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 crickets, katydids, and frogs. In sum, eavesdropping by unwanted receivers is often as important in shaping the structure of acoustic signals as is selection for transmission to intended receivers.

Keywords: eavesdropping, acoustic adaptation, aerial alarms, begging calls, soft songs, cue denial

In a seminal paper, Marler (1955) 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 behavior of other animals and that have evolved because of those effects (Wheeler et al. 2010), 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 (Morton 1975, Marten & Marler 1977, Marten et al. 1977, Wiley 1991, Boncoraglio & Saino 2007), 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 & Rand 1993, Ryan & Cummings 2013).

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, Myrberg 1981, McGregor & Dabelsteen 1996). 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 et al. 2015). In many cases, however, unintended receivers have negative effects on signaler fitness, as when the eavesdroppers are the signaler’s predators, parasites, or competitors (Ryan et al. 1982, Zuk & Kolloru 1998, Mougeot & Bretagnolle 2000, Bernal et al. 2006). When interception of the signal has a detrimental effect on signaler fitness, selection will favor 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.

Avian Alarm Calls

The first major test case for cue denial in avian acoustic signals emerged from an analysis by Marler (1955) of avian alarm calls. Marler (1955) divided the calls given by passerines in the presence of hawks and owls into two categories: those given while mobbing perched predators and those given in response to in-flight predators. Citing in particular the calls of the common chaffinch (*Fringilla coelebs*), Marler (1955) argued that whereas mobbing calls have “abundant location cues,” aerial alarms are adapted to deny such cues to predators. The aerial alarm of the chaffinch is a high frequency, continuous, narrow-band “seet” with a gradual onset and offset and little frequency modulation (Figure 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, 1c), as were the alarms of domestic chickens and even of some mammals (Marler 1955, 1957). Later work identified further examples of seet-like aerial alarms calls in New World passerines (Fig 1d) (Orians & Christman 1968, Vanderhoff & Eason 2009) and primates (Cäsar et al. 2012).

As Marler (1955) pointed out, the intended receivers of aerial alarms do not need to

79 know a signaler's location to receive the benefit of the warning, whereas disguising location
80 should reduce any cost from interception of the signal by a predator. Thus the hypothesis that
81 aerial alarms deny location cues solves the communication dilemma very neatly: the signal still
82 delivers its benefit to intended receivers while harmful effects from unintended receivers are
83 minimized. Despite its logical appeal, Marler's hypothesis has encountered a series of
84 objections. One objection is that many aerial alarms, particularly those produced by Australian
85 passerines, do not have the structural features specified by the hypothesis (Rooke & Knight
86 1977, Jurisevic & Sanderson 1994, 1998). Some Australian passerines produce seet-like aerial
87 alarm calls similar to the chaffinch's (Fig 1e), but others have aerial alarms with rapid frequency
88 modulation as in some fairy-wrens (Fig 1f) (Fallow et al. 2011) or with multiple elements at
89 relatively low frequencies as in some of the honeyeaters (Fig 1g, 1h) (Wood et al. 2000, Rooke
90 & Knight 1977). Rooke and Knight (1977) argued that the structural features of honeyeater
91 alarms in particular ought to make their calls easy to locate by raptors and other predators.

92 Shalter (1978) raised a second objection to Marler's hypothesis: that its argument was
93 based "entirely . . . on inference from human auditory capacities" rather than on the sound
94 localization capacities of the predatory birds that are the actual threat when aerial alarms are
95 given (see also Klump & Shalter 1984). Knowledge of sound localization in birds was limited
96 when Marler (1955) proposed his hypothesis and has greatly increased since (Klump 2000). An
97 especially important development is the proposal that birds in part localize sounds using a
98 pressure difference mechanism (Lewis & Coles 1980, Rosowski & Saunders 1980, Klump
99 2000). Marler (1955) assumed that birds use a sound-pressure mechanism, which compares
100 time, intensity, and phase of sounds arriving at the outside of the two tympanic membranes. In a
101 pressure difference mechanism, the two ears are acoustically coupled internally, so that a
102 sound affects both sides of a single tympanic membrane and intensity and phase interact
103 across the membrane (Lewis & Coles 1980). A pressure difference mechanism should be more
104 sensitive to changes in the angle of sound incidence (Klump 2000) and may be less restricted

