Essay

Begging and ectoparasite attraction

Gustavo Tomás^{a,b,*} Juan J. Soler^a

^a *Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (EEZA-CSIC), La Cañada de San Urbano, Almería, Spain*

^b *Departamento de Ciencias Naturales, Universidad Técnica Particular de Loja (UTPL), Loja, Ecuador*

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* Correspondence: G. Tomás, Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas, EEZA-CSIC (Consejo Superior de Investigaciones Científicas). Carretera de Sacramento, s/n. 04120 La Cañada de San Urbano, Almería, Spain.

E-mail address: gtomas@eeza.csic.es

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.

Keywords: acoustic communication, auditory cues, begging costs, ectoparasite attraction, honest signalling, host location mechanisms, interspecific eavesdropping, nestling begging calls, parent-offspring conflict, phonotaxis.

Begging behaviour, the mechanism by which offspring solicit food 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, 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 CO₂ 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.

<H1>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.

<H1>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.

Eavesdropping on nestling begging calls might be used by nonflying ectoparasites such as fleas, mites and ticks (Webb et al., 1977), although it may be especially important for long-distance detection of hosts by flying ectoparasites of birds such as mosquitoes (Culicidae), biting midges (Ceratopogonidae), black flies (Simuliidae), carnid flies (Carnidae), louse flies (Hippoboscidae) or Corethrellidae and flies that have haematophagous larvae such as blow flies (Calliphoridae) and *Philornis* bot flies (Muscidae). When detecting senders from a distance, auditory signals might inform receivers about sender location more precisely than olfactory signatures, because the latter are much more dependent on wind direction, speed and lateral turbulence (Conover, 2007; Gibson & Torr, 1999). For instance, host detection based on olfactory cues may be constrained in the absence of wind, as no clear odour plume is generated (e.g. Preiss & Kramer, 1986; Willis & Cardé, 1990; Willis, Avondet, & Finnell, 2008). In addition, flying ectoparasites using olfactory signals to locate hosts would be forced to fly upwind until they could see the hosts, but many ectoparasites are relatively poor flyers under windy conditions (Baldacchino, Puech, Manon, Hertzog, & Jay-Robert, 2014; Gibson & Torr, 1999; Marquardt, Demaree, & Grieve, 2000; Martínez-de la

Puente et al., 2009; Sedda et al., 2012). Thus, in the absence of wind, and also with relatively strong winds, the use of auditory signals will greatly facilitate host detection.

<H1>PREDICTIONS

If begging calls attract ectoparasites, ectoparasite abundance and begging intensity should be related both within and between host species. Within species, those with more intense begging would show higher ectoparasite abundance than those with less intense begging calls. At the population level, as well as for interspecific comparisons, we expect that a high risk of ectoparasitism would promote attenuation and/or degradation of begging calls, in a similar way as occurs when predation risk increases (Briskie, Martin, & Martin, 1999; Redondo & Arias de Reyna, 1988). We also predict an increased risk of parasitism for parents during provisioning visits associated with an increased begging display of their young. Finally, we also expect that activity patterns of the host would determine activity patterns of their ectoparasites. Thus, diurnal host species should be more affected by ectoparasites with diurnal activity, while nocturnal host species, whose young beg for food at night, should be comparatively more affected by ectoparasites active at night.

Some nestling ectoparasites readily detect and colonize nests soon after egg hatching (e.g. *Carnus* flies: Liker, Márkus, Vozár, Zemankovics, & Rózsa, 2001; *Philornis* flies: Fessler, Sinclair, & Kleindorfer, 2006), while others do so when nestlings are at a certain age (e.g. *Protophormia* blow flies: Bennett & Whitworth, 1991; biting midges: Tomás et al., 2008). This synchronization, and the fact that characteristics of begging calls change with age (Leonard & Horn, 2006; also in other taxa such as mammals: e.g. Noirot, 1968), suggests that parasites may use age-specific begging cues to locate hosts of a certain age. Likewise, parasites may eavesdrop on nestling begging

calls to synchronize their emergence, or termination of diapause, with host egg hatching (Bartlett-Healy, Crans, & Gaugler, 2008b). This would be especially adaptive for nest-dwelling ectoparasites of birds, which are known to pupate or enter diapause within the nest materials or in the immediate surroundings of bird nests (e.g. Amat-Valero, Calero-Torralbo, & Valera, 2013; Burt, Chow, & Babbitt, 1991; Fessler et al., 2006; Harper, Marchant, & Boddington, 1992). Termination of diapause in insects has been traditionally considered to be triggered by abiotic factors such as temperature, humidity or photoperiod (Tauber, Tauber, & Masaki, 1986). Yet it is known that mechanical stimulation can trigger emergence of certain parasites such as fleas (Humphries, 1963), which raises the possibility that auditory cues can also be involved in parasite emergence. Therefore, begging calls of different nestling ages could attract different parasites, or trigger termination of diapause, according to synchronization needs of parasites with the appropriate nestling stage.

