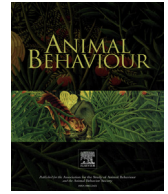




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## Eavesdropping and cue denial in avian acoustic signals

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Although some signals seem adapted to maximize transmission of cues to intended receivers, others appear to have been selected to deny specific types of cues to unwanted receivers. We review three categories of avian vocal signals that have been suggested to show adaptation for cue denial: aerial predator alarm calls, begging calls, and soft songs and calls. Evidence supports the conclusion that aerial alarm calls are adapted to deny localization cues and that begging calls and soft songs are adapted to deny detection. Selection for denial of cues in acoustic signals has also been documented in a variety of other animals. In summary, eavesdropping by unwanted receivers is often as important in shaping the structure of acoustic signals as is selection for transmission to intended receivers.

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In a seminal paper, Marler (1955, page 8) proposed the principle that animal sounds 'have not been chosen arbitrarily, but are directly adapted in structure to the function they have to perform'. An obvious aspect of such adaptation is that acoustic signals are selected for traits that facilitate communication with intended receivers. If we define acoustic signals as sounds that affect the behaviour of other animals and that have evolved because of those effects (Wheeler et al., 2011), then by definition all acoustic signals have intended receivers – the class of others that the signals have evolved to affect. Much evidence has accumulated that animal sounds are indeed adapted to facilitate communication with intended receivers, for example via traits that maximize transmission through the relevant habitat (Boncoraglio & Saino, 2007; Marten & Marler, 1977; Marten, Quine, & Marler, 1977; Morton, 1975; Wiley, 1991), that mesh well with the sensory capabilities and psychology of intended receivers (Guilford & Dawkins, 1991; Miller & Bee, 2012), or that exploit receivers by taking advantage of their sensory biases (Ryan & Cummings, 2013; Ryan & Rand, 1993).

Marler (1955) also proposed a second, less obvious aspect of acoustic signal adaptation: that signals may be adapted to deny

cues to unintended receivers. Acoustic signals often have receivers other than those the signals have evolved to affect (Marler, 1955; McGregor & Dabelsteen, 1996; Myrberg, 1981). These unintended receivers may be essentially benign, as in the case of animals that eavesdrop on the alarm calls of other species vulnerable to the same predators (Magrath, Haff, Fallow, & Radford, 2015). In many cases, however, unintended receivers have negative effects on signaller fitness, as when the eavesdroppers are the signaller's predators, parasites or competitors (Bernal, Rand, & Ryan, 2006; Mougeot & Bretagnolle, 2000; Ryan, Tuttle, & Rand, 1982; Zuk & Kolluru, 1998). When interception of the signal has a detrimental effect on signaller fitness, selection will favour acoustic traits that prevent detection of the signal by unintended receivers or, failing that, curtail the amount of information transmitted to those receivers.

Acoustic signal evolution is thus often subject to conflicting selection pressures: selection for maximizing communication to intended receivers and for minimizing communication to unintended ones. Here we explore three categories of avian acoustic signals that have been subject to such a conflict: alarm calls, nestling begging calls and soft vocalizations. One goal is to examine the extent to which selection to deny cues to unintended receivers has shaped the structure of avian vocal sounds. A second goal is to understand how the conflict between facilitating communication to intended receivers and minimizing communication to unintended receivers has been resolved.

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## AVIAN ALARM CALLS

The first major test case for cue denial in avian acoustic signals emerged from an analysis by Marler (1955) of the aerial alarm calls of birds. Aerial alarms are signals given in response to in-flight predators such as hawks and owls. The intended receivers for aerial alarms may be other prey individuals, in which case the alarmer may benefit either by saving genetic relatives from predation (Maynard Smith, 1965; Sherman, 1977) or by manipulating receivers to behave in ways that make the signaller safer (Charnov & Krebs, 1975; Sherman, 1985). Another possibility is that the predator is the intended receiver, and that the alarm somehow functions to discourage the predator from attacking, for example by revealing that the alarmer has detected it (Woodland, Jaafar, & Knight, 1980; Zuberbühler, Jenny, & Bshary, 1999). Some birds are more likely to give alarms in response to aerial predators when other conspecifics are nearby than in the absence of such an audience (Evans & Marler, 1992; Gyger, Karakashian, & Marler, 1986; Sullivan, 1985), which supports the idea that other prey are the intended receivers for the alarms. Regardless of the intended audience, producing alarms when a predator is nearby may have a cost in drawing the predator's attention to the alarmer, as Sherman (1977) showed for terrestrial predator alarms in Belding's ground squirrels, *Urocitellus beldingi*. Marler (1955) hypothesized that to counter such a cost, the acoustic structure of aerial alarms has evolved to deny the predator cues to the alarmer's location.

As evidence for his hypothesis, Marler (1955) used the structure of the aerial alarm of the common chaffinch, *Fringilla coelebs*. This alarm is a high-frequency, continuous, narrowband 'seet' with a gradual onset and offset and little frequency modulation (Fig. 1a). Marler (1955) noted that mammals and birds localize sounds using interaural differences in phase, intensity and time. The lack of abrupt starts and stops in the seet call together with the absence of frequency modulation denies interaural time difference cues to a receiver. Marler (1955) further argued that the frequency of the seet was too high for effective interaural phase comparisons and too low for effective interaural intensity comparisons. The aerial alarms of other Eurasian species were claimed to have similar acoustic properties (see Fig. 1b, c), as were the alarms of domestic chickens and even of some mammals (Marler, 1955, 1957). Later work identified further examples of seet-like aerial alarm calls in New World passerines (Fig. 1d) (Orians & Christman, 1968; Vanderhoff & Eason, 2009) and mammals (Cäsar, Byrne, Young, & Zuberbühler, 2012; Sherman, 1985).

