

## Do avian brood parasites eavesdrop on heterospecific sexual signals revealing host quality? A review of the evidence

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**Abstract** Eavesdropping can be defined as the extraction of information from the interactions between other individuals. It provides a relatively cheap way of gathering relevant information for fitness enhancement. Here, we propose that obligate avian brood parasites, which always lay their eggs in foreign nests of individuals of other species, may eavesdrop on their host sexual signals to locate nests of high quality individuals in which to lay their parasitic eggs. Sexual signal variation can honestly signal parental quality. Thus, by eavesdropping on sexual signals, parasites may select high quality foster parents for their own offspring. Such a use of sexual signals within host populations by brood parasites differs from signal exploitation theory that proposes that parasite only use signals to locate potential host independently from signaller quality. Here, we review the avian literature concerning host choice within a host species by obligate avian brood parasites and find evidence for host selection within individuals of a host species on the basis of cues potentially functioning as sexually selected traits, or at least revealing parental abilities. We have also found support for the existence of benefits linked to host selection by avian brood parasites. Finally, one study reported on the attenuation of a sexual ornament in host populations under strong pressure by brood parasites. Most of these findings have been interpreted as evidence for host selection by avian brood parasites based on the conspicuousness of sexual signals. We suggest, however, that these findings may in fact reveal eavesdropping on host signalling performance by brood parasites which would

use the information extracted to choose the better individuals among conspecifics of a given host. This provides a new perspective for the study of host selection in obligate brood parasites, and raises interesting questions for the study of animal cognition that would deserve experimental studies.

**Keywords** Brood parasitism · Heterospecific eavesdropping · Host choice · Public information · Sexual ornaments

### Introduction

Signals used to provide information among organisms usually occurs in communication networks in which multiple signallers and receivers, both conspecifics and heterospecifics, are present. Hence, signals may inform individuals other than those interacting with the signaller. Eavesdropping is the behaviour involving the extraction of information from signalling interactions between others (McGregor and Dabelsteen 1996) which provides a relatively low-cost method of assessment, thereby reducing uncertainty. Signals used during this information process may belong to acoustic/vocal, visual, olfactory, chemical or other communication modalities, whenever their range allows receivers access to the information transmitted (McGregor 1993). Moreover, a single individual may simultaneously provide information by means of several signals and through several sensory channels, which may lead to the use of multimodal cues by eavesdroppers.

Eavesdropping has been demonstrated in a conspecific context for such phylogenetically distant organisms as fishes (e.g. Oliveira et al. 1998; Doutrelant and McGregor 2000), birds (e.g. Naguib et al. 1999) and mammals (e.g. Barclay 1982; Madsen et al. 2002). For instance, male Siamese

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fighting fishes (*Betta splendens*) use the information gained through eavesdropping on visual-display interactions among other males to assess their future opponents and they later behave more aggressively towards the loser of the interaction than towards the winner (Oliveira et al. 1998). It has also been demonstrated that male territorial nightingales (*Luscinia megarhynchos*) assess opponents by eavesdropping on vocal interactions between other males: eavesdroppers responded more aggressively to the individual singing the first, which is perceived as a more serious rival (Naguib et al. 1999). Also, female fighting fishes preferred males that won the interactions with other males when they saw the interactions. Meanwhile, females that had not seen the interaction did not behave differently against the two males (Doutrelant and McGregor 2000). Moreover, some mammals, such as bats and whales, may use the conspecifics' echolocation calls to locate and assess foraging patches (Barclay 1982; Madsen et al. 2002). Eavesdropping may also occur in a heterospecific context if the signal informs on something useful to heterospecifics. For instance, eavesdropping has been shown to be useful for foraging bees, *Trigona spinipes*, which can detect and orient towards odour marks deposited by a competitor, *Melipona rufiventris*, and then rapidly monopolize the food source, expelling or killing their competitors (Nieh et al. 2004). Túngara frogs, *Physalaemus pustuosus*, eavesdrop calls of a sympatric heterospecific, *Leptodactylus labialis*, in mixed-species choruses to evaluate predation risk (Phelps et al. in press). Tuttle and Ryan (1981) demonstrated that bats (*Trachops cirrhosus*) eavesdrop frog mating calls to choose the best prey (palatable versus poisonous and normal versus very large species) among available frog species. One last example of eavesdropping among heterospecifics is provided by harbour seals, *Phoca vitulina*, that are able to discriminate between calls of dangerous and harmless killer whales and respond to them consequently (Deecke et al. 2002).

