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2 Essay

3 Begging and ectoparasite attraction

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

38

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

42 Begging behaviour, the mechanism by which offspring solicit food from their
43 parents, represents a classic example of a conflict of interest between parents and
44 offspring (Trivers, 1974). Through begging, offspring try to manipulate their parents to
45 receive the maximum possible amount of care, while the parents are compelled to make
46 carefully informed decisions to adjust their parental effort and to allocate food within
47 the brood in order to maximize fitness (Wright & Leonard, 2002). Consequently, the
48 parent-offspring conflict of interest arises because the fitness gain of the caring parent
49 and that of the signalling offspring do not coincide (Godfray, 1995; Trivers, 1974). In
50 the face of this conflicting genetic interest, mechanisms ensuring reliability of signals of
51 need are necessary for the evolution of adaptive parental responses and efficient parent-
52 offspring communication (Godfray, 1995; Mock, Dugas, & Strickler, 2011; Wright &
53 Leonard, 2002). Most mechanisms proposed to explain reliability of begging-related
54 signals include the existence of costs that limit the exaggeration of begging displays
55 (e.g. Godfray, 1991, 1995; Godfray & Johnstone, 2000; Grafen, 1990; Mock et al.,
56 2011; Zahavi & Zahavi, 1997).

57 Three main costs of offspring begging have been traditionally recognized:
58 energy expenditure (Chappell & Bachman, 2002), loss of inclusive fitness (Price,
59 Ydenberg, & Daust, 2002) and attraction of predators (Haskell, 2002). Although
60 evidence supporting the assumption of costly begging behaviour has accumulated
61 (Magrath, Haff, Horn, & Leonard, 2010; Martín-Gálvez, Pérez-Contreras, Soler, &
62 Soler, 2011; Moreno-Rueda, 2007; Roulin, 2001), no clear consensus exists on whether
63 or not these costs are sufficient or needed to guarantee reliability of begging signals
64 (Higham, 2014; Mock et al., 2011; Searcy & Nowicki, 2005; Számadó, 2011). While
65 some studies have suggested negligible energetic costs of begging in terms of oxygen
66 consumption (McCarty, 1996; Schleich & Busch, 2004), others have detected reduced

67 growth (e.g. Kilner, 2001; Rodríguez-Gironés, Zúñiga, & Redondo, 2001; but see
68 Leonard, Horn, & Porter, 2003) and immune response (e.g. Moreno-Rueda & Redondo,
69 2011) or increased oxidative stress (Moreno-Rueda, Redondo, Trenzado, Sanz, &
70 Zúñiga, 2012; Noguera, Morales, Pérez, & Velando, 2010). A loss of inclusive fitness
71 may be an important cost of begging, and there is evidence for this cost (Briskie,
72 Naugler, & Leech, 1994; Moreno-Rueda, 2007). Finally, there are only a handful of
73 studies showing that begging can attract predators (Haff & Magrath, 2011; Haskell,
74 1994; Ibáñez-Álamo, Arco, & Soler, 2012; Leech & Leonard, 1997; McDonald, Wilson,
75 & Evans, 2009).

76 Here, we postulate that, in a similar way as has been suggested for predators,
77 ectoparasites may eavesdrop on begging signals to locate their hosts, a potential cost of
78 begging not hitherto suggested. Begging behaviour usually comprises acoustic and
79 different nonacoustic signals including gaping, posturing or correlated cues such as CO₂
80 production (Wright & Leonard, 2002), which may all be involved in attraction of
81 ectoparasites. However, we mainly focus on acoustic signals as these are likely to be the
82 most conspicuous begging signals available to most parasites, while at the same time
83 acoustic signals are more specific to begging than nonacoustic signals or correlated
84 cues. Similarly, eavesdropping on acoustic begging signals by parasites may be
85 widespread in young birds and mammals and some reptiles and insects that display
86 parental care of juveniles. However, we support our argumentation mainly with
87 examples derived from avian begging behaviour because this has been the most studied
88 system regarding parent-offspring communication and the evolution of begging (Wright
89 & Leonard, 2002).