Figure 1. Spectrograms of aerial predator alarms of birds. Seet alarms of (a) the common chaffinch, from Marler (1955), (b) the common blackbird, from Marler (1955), (c) the great tit, from Klump and Shalter (1984), (d) the American robin, from Vanderhoff and Eason (2009), and (e) an Australian passerine, the white-winged fairy wren, from Fallow et al. 2011. Aerial alarms with non-seet structures from additional Australian passerines including (f) the superb fairy-wren, from Fallow et al. (2011), (g) the New Holland honeyeater, from Wood et al. 2008, and (h) the noisy miner, from Wood et al. (2008). (a) and (b) are reprinted by permission of Macmillan Publishers Ltd Nature 1955; (c) by permission of John Wiley and Sons; (e) and (f) by permission of Oxford University Press; and (h) and (i) by permission of CSIRO Publishing.

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 et al. 1980, Rosowski & Saunders 1980, Klump & Larsen 1992). 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 (*Tyta alba*) to the aerial “seet” alarm of a clay-colored robin (*Turdus grayi*). Similarly, Shalter (1978) found correct orientation in 100% of the responses given by goshawks (*Accipiter gentilis*) and pygmy owls (*Glacidium perlatum* and *G. brasilianum*) towards the seet call of a European 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 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 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 et al. 1986b). 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 narrow-band sounds and compared to broad-band sounds such as mobbing and distress calls. Narrow-band sounds as a whole were more difficult for the raptors to localize than were broad-band sounds, but conclusions cannot be drawn specifically for aerial alarms. Wood et al. (2000) tested a single species of Australian raptor, the brown falcon (*Falco berigora*), for response to aerial alarms of four species of birds and to a variety of broad-band calls. Three of the four aerial alarms were from Australian passerines. These three alarms had narrow frequency bandwidths like seet calls but were lower in frequency, had greater frequency modulation, and were broken into multiple separate notes. Nevertheless, brown falcons found the four aerial alarms more difficult to localize than broad-band calls, as also did two species of passerine birds. These results thus suggest narrow frequency bandwidth is the most important acoustic feature in denying localization cues. Work with artificial sounds has confirmed that bandwidth strongly affects localizability for birds, with broad-band sounds being more accurately localized than narrow-band signals by both owls and passerines (Knudsen & Konishi 1979, Klump & Shalter 1984, Park & Dooling 1991).

Klump and Shalter (1984) suggested that aerial alarms might be selected for features that prevent detection by the predator, in addition to or instead of features that prevent localization. Klump et al. (1986a) subsequently compared the hearing of great tits (*Parus major*) and one of their principal predators, the European sparrowhawk (*Accipiter nisus*), at the frequency of the great tit's aerial alarm. This alarm is a classic seet call: a single, continuous note of almost constant frequency emitted at about 8 kHz. Klump et al. (1986a) found that the hearing of the predator was better than its prey's at most frequencies, but that at 8 kHz the predator's thresholds were about 30 dB higher. Consequently, great tits were estimated to be able to detect their seet alarms at 40 meters from a signaler, whereas sparrowhawks would

have to be within 10 meters to detect them. This case presents a second solution to our signaling dilemma: signals can be adapted to exploit differences in the sensory capabilities of intended and unintended receivers in ways that allow the signals to provide cues to intended receivers while denying them to unintended ones.

A third explanation for the acoustic features of seet calls is that these calls have been selected directly for convergence to facilitate interspecific use of alarms. Scores of species of birds and mammals have been shown to use the alarm calls of heterospecifics (Magrath et al. 2015). In some cases, birds respond more strongly to heterospecific alarms the more closely those alarms resemble their own alarms (Fallow et al. 2011, Fallow et al. 2013). Attending to the alarms of other species has clear selective advantages, through greater safety from predation, reduced vigilance, and greater foraging efficiency (Magrath et al. 2015). What is needed to generate selection for convergence, however, is a benefit to the signaler rather than a benefit to the receiver, and how signalers in general might benefit from eliciting alarm responses in other species is not clear. A few cases are known where birds benefit from producing false alarms, that is alarms given in the absence of predators, through manipulating the behavior of heterospecifics to increase the alarmer's access to food (Munn 1986, Møller 1988, Flower 2011). In one case it has been shown that deception is more effective when the species giving the false alarms mimics the alarms of target species (Flower et al 2014). False alarming, however, is fairly rare across birds, and is therefore unlikely to provide an explanation for widespread convergence in alarm calls.