Eavesdropping may impose severe costs to signal emitters which may unbalance the trade-off between the cost of producing a signal and the benefit of influencing the behaviour of the targeted receivers (Johnstone 1998). The use of information by eavesdroppers may then act as a strong selective pressure on the evolution of communication systems. Indeed, eavesdroppers may either favour the maximization of the signals as happens during male–male interactions in the fighting fish (the fighting rate of males increases in the presence of a female audience; Doutrelant et al. 2001), or prevent it, which is likely to occur when eavesdroppers are predators, preys or parasites (Endler 1992; Wiley 1994) or more generally when their use of information involves a cost for the signallers. However, this process will also depend on the communication modality involved. Indeed, some signals, such as those related to morphological traits which involve the visual channel, are long-lasting and the emitters have no capacity to stop their emission. Therefore, selec-

tion by eavesdroppers may directly act on the signaller trait or indirectly modifying the behavioural displays allowing the reception of the signal (e.g. trait hiding when facing eavesdroppers).

Obligate avian brood parasites and their hosts may provide good examples of heterospecific eavesdropping. Brood parasitism is a form of breeding in which the parasite lays its eggs in the nest of another individual from the same or a different species, the host, which incubates and rears the young (Rothstein 1990). Brood parasites may be either facultative or obligate, the former being able to rear their own offspring while obligate brood parasites must always lay their eggs in foster nests of other species in which host parents raise the parasite young (i.e. parasites and hosts share the nest and food). Successful parasitism often reduces host reproductive outcome (e.g. Rothstein 1990), which favours the evolution of host defences, which at the same time selects for counter-adaptations by the parasite (e.g. Davies 2000). This escalation of adaptations and counter-adaptations by both sides is assumed to be a classical example of coevolutionary “arms race” (Dawkins and Krebs 1979). In this context, host choice by obligate avian brood parasites is expected to be under strong selective pressure since host ability to raise parasite offspring determines parasites' fitness (Davies 2000). Irrespective of brood parasitism, hosts must mate before reproduction and in this process conspicuous sexually selected signals are likely to participate. Consequently, the degree of expression of sexual ornaments or sexually selected behaviours may greatly vary among hosts of avian brood parasites. Obligate brood parasites, however, might use sexually selected signals displayed by hosts as location cues when searching potential host species (e.g. Wiley 1988; Garamszegi and Avilés 2005). Sexual signals may be selected to honestly reveal parental quality to potential mates. Therefore, parasites might recognize and use these signals as indicators of host raising capacities, whenever the ornament or behaviour would signal the level of parental care (Soler et al. 1995). Sexual signals of hosts may therefore be important to parasites for two reasons: (i) they may provide a good way to find species to parasite since ornaments are conspicuous and parasites may detect ornamented species more easily than non-ornamented species; (ii) they may provide a good way to choose hosts to parasite within a population, that is to choose individuals among conspecifics of a host, if ornaments or behaviours signal the quality of parental care. This idea would imply that parasites have the ability of making comparisons among host species to choose the best one to parasite and also among conspecifics of each host species to choose the better individuals with respect to a given phenotypic trait.

The use of signals by obligate avian brood parasites during the choice of an individual within a species as a host differs from signal exploitation theory (see Zuk and