90 The possibility that ectoparasites are attracted by nestling begging calls may help
91 the interpretation of previous apparently contradictory or unexpected results. For

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

111 In this essay, we first identify evidence suggesting that ectoparasites can use
112 begging calls to locate hosts. We consider that, within begging signalling systems,
113 eavesdropping on auditory signals can be one of the mechanisms for host detection by
114 ectoparasites. We then enumerate some advantages of auditory cues for host detection
115 by ectoparasites. Finally, we propose some predictions of the hypothetical role of

116 ectoparasites eavesdropping on begging calls, explaining the evolution of begging
117 behaviour and parent-offspring communication.

118

119 <H1>Eavesdropping Evidence

120 Host detection by ectoparasites has been assumed to rely chiefly on olfactory
121 and visual cues (Allan, Day, & Edman, 1987; Gibson & Torr, 1999; Lehane, 2005;
122 Waladde & Rice, 1982). However, comprehensive knowledge is incomplete for many
123 ectoparasitic taxa. The possible use of auditory cues for host detection by ectoparasites
124 has scarcely been investigated, although arthropods possess highly efficient auditory
125 systems that solve the physical problems of directional hearing imposed by a small body
126 size (Robert & Hoy, 2007; Römer, 2015). In insects, tympanal organs have evolved
127 independently no less than 19 times (Yager, 1999), being present in all major Orders
128 (Matthews & Matthews, 2010). As for other animals, the evolution of auditory systems
129 in insects has been favoured in scenarios such as conspecific identification, intraspecific
130 communication, mate finding, courtship or predator avoidance (Fournier, Dawson,
131 Mikhail, & Yack, 2013; Matthews & Matthews, 2010; Robert & Hoy, 2007; Yuval,
132 2006). In the case of ectoparasites, facilitation of host detection may have also
133 contributed to the evolution of these auditory systems.

134 Current knowledge points out that this may be the case, as several parasitic
135 insects do locate their hosts using the host's acoustic cues (Table 1). Sarcophagidae
136 parasitoid flies orient to calls of cicadas (Farris, Oshinsky, Forrest, & Hoy, 2009; Soper,
137 Shewell, & Tyrrell, 1976) and Tachinidae flies to calls of crickets (Cade, 1975;
138 Lehmann, 2003). Furthermore, blood-feeding parasites of frogs such as Chaoboridae
139 phantom midges (Toma, Miyagi, Higa, Okazawa, & Sasaki, 2005), Corethrellidae frog-
140 biting midges (Borkent, 2008; McKeever, 1977) and Culicidae mosquitoes (Borkent &

141 Belton, 2006; Toma et al., 2005) are actively attracted to frog calls. Entomologists
142 indeed take advantage of this feature by using frog-call traps to sample biting flies
143 (Borkent, 2008).

144 Some anecdotal evidence even suggests that ectoparasites are able to detect and
145 orient towards bird sounds (Table 1). Three studies exploring parasite phonotaxis to
146 amphibian vocalizations unexpectedly found that large numbers of Corethrellidae
147 (Bernal, 2004; Camp, 2006) and female mosquitoes (Bartlett-Healy, Crans, & Gaugler,
148 2008a) were attracted towards calls or songs of different bird species used as the control
149 treatment. Moreover, it was shown that blood-sucking ticks *Ornithodoros concanensis*
150 are attracted to vocalizations of cliff swallow, *Petrochelidon pyrrhonota*, nestlings, and
151 to artificially generated sound matching the natural frequencies of nestlings' calls
152 (Webb, 1976, 1979; Webb, George, & Cook, 1977). The observed attraction of ticks
153 towards vocalizing nestlings is, however, unlikely to be related to nestling begging
154 behaviour, mainly because this tick is active only at night (Webb, 1976, 1979; Webb et
155 al., 1977), when nestlings of diurnal species do not beg for food. Furthermore, sound
156 invariably induces substrate-borne vibration (Hoy & Robert, 1996), and because no
157 control sound was used, it is still possible that ticks oriented towards nestling
158 vocalizations using vibrational rather than auditory cues (Kilpinen, 2005).
159 Distinguishing between these two possibilities is important to explore mechanisms of
160 host detection by ticks, and it is imperative for the hypothesis of ectoparasites
161 eavesdropping on begging calls. It could be the case that nonflying ectoparasites rely
162 mainly on vibrational cues for host detection, while flying ectoparasites would rely
163 primarily on eavesdropping on auditory signals.