Overall, the evidence seems strong that the acoustic characteristics of aerial alarms have been shaped by selection to deny location cues to predators, as Marler (1955) proposed. Selection to deny detection by predators may also play a role, though this hypothesis relies on differences between the hearing of predators and their prey that may not be general. Direct selection for convergence seems a less likely explanation for the properties of aerial alarms.

194 Nestling Begging Calls

195 The begging calls of nestling birds provide a second test case for cue suppression. When
 196 parents arrive at a nest carrying food, their nestlings give begging calls while also jostling for
 197 position, extending their heads upward, and displaying their sometimes colorful gapes
 198 (Redondo & Castro 1992, Kilner 2002). Begging is much less frequent in the absence of the
 199 parents (Leonard & Horn 2001a), and young often turn on their begging in response to cues that
 200 their parents are nearby (Lock & Hauber 2012), supporting the common sense inference that
 201 the parents are the intended receivers of begging signals. Experiments in which begging calls
 202 are played from speakers placed near nests show that in most cases parents respond to
 203 augmented calling by increasing their rate of feeding visits to the brood (Muller & Smith 1978,
 204 Bengtsson & Ryden 1983, Burford et al. 1998, Price 1998, Kilner et al. 1999, Tarwater et al.
 205 2009, but see Clark & Lee 1998). A variety of evidence suggests that parents are also
 206 influenced by begging intensity in allocating feedings among the young within broods (Smith &
 207 Montgomerie 1991, Kacelnik et al. 1995, Rosivall et al. 2005, Tanner et al. 2008, Krauss &
 208 Yasukawa 2013), but this evidence is compatible with parents responding to visual rather than
 209 auditory components of begging. To our knowledge, only one study has experimentally isolated
 210 an effect of auditory signals on allocation within broods. Leonard and Horn (2001b) gave parent
 211 tree swallows (*Tachycineta bicolor*) choices between feeding two non-begging young, each
 212 associated with an earbud speaker playing contrasting begging call treatments. Parents showed
 213 preferential response to high rates of begging calls over lower rates, and a suggestive but not
 214 significant preference for loud calls over softer ones.

215 The important unintended receivers of begging calls are again predators. One way to
 216 test the effect of begging on predation is to compare predation rates during the nestling stage
 217 (with begging) and the incubation stage (without begging); these comparisons have given mixed
 218 results (Slagsvold 1982, Cresswell 1997, Roper & Goldstein 1997, Yasukawa in press). An
 219 experimental approach is to test the effect of playback of begging near a nest on the likelihood

that the nest's contents will be attacked. Such experiments have generally found that begging calls increase predation risk at both artificial nests (Haskell 1994, Leech & Leonard 1997, Dearborn 1999, McDonald et al. 2009) and natural ones (Haff & Magrath 2011), though a recent experiment with red-winged blackbirds found no evidence that begging calls increase predation (Yasukawa in press). As might be expected, the effect of begging calls on predation appear to be stronger for calls played at high rates or amplitudes than for calls played at low rates or amplitudes (Haskell 1994, Dearborn 1999). In addition, some evidence suggests that the effect of begging on predation is stronger for nests placed on or near the ground than for nests placed higher in trees (Haskell 1994).

Three different perspectives have been proposed on the effects of intended and unintended receivers on the evolution of begging call structure. First, Marler (1955) suggested that the acoustic features of nestling begging calls have evolved to deny localization cues to unwanted receivers, just as he argued for aerial alarm calls. Second, Redondo and Arias de Reyna (1988) proposed that intended receivers have selected for good localization properties in begging calls while unintended receivers have selected for poor detectability. The rationale is that parents allocating food among their young would preferentially feed those with the most easily localizable calls, producing selection for call traits that enhance localization. Predators by contrast would preferentially attack nests with detectable calls, and thus would exert selection for structural features that lower call transmission. Third, Horn and Leonard (2002) and Leonard and Horn (2005) proposed that begging calls are adapted principally for good detectability by intended receivers. Here the rationale is that parents will allocate food preferentially to the nestlings with the most detectable calls, selecting for good transmission properties within the limited confines of the nest.