Kolluru 1998 for a review), at least if we consider the point of view of the parasite. According to that theory, sexual signals may be conspicuous to potential unintended exploiters, hence leading to a high detectability by natural enemies such as predators and parasites, thus increasing risks for signallers (e.g. Burk 1982; Verrell 1991; Endler 1992). The use of sexual signals as location cues by avian brood parasites within host species mainly predicts a positive relationship between the degree of expression of sexual signals and the occurrence of parasitism. Here, we propose that beyond their inherent conspicuousness, sexual signals reflecting parental quality may be used by unintended exploiters, i.e. eavesdroppers, to evaluate the relative quality of signallers within a host population, and subsequently choose the best available individuals with respect to the given trait or behaviour. Eavesdropping predicts a positive association between the degree of expression of sexual signals and the occurrence of parasitism within a parasitized population. Furthermore, if brood parasites eavesdrop on host sexual communication, we predict a within-species positive relationship between the degree of expression of sexual signals of nests' owners and the occurrence of parasitic eggs and their success. Therefore, the two mechanisms share one similar prediction though the exploitation approach makes predictions within and among species while the eavesdropping approach makes predictions only among individuals within a given population of hosts. This overlap is due to the fact that sexual signals are simultaneously selected to be conspicuous and hold information on bearer quality. In summary, the exploitation theory (see details mentioned earlier) deals with the issue of selecting among potential host species and secondarily among individuals within a population of hosts, while the eavesdropping approach we develop here deals with the issue of selecting among individuals within a population of hosts.

Although the predictions of the two mechanisms only differ by some subtle aspects, their evolutionary outcomes are likely to differ significantly. From the host point of view, a decrease in sexual ornamentation is expected under both mechanisms because pairs with exaggerated traits or behaviours are highly parasitized both if parasites rely on variation in conspicuousness among species and/or within populations and on variation among parental quality within populations as expressed by sexual signals. However, the selective pressures acting on host signalling might differ if brood parasites ignore inter-individual variations in the information conveyed by signals as it is implied under the exploitation mechanism. From the parasite point of view, the evolutionary outcome of host choice strategies based on the localisation only versus on variations in information conveyed by signals is likely to differ. In the context of breeding habitat selection, a game-theoretical approach showed that a strategy using performance of others (namely public information *sensu* Danchin et al. 2001) is likely to be the evolutionary

stable strategy (ESS) under most natural conditions, while a strategy exploiting only the localisation of others is unlikely to be selected for (Doligez et al. 2003). Nonetheless, the major difference between our hypothesis and the “signal exploitation” theory is in the nature of the information that is used by the parasite. Eavesdropping here involves public information (Danchin et al. 2004), the level of sexual signalling in this case, while the signal exploitation approach ignores the information carried out by the signal regarding host performance and focuses on the fact that sexual signals per se allow the localisation of the host pair. According to eavesdropping, brood parasites cue on the relative quality of sexual signals whereas signal exploitation by brood parasites just involves variation in signal conspicuousness as a potential location cue.

A recent study suggested that in the facultative brood parasite common goldeneye (*Bucephala clangula*) females can prospect nests of conspecifics after fledging to assess the breeding performance of conspecifics and select the nest in which to lay parasitic eggs in the next breeding season (Pöysä 2006). Here, we generalise that idea in connecting public information to obligate avian brood parasitism, and by suggesting that eavesdropping on heterospecific sexual signals may be used by obligate brood parasitic females to locate high quality foster parents within the current breeding season. To that purpose we performed a review of the evidence on the choice of individuals within a host population by obligate avian brood parasitism and reinterpreted results of previous authors as evidence for eavesdropping by parasitic female brood parasites.

## Studies reviewed

We reviewed the literature on host selection within populations by obligate avian brood parasites and focused on: 1) the cues used by parasites for host selection; 2) the functioning of these cues as sexually selected signals that could reveal parental abilities; and 3) the benefits that host selection provided to the parasite. Our goal was to assess whether avian brood parasites may constitute a particular case of heterospecific eavesdropping on sexual signals, or some other traits correlated with parental abilities. Studies published since 1972 on the topic were found by performing a search on the two keywords “host selection” and “brood parasitism” in ISI Web of Science (<http://isi1.newisiknowledge.com/>) in October of 2006 as well as in our own databases.

