, within begging signalling systems, eavesdropping on auditory signals can be one of the mechanisms for host detection by ectoparasites. We then enumerate some advantages of auditory cues for host detection by ectoparasites. Finally, we propose some predictions of the hypothetical role of ectoparasites eavesdropping on begging calls, explaining the evolution of begging behaviour and parent–offspring communication.

EAVESDROPPING EVIDENCE

Host detection by ectoparasites has been assumed to rely chiefly on olfactory and visual cues (Allan, Day, & Edman, 1987; Gibson & Torr, 1999; Lehane, 2005; Waladde & Rice, 1982). However, comprehensive knowledge is incomplete for many ectoparasitic taxa. The possible use of auditory cues for host detection by ectoparasites has scarcely been investigated, although arthropods possess highly efficient auditory systems that solve the physical problems of directional hearing imposed by a small body size (Robert & Hoy, 2007; Römer, 2015). In insects, tympanal organs have evolved independently no less than 19 times (Yager, 1999), being present in all major Orders (Matthews & Matthews, 2010). As for other animals, the evolution of auditory systems in insects has been favoured in scenarios such as conspecific identification, intraspecific communication, mate finding, courtship or predator avoidance (Fournier, Dawson, Mikhail, & Yack, 2013; Matthews & Matthews, 2010; Robert & Hoy, 2007; Yuval, 2006). In the case of ectoparasites, facilitation of host detection may have also contributed to the evolution of these auditory systems.

Current knowledge points out that this may be the case, as several parasitic insects do locate their hosts using the host's acoustic cues (Table 1). Sarcophagidae parasitoid flies orient to calls of cicadas (Farris, Oshinsky, Forrest, & Hoy, 2009; Soper, Shewell, & Tyrrell, 1976) and Tachinidae flies to calls of crickets (Cade, 1975; Lehmann, 2003). Furthermore, blood-feeding parasites of frogs such as Chaoboridae phantom midges (Toma, Miyagi, Higa, Okazawa, & Sasaki, 2005), Corethrellidae frog-biting midges (Borkent, 2008; McKeever, 1977) and Culicidae mosquitoes (Borkent & Belton, 2006; Toma et al., 2005) are actively attracted to frog calls. Entomologists indeed take advantage of this feature by using frog-call traps to sample biting flies (Borkent, 2008).

Some anecdotal evidence even suggests that ectoparasites are able to detect and orient towards bird sounds (Table 1). Three studies exploring parasite phonotaxis to amphibian vocalizations unexpectedly found that large numbers of Corethrellidae (Bernal, 2004; Camp, 2006) and female mosquitoes (Bartlett-Healy, Crans, & Gaugler, 2008a) were attracted towards calls or songs of different bird species used as the control treatment. Moreover, it was shown that blood-sucking ticks *Ornithodoros concanensis* are attracted to vocalizations of cliff swallow, *Petrochelidon pyrrhonota*, nestlings, and to artificially generated sound matching the natural frequencies of nestlings' calls (Webb, 1976, 1979; Webb, George, & Cook, 1977). The observed attraction of ticks towards vocalizing nestlings is, however, unlikely to be related to nestling begging behaviour, mainly because this tick is active only at night (Webb, 1976, 1979; Webb et al., 1977), when nestlings of diurnal species do not beg for food. Furthermore, sound invariably induces substrate-borne vibration (Hoy & Robert, 1996), and because no control sound was used, it is still possible that ticks oriented towards nestling vocalizations using vibrational rather than auditory cues (Kilpinen, 2005). Distinguishing between these two possibilities is important to explore mechanisms of host detection by ticks, and it is imperative for the hypothesis of ectoparasites eavesdropping on begging calls. It could be the case that nonflying ectoparasites rely mainly on vibrational cues for host detection, while flying ectoparasites would rely primarily on eavesdropping on auditory signals.

ADVANTAGES OF AUDITORY CUES

Auditory signals transmit very fast, allowing near-instantaneous transmission of valuable information and accurate source localization. Moreover, information in auditory signals can be encoded across multiple channels such as frequency or amplitude, while efficient transmission is independent of light availability, visual contact or immediate proximity between sender and receiver (Endler, 1993; Wiley & Richards, 1982). Thus, in this instance, hearing might be advantageous for ectoparasites with crepuscular or nocturnal habits parasitizing nocturnal hosts, because visual signals are largely constrained at night.