These competing hypotheses have been tested using comparative data on begging call structure. Two acoustic features have been emphasized in such comparisons: frequency bandwidth and frequency. Frequency bandwidth is relevant in particular to localization; as we

have seen, sounds with wider bandwidth are more easily localized. Frequency may also be relevant to localization but is more directly relevant to detection because of its effects on excess attenuation. Excess attenuation is the amount by which attenuation with distance exceeds what is expected from spherical spreading of sound energy. Excess attenuation due to heat losses and scattering increases with increasing sound frequency, so at least for birds vocalizing from elevated perches (away from ground interference) the higher the frequency the greater the excess attenuation and the lower the transmission distance (Marten & Marler 1977, Bradbury & Vehrencamp 2011).

The hypotheses concerning how selection on detectability and localizability have shaped begging calls can be tested by examining features such as bandwidth and frequency. As one example, the begging calls of red-winged blackbirds show the high frequencies that would minimize transmission but not the narrow bandwidth that would minimize localizability (Fig 2).

Figure 2. Spectrogram of begging calls of red-winged blackbirds. Some features of these calls such as broad frequency bandwidth, frequency modulation, and sharp on- and off-sets should facilitate localization, whereas other features such as relatively high frequency (4–8 kHz) and low amplitude (Briskie et al. 1994) may represent adaptations to reduce detection by eavesdropping predators.

Four comparative studies have tested the predictions of the competing hypotheses more systematically. 1) Redondo and Arias de Reyna (1988) compared begging call structure in 14 open nesting and 10 hole nesting species, under the assumption that hole nesters are less exposed to nest predation. Frequency bandwidth was significantly lower in open nesting species, suggesting that predation on these species has selected for reduced localization. Call frequency (controlling for body size) was higher in open nesting species, suggesting that predation also has selected for poor transmission and hence poor detectability. (2) Popp and Ficken (1991) compared the begging calls of hole nesting and open nesting species, with a larger sample (75 species). Frequency bandwidth was higher in hole nesting than in open nesting species, but the difference was not significant. Maximum and minimum frequencies were not much different in the two groups. 3) Haskell (1999) compared begging calls of ground nesting and tree nesting warblers; here ground nesters are the group assumed to be more exposed to nest predation. The calls of five ground nesting species had significantly higher frequencies than the calls of five tree nesting species. The two groups did not differ consistently in bandwidth or in amplitude. 4) Briskie et al. (1999) measured predation rates on 24 species of woodpeckers and passerines, and related those rates to begging call structure while controlling for body size. The analysis also controlled for phylogeny, a step not taken by studies 1–3 and which is definitely recommended in modern comparative work. Dominant frequency increased with predation risk, while amplitude decreased. Frequency bandwidth showed no association with predation. An additional, experimental study is also relevant: McDonald et al. (2009) found that playback of nestling vocalizations was just as effective as playback of broad-band white noise in increasing nest predation on bell miners (*Manorina melanophrys*), suggesting that localizability of calls was not important.

The one experimental study together with the comparative analyses of begging call structure best support the hypothesis that predators have selected for features that minimize detectability rather than localizability in begging calls. Given the evidence that parents

preferentially allocate food to nestlings with more detectable calls, selection due to intended receivers must act in the opposite direction. Thus the current structure of begging calls must be a compromise between selection from unintended receivers for reduced detectability and from intended receivers for greater detectability. An exciting possibility is that begging calls can be adapted for the transmission properties of the specific nest environment (Fairhurst et al. 2013), perhaps without producing increased transmission outside the nest.