## Discussion

We found evidence of non-random host choice in three obligate avian brood parasite species exploiting nests of 10

**Table 1** Review of the evidence on host selection at the intra-specific level by obligate avian brood parasites

Parasitic species	Host species	Correlates	Reference
<i>Molothrus ater</i>	<i>Melospiza melodia</i>	Female age: Parasites choose adult versus young females	Smith 1981; Smith et al. 1984; Smith and Arcese 1984
<i>Molothrus ater</i>	<i>Melospiza melodia</i>	Nest mass: Parasites choose nests with a great amount of material	McLaren and Sealy 2003
<i>Molothrus ater</i>	<i>Empidonax traillii</i>	Noise performed by adult hosts: Parasites choose noisier individuals during incubation	Uyehara and Narins 1995
<i>Molothrus ater</i>	<i>Setophaga ruticilla</i> , <i>Empidonax oberholseri</i> , <i>Vireo gilbus</i> and <i>Dendroica petechia</i>	Parental activity rate during nest construction: Parasites choose nests with higher activity rate and males that sing more	Banks and Martin 2001
<i>Molothrus ater</i>	<i>Agelaius phoeniceus</i>	Dominance status of females: Parasites choose dominant females which raise parasite chicks faster and with less variability	Grant and Sealy 2002
<i>Molothrus ater</i>	<i>Agelaius phoeniceus</i>	Nest location and vocalizations made by females: Parasites choose host nests nearer to trees and with noisier females. No relationship with male singing activities	Clotfelter 1998
<i>Cuculus canorus</i>	<i>Cercotrichas galactotes</i>	Brood volume: Parasites choose nests with larger eggs	Álvarez 2000
<i>Cuculus canorus</i>	<i>Acrocephalus arundinaceus</i>	Nest location and volume: Parasites choose host nests nearer to perches and bigger nests endure higher rate of multiple parasitism	Moskát and Honza 2000
<i>Clamator glandarius</i>	<i>Pica pica</i>	Nest volume: Parasites choose larger nests whose owners are better parents	Soler et al. 1995

*Note.* The table provides details of the correlates with the parasite choice. Information on the studies performed on the topic was obtained by searching the terms “host selection” and “brood parasitism” in the ISI Web of Science as well in authors’ databases

different host species (Table 1). Evidence comes from 11 papers in which host selection by brood parasites was studied at the intra-specific level.

#### Cues used in host selection

Three studies on brown headed cowbirds (*Molothrus ater*) found that parasitism rate increases with female host age (song sparrow, *Melospiza melodia*; Smith 1981; Smith and Arcese 1984; Smith et al. 1984; Table 1). As a matter of fact, attribute preferred by cowbirds may not be female age itself but some related trait or behaviour revealing either location and/or her quality. Adult female song sparrows had a higher breeding success and showed a stronger mobbing response than young females (Smith 1981; Smith and Arcese 1984). The latter behaviour may be efficient against enemies at the nest (Smith and Arcese 1984), which may benefit the parasites secondarily. However, vigorous hosts may also defend their nests more vigorously against parasites, which may counterbalance their attractiveness. In addition, one study of the European cuckoo (*Cuculus canorus*) found that the rate of parasitism increases with host brood egg volume (in rufous bush chats *Cercotrichas galactotes*; Álvarez 2000), a cue likely revealing parental host quality as larger eggs usu-

ally have higher fledging success. However, it is likely that cuckoos rely on some correlate of egg volume rather than on egg volume itself because parasites lay their eggs prior to host clutch completion. For instance, clutch size is positively correlated with the amount of nest material in rufous bush chats (Palomino et al. 1998).

The remaining seven studies, while investigating host selection by parasites, found significant relationships between the expression of traits potentially functioning as host sexual signals (nest size, nest building activity, song outcome and female status) and rate of parasitism by brown headed cowbirds or great spotted cuckoos *Clamator glandarius* (Table 1). One of these studies on brown headed cowbirds found a positive relationship between parasitism rate and the vocalizations performed by female host red-winged blackbirds, *Agelaius phoeniceus* (Table 1). Vocalizations made by female hosts are interpreted as a behaviour related to nest defence (Clotfelter 1998), which might benefit the parasite. But cowbirds’ parasitism was not related to male blackbird song outcome (Clotfelter 1998) in spite of the fact that song is assumed to be a sexually selected trait in birds. However, male red-winged blackbirds sing from many spots within their territories (Orians and Christman 1968) and may therefore provide little information about the location or the quality of