Marler (1955) argued that the intended receivers of aerial alarms do not need to know a signaller's location to receive the benefit of the warning, whereas disguising location should reduce any cost from interception of the signal by a predator. If so, the hypothesis that aerial alarms deny location cues solves the communication dilemma very neatly: the signal still delivers its benefit to intended receivers while harmful effects from unintended receivers are minimized. Despite its logical appeal, Marler's hypothesis has encountered a series of objections. One objection is that many aerial alarms, particularly those produced by Australian passerines, do not have the structural features specified by the hypothesis (Jurisevic & Sanderson, 1994, 1998; Rooke & Knight, 1977). Some Australian passerines produce seet-like aerial alarm calls similar to the chaffinch's (Fig. 1e), but others have aerial alarms with rapid frequency modulation as in some fairy-wrens (Fig. 1f) (Fallow, Gardner, & Magrath, 2011) or with multiple elements at relatively low frequencies as in some of the honeyeaters (Fig. 1g, h) (Rooke & Knight, 1977; Wood, Sanderson, & Evans, 2000). Rooke and Knight (1977) argued that the structural features of honey-eater alarms in particular ought to make their calls easy to locate by raptors and other predators.

Shalter (1978, page 260) raised a second objection to Marler's hypothesis: that its argument was based 'entirely ... on inference from human auditory capacities' rather than on the sound localization capacities of the predatory birds that are the actual threat when aerial alarms are given (see also Klump & Shalter, 1984). Knowledge of sound localization in birds was limited when Marler (1955) proposed his hypothesis and has greatly increased since (Klump, 2000). An especially important development is the proposal that birds in part localize sounds using a pressure difference mechanism (Klump, 2000; Lewis & Coles, 1980; Rosowski & Saunders, 1980). Marler (1955) assumed that birds use a sound pressure mechanism, which compares time, intensity and phase of sounds arriving at the outside of the two tympanic membranes. In a pressure difference mechanism, the two ears are acoustically coupled internally, so that a sound affects both sides of a single tympanic membrane, and intensity and phase interact across the membrane (Lewis & Coles, 1980). A pressure difference mechanism should be more sensitive to changes in the angle of sound incidence (Klump, 2000) and may be less restricted by sound frequency than Marler assumed (Lewis & Coles, 1980). The interaural canal of birds provides the kind of internal coupling of the two ears that the pressure difference mechanism requires (Hill, Lewis, Hutchings, & Coles, 1980; Klump & Larsen, 1992; Rosowski & Saunders, 1980). How reliant birds are on such a mechanism is still debated (Klump, 2000).

Even if we are uncertain about the mechanisms birds use to localize sound, we can still directly measure the effects of alarm call traits on the accuracy of localization. A number of studies have measured localization in predatory birds using their tendency to turn their heads towards the source of sounds. Using this method, Shalter and Schleidt (1977) found correct orientation in 100% of the responses given by barn owls, *Tyto alba*, to the aerial 'seet' alarm of a clay-coloured robin, *Turdus grayi*. Similarly, Shalter (1978) found correct orientation in 100% of the responses given by goshawks, *Accipiter gentilis*, and pygmy owls (*Glaucidium perlatum* and *Glaucidium brasilianum*) towards the seet call of a common blackbird, *Turdus merula*. Although these two studies showed that aerial alarms are localizable by predatory birds, responses in these tests were always correctly oriented for control stimuli as well as for alarms, suggesting that the localization problems in these studies were too simple to reveal differences in localizability. Subsequently, Brown (1982) tested red-tailed hawks, *Buteo jamaicensis*, and great horned owls, *Bubo virginianus*, for their ability to localize the seet call of an American robin, *Turdus migratorius*, and the mobbing calls of a red-winged blackbird, *Agelaius phoeniceus*, using more precise measurements of head turning. Errors in orientation were on average more than twice as great for the seet call (124.5°) as for mobbing calls (51.5°). Similarly, Jones and Hill (2001) tested eight species of North American hawks and owls for their ability to localize the seet call of an American robin and the mobbing call of a tufted titmouse, *Baeolophus bicolor*. Accuracy of orientation was significantly greater for mobbing calls than for seet calls. Passerines have also been shown to have difficulty localizing seet calls (Klump, Windt, & Curio, 1986). The results of these studies thus support Marler's prediction that seet alarms are particularly difficult for birds to localize.

Two studies have extended such work to the rather different aerial alarms of Australian passerines. Jurisevic and Sanderson (1998) tested 11 species of Australian raptors for head turning towards aerial alarms and other sounds. Aerial alarms of Australian passerines were lumped in the analysis with other narrowband sounds and compared to broadband sounds such as mobbing and distress calls. Narrowband sounds as a whole were more difficult for the raptors to localize than were broadband sounds, but conclusions cannot be drawn specifically for aerial alarms. Wood et al. (2000) tested a single species of Australian raptor, the brown falcon,

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