Soft Songs and Calls

Low amplitude “soft” songs and calls provide a third test case for cue denial in avian acoustic signals. Soft songs function, as do broadcast songs, in courtship and aggression (Dabelsteen 1998, Searcy et al. 2006, Reichard & Welkin 2015). Soft calls of a variety of functional categories are produced by birds as a whole (Reichard & Weklin 2015), including soft alarm calls and contact calls, but we discuss here only those soft calls that function similarly to soft song, that is in courtship and aggression. Dabelsteen et al. (1998) first drew attention to the widespread occurrence of soft song in birds; since then, soft songs and calls have been described in an ever-expanding number of bird species (Morton 2000, Reichard & Welkin 2015, Reichard & Anderson 2015).

Among temperate songbirds at least, soft song is chiefly a male signal, given in some species primarily in courtship, in other species primarily in aggressive encounters with rival males, and in yet other species in both courtship and aggression (Dabelsteen et al 1998, Reichard & Anderson 2015). Thus the intended receivers of soft songs may be conspecific females, conspecific males, or both. Unintended receivers may include predators, as with the other signal categories we have discussed. With soft song, however, additional categories of unintended receivers are possible (Dabelsteen et al. 1998, Searcy & Nowicki 2006, Akçay et al 2015). Rival males who are not at the moment confronting the signaler might eavesdrop on aggressive song to locate territorial males who are struggling with intruders, or they might

eavesdrop on courtship song so that they can interfere with courtship. Conspecific females who are not currently being courted might intercept aggressive song to determine which males are experiencing difficulty holding territory, or they might intercept courtship song to determine whether their mate is seeking extra-pair copulations. Features of soft song are thus subject to selection stemming from effects on a variety of unintended receivers.

The defining feature of soft vocalizations is low amplitude, but few rigorous measurements of their actual amplitudes have been made. Anderson et al. (2008) recorded soft song in song sparrows using a calibrated microphone and holding the distance of the singers to the microphone constant. In a sample of 326 songs recorded from 12 males, amplitudes varied continuously from 50 to 86 dB SPL. A human observer subjectively classified those songs ≤ 77 dB as soft, and this cutoff corresponded well with the boundary between a peak of high-amplitude songs and a tail of low-amplitude ones. The median soft song was about 14 dB lower than the median loud song. Rek and Osiejuk (2011) used a sound level meter positioned 0 to 2 m from male corncrakes (*Crex crex*) to estimate the amplitudes of calls, and found a mean of 70 dB (range 65-76) for soft calls and a mean of 96 dB (range 80-101) for loud ones (SPL at 1 m) (Rek 2013). Thus the average soft call is about 26 dB lower than the average loud call.

A logical explanation for the low amplitude of soft song is that this feature has evolved to minimize detection of the signal by unwanted receivers (Dabelsteen et al. 1998). Soft song is almost universally directed at conspecifics that are in very close proximity to the singer. Lowering the amplitude of song inevitably lowers its transmission distance; for example, the 14 dB median difference in the amplitude of loud and soft songs in song sparrows should reduce transmission distance by more than a factor of 4. If the intended receiver is close and unintended receivers are more distant, then low amplitude provides another neat solution for our communication dilemma: communication with the intended receiver is achieved while communication with unintended receivers is minimized.

Although this “eavesdropping avoidance hypothesis” is logically compelling, many other explanations for the occurrence of soft song have also been proposed (Akçay et al. 2015, Reichard & Anderson 2015). Most of these hypotheses apply to soft vocalizations used in aggression rather than to those used in courtship. Soft songs and soft calls are among the most reliable signals of aggressive intentions in a number of species of birds (Searcy & Nowicki 2006, Ballentine et al. 2008, Hof & Hazlett 2010, Rek & Osiejuk 2011, Akçay et al. 2013, Xia et al. 2013). The readiness hypothesis proposes that soft song is tied to aggression in birds because the postures from which attacks can be launched are more compatible with singing at low amplitude than at high amplitude (Akçay et al. 2011, Akçay & Beecher 2012). The vulnerability handicap hypothesis proposes that singing soft song increases the vulnerability of singers to injury by opponents, and therefore low amplitude imposes a signal cost that makes soft song a reliable signal of aggression (Vehrencamp 1980, Lairde & Vehrencamp 2008). A third alternative is that soft songs are conventional signals, that is signals whose design, including their low amplitude, is arbitrary with respect to their message (Guilford & Dawkins 1995).