the nest (Clotfelter 1998). All the remaining studies (Soler et al. 1995; Uyebara and Narins 1995; Moskát and Honza 2000; Banks and Martin 2001; Grant and Sealy 2002; McLaren and Sealy 2003) found positive relationships between the expression of traits likely to function as sexual signals and the rate of parasitism (Table 1). These patterns could be explained either by an easier location of more conspicuous host individuals (e.g. Banks and Martin 2001), or by an active selection of high quality hosts that parasites may assess on the basis of signals. Indeed, nest size (Soler et al. 1998; 2001; de Neve et al. 2004; Szentirmai et al. 2005) and nest building activities (Soler et al. 1995; Palomino et al. 1998; Szentirmai et al. 2005) have been shown to be sexually selected signals revealing parental quality (e.g. Soler et al. 1998; Szentirmai et al. 2005). Similarly, song in birds is known to be a secondary sexual trait reflecting male quality to potential females (Andersson 1994; Catchpole and Slater 1995). Moreover, in the red-winged blackbird *Agelaius phoeniceus*, a usual host of the brown headed cowbirds, female dominance status seems to be under sexual selection since males provide more food for their offspring when mated with dominant than subordinate females (Searcy and Yasukawa 1995).

#### Benefits of non-random host selection

Interestingly, the two studies that analysed the benefits for the brood parasite revealed host selection based on parental quality as expressed by sexual signals. Naturally parasitized magpies *Pica pica* raised more parasite great-spotted cuckoo chicks than experimentally parasitized pairs (Soler et al. 1995). Similarly, the chosen dominant female red-winged blackbirds raised parasite cowbird chicks with faster and more stable growth than non-chosen subordinate females (Grant and Sealy 2002). These two results could be explained by either the eavesdropping or the signal exploitation mechanisms. For instance, naturally parasitized magpies had bigger nests than experimentally parasitized pairs and big nests are both conspicuous and indicators of parental quality (Soler et al. 1995).

Public information extracted from potential host breeding performance has been recently shown to play a role in host choice of the facultative brood parasite common goldeneye (Pöysä 2006). Facultative brood parasites are able to raise their own offspring within the same season they parasitize or change from normal nesting to parasitic laying between years. Concretely, Pöysä (2006) showed that: (1) the occurrence of parasitism in a given nest-site was associated with prospecting rate in the same site at the end of the previous year; (2) prospecting rate was higher in successful than in unsuccessful boxes; and (3) successful nest-sites were more parasitized than unsuccessful ones. These findings together provide support for the use of public information in host selection by parasitic goldeneyes. Thus, host selection by

brood parasites based on public information seems to be at work even in facultative brood parasite in which the benefits of host choice are less important than in obligate brood parasitism.

#### Benefits of relying on sexual signals

Although many examples of heterospecific eavesdropping have been given in animals (e.g. Tuttle and Ryan 1981; Deecke et al. 2002; Nieh et al. 2004), many authors refer to the use of information only as a way to locate hosts, preys, predators or food (what has been called exploitation of signals by Zuk and Kolluru 1998). However, these results might in fact show that eavesdroppers may gather information reflecting fitness prospects. Such public information use should thus help avian brood parasites to select the best among all available individuals within a host population.

More generally, we suggest that sexual signals may be a source of Inadvertent Social Information (*sensu* Danchin et al. 2004) about heterospecifics. Sexual signals may provide valuable information to heterospecifics as useful as other integrative cues used in animal decision-making (e.g. reproductive performance of others when selecting a breeding habitat, Danchin et al. 1998; Doligez et al. 2002; Parejo et al. 2005). For avian brood parasites, cues such as sexual signals provide advantages as they may have been selected to provide honest information on host quality. Unlike other cues such as the reproductive success that must be evaluated one year to be used in the following one, sexual signals can be used immediately to decide where to lay parasitic eggs. Furthermore, the assessment of quality by means of sexual signals is likely to be easy because sexual signals are generally conspicuous ornaments. Therefore, avian brood parasites relying on sexual signals may gather information from a distance thereby reducing the costs of aggressive encounters with their hosts.