<H1>EXTENSION OF THE HYPOTHESIS

Eavesdropping on begging signals may have evolved in those parasites searching for hosts that display begging behaviours related to parental care of juveniles. Acoustic begging displays in particular are performed not only by birds but also by mammals and some reptiles and insects (Royle, Smiseth, & Kölliker, 2012). Eavesdropping on begging signals might explain, for instance, the reported attraction of ticks to sound produced by feeding cattle and by barking dogs (Waladde & Rice, 1982). Moreover, young mammals from rodents to bats are known to display an array of acoustic signals to solicit parental care, including ultrasonic vocalizations (Knörnschild & von Helversen, 2008; Madden, Kunc, English, Manser, & Clutton-Brock, 2009; Portfors & Perkel, 2014) to which many parasites might be sensitive (Matthews &

Matthews, 2010; Yager, 1999, 2012). Among reptiles, juveniles of all extant species of crocodilians produce different types of vocalizations during the first few weeks after hatching, which play a major role particularly in interactions with adults (Vergne, Pritz, & Mathevon, 2009). Regarding insects, auditory begging signals are displayed, for instance, by some Coleoptera species, although chemical begging signals are most common (Mas & Kölliker, 2008), and both types of signal might be eavesdropped on by parasites. All these could represent potentially fruitful research avenues.

Ectoparasites, through eavesdropping, may have also shaped the evolution of other acoustic signals such as birdsong (following the same rationale as applied for predators and parasitoids: Peake, 2005; Zuk & Kolluru, 1998). Among singing displays, song performance during the dawn and dusk choruses may be especially costly (Poesel, Kunc, Foerster, Johnsen, & Kempenaers, 2006) and may honestly reflect bird quality (Zahavi & Zahavi, 1997). Many ectoparasite groups are more active at dawn and at dusk, and may be attracted to birds by their dawn and dusk singing activities, when birds remain relatively stationary near their roosting location (many birds, both nocturnal and diurnal, vocalize also at night: La, 2011). This would reinforce the honesty of the sexual signal, as only birds with a higher degree of resistance to parasites would be able to display the signal at a higher level (Hamilton & Zuk, 1982).

<H1>CONCLUDING REMARKS

We postulate that ectoparasites could eavesdrop on begging signals for host location. It is likely that communication nearly always involves redundancy, because several different sensory modalities are likely to be acting simultaneously and reinforcing one another's messages (Matthews & Matthews, 2010). Thus, begging auditory signals, in concert with other begging-related cues, such as visual and chemical

cues, would provide the most likely cues for host searching and detection by ectoparasites. Among terrestrial animals, only vertebrates and insects have a good sense of hearing (Robert & Hoy, 2007), which raises the possibility that both groups interact acoustically. Dependent offspring expend considerable amounts of time and energy producing begging-related signals including loud, conspicuous calls that are detectable at long distances, which would be of great advantage for ectoparasites as cues for host detection. This hypothesis would help us understand two important issues that have long puzzled evolutionary biologists. First, it may shed light on the mechanisms of host detection by parasites, which are poorly known for many ectoparasitic taxa despite its key importance for understanding coevolution between hosts and parasites. Second, it would represent a never considered but potentially generalized cost of begging that may be crucial for explaining the evolution of signalling behaviours of need and thereby for the resolution of parent-offspring conflicts. To conclude, because sound is a fundamental form of energy, it is not surprising that its use has evolved in many organisms for an array of ecological processes. Even plants have recently been shown to produce and respond to sound in a life history context (Gagliano, Mancuso, & Robert, 2012)! To our knowledge, ectoparasites have never been suggested as potential eavesdroppers of offspring begging signals. This neglect appears unjustified and the hypothesis warrants detailed investigation.

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Table 1. Overview of parasites known to eavesdrop on (insect and amphibian) or suspected to eavesdrop on (bird) host auditory signals for host location.

	Parasite	Parasite species	Host	Comments	Source
	family				
Insects					
	Sarcophagidae	<i>Emblemasona auditrix</i>	Cicadas (Homoptera: Cicadidae)	<i>E. auditrix</i> attracted by calls of at least 3 species of cicada	Farris et al., 2009; Soper et al., 1976
	Tachinidae	Cricket-flies (<i>Ormia</i> spp., <i>Therobia</i> spp., <i>Homotrixa</i> spp., etc.)	Crickets and bushcrickets (Orthoptera: Gryllidae, Tettigoniidae)	11 of 67 known cricket-flies attracted by calls of a wide spectrum of host species	Cade, 1975; Lehmann, 2003
Amphibians					
	Corethrellidae	<i>Corethrella</i> spp.	Frogs	Nearly 100 parasite species parasitize at least 23 frog species	Borkent, 2008; McKeever, 1977
	Chaoboridae	Phantom midges	Frogs	2 parasite species attracted to frog calls	Toma et al., 2005
	Culicidae	Mosquitoes (<i>Culex territans</i> , <i>Mimomyia luzonensis</i> , <i>Uranotaenia</i> spp.)	Frogs	At least 4 mosquito species are attracted to frog calls	Borkent & Belton, 2006; Toma et al., 2005
Birds					
	Corethrellidae	<i>Corethrella brakeleyi</i> , <i>C. wirthi</i> , etc	Amphibians, (birds?)	Attracted to call of common raven and other birds	Bernal, 2004; Camp, 2006
	Culicidae	Mosquito (<i>Culex territans</i>)	Amphibians, (birds?)	Attracted to songs of birds (sparrows, finches, grosbeaks and buntings)	Bartlett-Healy et al., 2008a
	Argasidae	Tick (<i>Ornithodoros concanensis</i>)	Cliff swallow, <i>Petrochelidon pyrrhonota</i> , cave bats	Could not ascertain if oriented towards vocalization (not begging), sound per se or substrate-borne vibration	Webb, 1976; Webb et al., 1977