Not only are there alternatives to the eavesdropping avoidance hypothesis, there is also experimental evidence against specific predictions of the hypothesis. One such prediction is that if soft song functions to minimize detection by predators, then use of soft song should increase in contexts in which the danger from predators is high. This prediction has been tested in two experiments with song sparrows in which predator danger was simulated with playback of song sparrow alarm calls (Searcy & Nowicki 2006) or of the calls of a bird-eating Cooper’s hawk (*Accipiter cooperi*) (Akçay et al in press). In both experiments, use of soft song did not increase in the predator context, counter to the prediction. A second prediction applies to a different eavesdropping scenario, one in which rival conspecific males use singing interactions between a territory owner and an intruder to target territories for their own intrusions. Working again with song sparrows, Searcy and Nowicki (2006) used loudspeakers to simulate owner/intruder interactions in which the owner sang either soft songs or broadcast songs. Contrary to

prediction, intrusions by third party males were actually more common when owners appeared to use soft song than when they used loud song.

Although some predictions of the eavesdropping avoidance hypothesis have not been supported, the falsified predictions are specific to particular categories of eavesdroppers and particular contexts of eavesdropping, and the tests have been done in only a single species. Even in song sparrows, additional categories of eavesdroppers have not been tested at all. In particular, the possibility remains that eavesdropping by conspecific females is costly for males in certain contexts, and that soft song has evolved in response to this form of eavesdropping (Akçay et al. 2015).

A more general prediction of the eavesdropping avoidance hypothesis exists that applies across all possible categories of eavesdroppers and all contexts of eavesdropping. The logic is that if selection has favored low amplitude in soft vocalizations to minimize eavesdropping (whatever the context), then other acoustic traits of soft vocalizations should also be adapted to decrease transmission (Dabelsteen et al. 1998, Rek 2013, Akçay et al. 2015). This prediction brings us squarely back to the question of how important unintended receivers have been in shaping the structure of soft songs and calls.

As we have seen, high frequency is one acoustic trait that lowers sound transmission. Frequency also affects the degree to which acoustic signals are masked by noise; such masking greatly affects the detectability of sounds (Klump 1996, Lohr et al. 2003). In open habitats, noise is often largely wind-generated, and is mainly low frequency (< 2 kHz) (Ryan & Brenowitz 1985, Bradbury & Vehrencamp 2011). In tropical forests, environmental noise is often dominated by insect sounds that occur at higher frequencies (> 4 kHz) (Ryan & Brenowitz 1985, Slabbekorn 2004). Thus selection for low detectability via masking may select for different sound frequencies depending on the habitat. It has also been suggested that stereotypical, redundant sounds will be detectable at a greater distance than more variable ones (Wiley 1994,

Reichard & Anderson 2015), so increasing the variability of a signal would be another method for decreasing its transmission distance.

The eavesdropping avoidance hypothesis thus makes specific predictions about the structure of soft vocalizations: compared to control songs or calls, soft sounds should be emitted at higher frequencies, should overlap more with environmental noise, and should have more variable elements. The logical control sounds to use in testing these predictions are loud songs or loud calls of similar function. Anderson et al. (2008) have published measurements of soft songs in song sparrows that allow tests of these predictions. One complication is that song sparrows have two forms of soft song: crystallized soft songs, which are song types from the broadcast repertoire sung at lower amplitude, and warbled soft song, specialized song types that are sung only at low amplitude. Although crystallized soft songs are identifiable as broadcast song types, they often have some additional notes, so their acoustic structure is not identical to broadcast song. In a large sample of songs of all three types, warbled soft songs had significantly higher maximum frequencies than did either broadcast song or crystallized soft song, while the latter two were indistinguishable. Minimum frequencies were just above 2000 kHz for broadcast song, and were significantly lower for warbled soft song, with crystallized soft song intermediate; thus overlap with low frequency noise should be greater for the two categories of soft song. A measure of song variability, the number of note types per note, was significantly higher for warbled soft song than for the other two categories. In sum, warbled soft song met all three structural predictions, whereas crystallized soft song met only one.