#### Cognitive prerequisites for relying on quality

The use of information provided by the association of ornaments with potential fitness benefits may create cognitive demands on parasite information processing. Indeed, evidence seems to suggest that avian brood parasites have evolved fine cognitive-based mechanisms of recognition that could be useful when facing a host choice. Parasitic cowbirds have a larger hippocampus volume, which is a brain region implicated in several types of memory-based cognitive process (O'Keefe and Nadel 1978), than non-parasitic species (Reboreda et al. 1996). Also, the volume of the hippocampus in these species is larger in the sex implicated in nest searching (females) (Reboreda et al. 1996). Furthermore, obligate avian brood parasites have shown other special cognitive abilities such as the capacity to learn to recognize conspecifics (Soler and Soler 1999) or the memory for relocating nests searched



before (Astié et al. 1998). Finally, it has recently been shown that an obligate brood parasite, the shiny cowbird, *Molothrus bonariensis*, is able to locate both active and deserted host nests but it needs to associate host activity to nests to parasitize (Fiorini and Reboreda 2006).

### Consequences on avian signalling

Eavesdropping on sexual signals by obligate avian brood parasites may constrain the exaggeration of host sexually selected signals. Exaggerated sexual signals benefit hosts to attract mates but involve costs due to a higher vulnerability to avian brood parasitism. Hence, the cost of brood parasitism may prevent a rampant escalation of the expression of sexual signals. The evolutionary influence of eavesdropping by avian brood parasites on the degree of expression of sexual signals in hosts probably depends on the costs imposed by parasites. To date, only one study tested the evolutionary consequences of heterospecific eavesdropping by avian brood parasites on the degree of expression of a sexual ornament. Soler et al. (1999) found in the magpie that nest size, a trait under sexual selection (de Neve et al. 2004) that is used by great spotted cuckoo to select hosts (Soler et al. 1995), was smaller in European populations parasitized by the great spotted cuckoo than in non-parasitized ones. Nevertheless, the sensory modality of the signal involved should be also taken into account when assessing the evolutionary effect of avian brood parasitism on the degree of expression of sexual signals because the reception of some visual and chemical signals may not be controlled by the emitters. For instance, plumage colour in birds cannot be changed by the bird and the selective pressure exerted by avian brood parasitism in this case should be directed to limit the time in which the signal is visible, both to mates and parasites, rather than to reduce the plumage colour.

### Conclusion

We propose that avian brood parasites may act as heterospecific eavesdroppers potentially decoding the information in host sexual signals on quality as potential foster parents for their offspring. We hypothesise that, in general, linking the idea of eavesdropping on public information communicated by sexual signals to obligate avian brood parasitism provides a new key to understand the evolution of host selection in brood parasites. We reinterpreted previous results that had been mostly claimed (see however Soler et al. 1995; Alvarez 2000) to support host selection by avian brood parasites on the basis of the conspicuousness of sexual traits (signal exploitation *sensu* Zuk and Kolluru (1998)). Those results may well support our eavesdropping interpretation of brood parasite choice of a host nest. We further propose predictions that

allow differentiating those two mechanisms of host selection and show that published data tend to match predictions of eavesdropping better than those of signal exploitation.

Eavesdropping has some important cognitive prerequisites that need to be experimentally studied. Experiments in which artificial novel ornaments are provided to individuals within a host species in which the expression of a second ornament is naturally related to parental abilities could help to disentangle between the two alternatives. Specifically, under signal exploitation, we would predict a parasite preference for more ornamented (and thus more conspicuous) individuals regardless of the ornament. Alternatively, under the eavesdropping mechanism, we would expect parasite preference for individuals bearing higher expression of the ornament reflecting parental quality relative to an artificially generated signal of conspicuousness that is not used in that host species as revealing host parental ability. However, we are conscious that in such a species any new secondary sexual character (and in particular those manipulated by experimenters) are likely to be interpreted by parasites as revealing parental care capacities. Thus, the real ideal system might be a host species in which parental care would be only provided by the female. In such a system, we would expect an increase in the rate of parasitism of pairs with males with experimentally exaggerated traits under exploitation but not under eavesdropping because in species with monoparental care secondary sexual characters cannot reveal the male's parental abilities. Unfortunately, there are no, to our knowledge, any host species of obligate avian brood parasites with monoparental care.

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