164

165 <H1>ADVANTAGES OF AUDITORY CUES

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

174 Eavesdropping on nestling begging calls might be used by nonflying
175 ectoparasites such as fleas, mites and ticks (Webb et al., 1977), although it may be
176 especially important for long-distance detection of hosts by flying ectoparasites of birds
177 such as mosquitoes (Culicidae), biting midges (Ceratopogonidae), black flies
178 (Simuliidae), carnid flies (Carnidae), louse flies (Hippoboscidae) or Corethrellidae and
179 flies that have haematophagous larvae such as blow flies (Calliphoridae) and *Philornis*
180 bot flies (Muscidae). When detecting senders from a distance, auditory signals might
181 inform receivers about sender location more precisely than olfactory signatures, because
182 the latter are much more dependent on wind direction, speed and lateral turbulence
183 (Conover, 2007; Gibson & Torr, 1999). For instance, host detection based on olfactory
184 cues may be constrained in the absence of wind, as no clear odour plume is generated
185 (e.g. Preiss & Kramer, 1986; Willis & Cardé, 1990; Willis, Avondet, & Finnell, 2008).
186 In addition, flying ectoparasites using olfactory signals to locate hosts would be forced
187 to fly upwind until they could see the hosts, but many ectoparasites are relatively poor
188 flyers under windy conditions (Baldacchino, Puech, Manon, Hertzog, & Jay-Robert,
189 2014; Gibson & Torr, 1999; Marquardt, Demaree, & Grieve, 2000; Martínez-de la

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

192

193 <H1>PREDICTIONS

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

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

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

228

229 <H1>EXTENSION OF THE HYPOTHESIS

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

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

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

258

259 <H1>CONCLUDING REMARKS

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

265 cues, would provide the most likely cues for host searching and detection by
266 ectoparasites. Among terrestrial animals, only vertebrates and insects have a good sense
267 of hearing (Robert & Hoy, 2007), which raises the possibility that both groups interact
268 acoustically. Dependent offspring expend considerable amounts of time and energy
269 producing begging-related signals including loud, conspicuous calls that are detectable
270 at long distances, which would be of great advantage for ectoparasites as cues for host
271 detection. This hypothesis would help us understand two important issues that have long
272 puzzled evolutionary biologists. First, it may shed light on the mechanisms of host
273 detection by parasites, which are poorly known for many ectoparasitic taxa despite its
274 key importance for understanding coevolution between hosts and parasites. Second, it
275 would represent a never considered but potentially generalized cost of begging that may
276 be crucial for explaining the evolution of signalling behaviours of need and thereby for
277 the resolution of parent-offspring conflicts. To conclude, because sound is a
278 fundamental form of energy, it is not surprising that its use has evolved in many
279 organisms for an array of ecological processes. Even plants have recently been shown to
280 produce and respond to sound in a life history context (Gagliano, Mancuso, & Robert,
281 2012)! To our knowledge, ectoparasites have never been suggested as potential
282 eavesdroppers of offspring begging signals. This neglect appears unjustified and the
283 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 family	Parasite species	Host	Comments	Source
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