The inclusion of higher frequency elements, in the region above 4 kHz where excess attenuation is a particular problem, seems to be a fairly general phenomenon in soft vocalizations (Dabelsteen 1984, Dabelsteen et al. 1993, Titus 1998, Vargas-Castro 2015), though there are exceptions (Xia et al. 2013 Belinsky et al. 2015). Greater variability also seems to be fairly general across soft vocalizations (Xia et al. 2013, Vargas-Castro 2015). The soft calls of corncrakes, used in aggressive contexts, offer one case in which much of the energy of

a soft vocalization is at low enough frequencies ($\ll 2$ kHz) to make masking by wind noise important. The soft songs of the tropical white-throated thrush (*Turdus assimilis*) have all three properties expected to lower transmission (Figure 3): compared to broadcast song, their mean and maximum frequencies are higher, more of their energy overlaps with environmental noise (from insects), and they show greater variability (Vargas-Castro 2015). Thus analysis of the acoustic features of soft vocalizations in general upholds the predictions of the eavesdropping avoidance hypothesis.

Figure 3. Spectrograms of broadcast song and soft song of a white-throated thrush (from Vargas-Castro 2015). The soft syllables (H-M) are considerably higher in maximum, minimum, and mean frequency than broadcast syllables (a-g) and also overlap more with the band of environmental noise (from insects) visible between 4 and 5 kHz. Reprinted from Vargas-Castro 2015 Behaviour 152: 775-795 by permission of Brill.

A second, more direct prediction of the eavesdropping avoidance hypothesis requires an experimental test: after amplitudes are experimentally equalized, transmission distances should still be greater for soft vocalizations than for control sounds. Again, the logical control sounds for such a test are loud songs or loud calls of similar function. Dabelsteen et al. (1993) measured transmission of the (loud) motif elements and (soft) twitter elements of European blackbirds,

though without equalizing initial amplitudes. Twitter elements were found to have lower signal to noise ratios at all re-recording distances, but this result must be due at least in part to their lower initial amplitudes. What remains pertinent here is that excess attenuation was greater for twitter elements than for motif elements, which accords with prediction. Three experimental tests have been carried out with equalized initial playback amplitudes. 1) Balsby et al. (2003) compared transmission of high amplitude “perch song” and low amplitude “diving song” in whitethroats (*Sylvia communis*). After transmission across 12.5–50 m of natural habitat, excess attenuation was significantly higher and signal to noise ratios were significantly lower for diving song. 2) Rek (2013) compared transmission of the loud broadcast calls of corncrakes to transmission of gurgling and mewing notes from their soft calls. Excess attenuation at 40 m was about the same in mewing notes as in broadcast calls, and was actually significantly lower in gurgling notes. Nevertheless, signal to noise ratios were higher in broadcast calls at 40 m than in either type of soft notes, perhaps because the frequencies of the soft notes overlap more with environmental noise. (3) Vargas-Castro, Sandoval and Searcy (unpublished) compared transmission of soft and loud songs in the tropical white-throated thrush. At all re-recording distances (10, 20, and 40 m), excess attenuation was greater and signal to noise ratios were lower for soft song.

The results of transmission studies and comparisons of the acoustic features of soft and broadcast vocalization support the eavesdropping hypothesis. Thus both the low amplitude of soft vocalizations and their other acoustic features seem to have been shaped by selection to avoid detection by unwanted receivers.

Cue Suppression in Other Animals

Selection for cue suppression in auditory signals is also known for animals other than birds (Zuk & Kolluru 1998). An extreme case involves the calling song of the field cricket, *Teleogryllus oceanicus*, which is used by males to attract females. In Hawaii, where *T. oceanicus* has recently been introduced, it is attacked by the parasitoid fly *Ormia ochracea*, also a recent

introduction. *Ormia* typically finds crickets using their calling song (Cade 1975), and in these Hawaii populations male crickets are more likely to be parasitized if they produce longer songs with longer components (Zuk et al 1998). The parasitized Hawaiian populations produce song with shorter components than do males in parts of the range lacking the parasitoid (Zuk et al. 1993, Rotenberry et al. 1996), suggesting adaptation of acoustic structure to the pressure exerted by unwanted eavesdroppers. At the extreme, the majority of males in some Hawaiian populations have become entirely silent through a mutant wing morphology that lacks the stridulatory apparatus that produces the song (Zuk et al 2006). *Ormia* is known to exert selection on call traits in other cricket species as well (Wagner 1996, Gray & Cade 1999, Wagner & Basolo 2007).

A similar case is provided by the calling songs of neotropical katydids subject to predation by foliage gleaning bats. Calling by male katydids attracts bats as well as conspecific females (Belwood & Morris 1987). Different species of bats prefer different call features (Falk et al. 2015), but the overall effect of bat predation is to select for calls with lower bandwidths, higher frequencies, and lower duty cycles and for communicating via substrate vibrations rather than by calling (Belwood & Morris 1987, Römer et al. 2010). Low bandwidth presumably is favored to reduce localizability, as Marler (1955) predicted for avian alarms. Bats feature as unwanted receivers again in a final case of cue suppression, in the mate attraction calls of the túngara frog (*Engystomops pustulosus*). The male call is a whine followed by one or more chucks. Female frogs prefer to approach calls with chucks (Rand & Ryan 1981), but so do predatory bats (Ryan et al 1982) and blood-sucking flies (Bernal et al. 2006). Calls with chucks are more easily localized by bats (Page & Ryan 2008), but the same was not true for the flies (Bernal et al. 2006). Pressure from predators helps explain why chucks are not added to all calls despite the preferences of conspecific females.

Conclusions

For each of the categories of avian acoustic signals we have discussed, the structure of the sounds give evidence of having been shaped by selection to deny cues to unwanted receivers. Aerial alarms seem to have been selected for narrow bandwidth and in some cases for high frequency in order to deny localization cues to predators, as Marler (1955) originally hypothesized. Avian begging calls appear to have been selected for high frequency and perhaps low amplitude to deny detection by predators. Soft vocalizations seem to have been selected at least in some cases for high frequency, greater overlap with noise, and greater variability as well as for low amplitude, all to evade detection by various type of unwanted receivers. The acoustic signals of some crickets, katydids, and frogs also give evidence of adaptation to evade detection or localization by predators and parasites. In some cases the patterns produced by selection due to unwanted receivers seem weak, or to apply only to a subset of signalers (e.g. to open nesters but not cavity nesters), but it is important to remember that patterns produced by selection to facilitate communication with intended receivers can also be weak (Daniel & Blumstein 1998, Boncaraglio & Saino 2007). What are needed are comparative analyses that combine measures of selection by unwanted receivers with measures of effects of intended receivers while controlling for covariates such as phylogeny and body size, to see how much of the overall variation in the structure of acoustic signals can be explained by combining these factors.

We have also seen evidence of various ways in which signalers can evade the conflict between facilitating communication with intended receivers and minimizing communication with unwanted ones. First, signalers can exploit differences in the information needed by intended and unintended receivers, as in the case of aerial alarms, where unintended receivers need information on the location of an alarmer to exploit the signal and intended receivers do not. Second, signalers can exploit differences in the sensory sensitivities of intended and unintended receivers, as seems to be the case for the aerial alarms of great tits. Third, signalers can take advantage of differences in their average distance to intended and unintended receivers, as in

the example of soft vocalizations. In other cases, however, no evasion appears possible, because both intended and unintended receivers select for the same signal properties, as appears to be true for avian begging calls as well as for the mate attraction signals of Hawaiian crickets, neotropical katydids, and túngara frogs. In these cases, the properties of the signals are set as a compromise between conflicting selection pressures.

Acknowledgments

We thank Mike Beecher and Robert Seyfarth for their work in organizing this special issue. We are grateful to Luis Vargas Castro and Luis Sandoval for permission to cite unpublished results. W.A.S. thanks Steve Nowicki, Rindy Anderson, Susan Peters, Adrienne DuBois, Çağlar Akçay, Mike Beecher and others for their collaboration on soft song research. K. Y. thanks Jody Urish, Al Her, Erin Light, Jacy Bernath-Plaisted, Emily Dorjath, Stephanie Morgan and others for their collaboration on begging call research.

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