Why signal softly? The structure, function, and evolutionary significance of low-amplitude signals

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1 Acoustic signaling is a taxonomically widespread form of animal communication consisting of
2 long range, high-amplitude signals and short range, low-amplitude signals. Research on acoustic
3 communication has emphasized high-amplitude signals and often overlooked low-amplitude
4 signals, even though they are produced in behavioural contexts that directly influence fitness.
5 Low-amplitude signals are referred to by a variety of names such as soft songs, courtship songs,
6 whispers, close calls, contact calls, grunts, and moans, but all of these signals share a reduced
7 amplitude and an active space that is limited to close-proximity receivers. In this review, we
8 establish a general definition for low-amplitude signals and investigate the similarities and
9 differences between low- and high-amplitude signals with respect to their acoustic structure and
10 function. Then, we critically evaluate some proximate and ultimate evolutionary mechanisms
11 that may explain why these signals are produced at low amplitude using examples from a variety
12 of taxa. We conclude by suggesting priorities for future research on low-amplitude signals and
13 highlighting how studying these signals will lead to a more complete understanding of how and
14 why animals communicate acoustically.

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21 *Keywords:* communication, social behaviour, soft song, short-range song, amplitude, sexual
22 selection, eavesdropping
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Research on acoustic communication has provided important insights into the fields of sexual selection, sensory perception and the evolution of behaviour (Andersson, 1994; Bradbury & Vehrencamp, 2011; McGregor, 2005; Searcy & Nowicki, 2005). Until recently, most research on this topic has focused on high-amplitude signals that project over long distances and can simultaneously influence multiple types of receivers (Wiley & Richards, 1978, 1982). Because high-amplitude signals propagate widely, they can serve a variety of functions that directly influence an organism's fitness including attracting mates, competing with rivals, avoiding predators, and mediating social interactions within groups (Bradbury & Vehrencamp, 2011).

However, acoustic signals are produced over a wide range of amplitudes (e.g., Anderson, Searcy, Peters, & Nowicki, 2008), and the repertoires of some species include signals that are produced exclusively at low amplitudes (e.g., Titus 1998; Reichard and Welklin 2015). The occurrence of low-amplitude signaling has been documented for decades (e.g., Alexander, 1961; Nice, 1943), but this form of communication remains understudied and poorly understood. Low-amplitude signals are produced in the same social contexts as high-amplitude signals such as directed courtship (Rebar, Bailey, & Zuk, 2009; Reichard, Rice, Schultz, & Schrock, 2013), intense aggressive interactions (Ballentine, Searcy, & Nowicki, 2008; Hof & Hazlett, 2010; Searcy, Anderson, & Nowicki, 2006), alarm signaling (Greene & Meagher, 1998; Smith, 1978), group movements and foraging (Radford & Ridley, 2008; Townsend, Hollen, & Manser, 2010), and parent-offspring communication (Horn & Leonard, 2002). Low-amplitude signals appear to serve many functions that influence fitness, which raises the question of why selection has repeatedly favored the evolution of these signals in so many disparate social contexts. Furthermore, low-amplitude signals are taxonomically widespread, with evidence for these signals being present in amphibians, birds, fish, insects, and mammals (Table 1). Collectively,

low-amplitude signals present an interesting case study in behavioural evolution that has the potential to provide novel insights into topics such as honest signaling, audience effects, signal transmission and perception, physiological constraints on signal production, and signal development.

WHAT IS A LOW-AMPLITUDE SIGNAL?

Amplitude

Animals vary dramatically in the range of acoustic amplitudes they can produce and perceive (Dooling, Lohr, & Dent, 2000; Fay, 1988), making it impossible to establish a universal amplitude threshold below which signals are categorized as “low amplitude.” As an example of the difficulties in comparing amplitude between species, the low-amplitude songs of song sparrows (*Melospiza melodia*) range from 54-77 dB sound pressure level (SPL) measured at 1 m from the singer (Anderson et al., 2008), whereas the close-proximity courtship songs of multiple moth species (from families Noctuidae, Arctiidae, Geometridae and Crambidae) range from 43-76 dB SPL measured at 1 cm from the singer (Nakano, Takanashi, Fujii, Skals, Surlykke et al., 2009). The similarity in the decibel values here is misleading because the sparrow microphone was 100 times further from the signaler than the moth microphone. Sound pressure level decreases by about 6 dB with every doubling of distance when spherical spreading occurs (Wiley & Richards 1982). Thus, at a distance of 1 m the absolute amplitude of the moth’s song (3-36 dB SPL) is substantially lower than the sparrow’s song. The magnitude of this difference is particularly striking because amplitude is often perceived on a logarithmic scale, not a linear

scale. As an example, at most frequencies, humans perceive an increase of 10 dB as a doubling in loudness (Fletcher & Munson, 1933; Macmillan, 1990).

The differences in how the above amplitudes were reported highlights the challenges associated with measuring signal amplitudes. If the distance between the signaler and the microphone changes, which includes shifts in the subject's orientation (e.g., facing v. facing away from the microphone), the measurement of amplitude will be affected. Because of these limitations, most studies have not measured signal amplitudes in the field and have instead simply categorized signals as either loud or soft according to the perceptions of a human observer (e.g., Gustison, le Roux, & Bergman, 2012; Hedwig, Hammerschmidt, Mundry, Robbins, & Boesch, 2014; Searcy et al., 2006; but see Anderson et al., 2008; Brumm 2004). This approach can be problematic because auditory perceptions and sensitivities differ not only between human observers, but also between humans and the organisms that they are studying (Dooling, Zoloth, & Baylis, 1978; Fletcher & Munson, 1933; Green, 1975). In addition, categorizing signals as loud or soft implies two distinct amplitude classes rather than treating amplitude as a continuous variable.

Previous researchers have often relied on comparisons with the high-amplitude signals in a species' repertoire when defining a signal as low amplitude (e.g. Anderson et al., 2012; Bourne, Collins, Holder & McCarthy 2001; Hof & Hazlett, 2010; Ladich 2007; Reichard, Rice, Vanderbuilt & Ketterson, 2011, 2011). However, some species (moths, Nakano et al., 2009; beetles, Fleming, Lindeman, Carroll & Yack 2013), do not produce any high-amplitude signals, rendering this definition too narrow. As an alternative, we advocate defining low-amplitude signals according to a signal's active space, or the distance from the signaler at which the signal remains detectable to potential receivers (Brenowitz 1982). Specifically, we define low-

amplitude signals as those produced at amplitudes that limit the signal's active space to either a single receiver or a group of receivers nearby the signaler. Implicit in this definition is that low-amplitude signals are designed to function in short-range communication. Thus defined, the examination of low-amplitude signals requires consideration of signal amplitude at the source, the environmental conditions through which the signal propagates, and the perceptual capabilities of potential receivers (Brenowitz 1982; Henry & Lucas, 2010; Wiley 1994).

Structure

A common misconception about low-amplitude signals is that they are simply whispered versions of a species' high-amplitude signals. Many species do vary the amplitude of their broadcast signals, producing the same acoustic structure at low amplitude (e.g., Anderson et al., 2008; Hof & Hazlett, 2010; Morrison & Reiss, 2013; Reichard et al., 2013). In contrast, many species produce signals that are both acoustically distinct from the high-amplitude repertoire and produced exclusively at low amplitude (Figure 1). In several bird species for example, males produce both high- and low-amplitude versions of their broadcast vocalizations as well as a distinct vocalization that is only produced at low amplitude during close-proximity interactions with conspecifics (e.g., Anderson et al., 2008; Ballentine et al., 2008; Hof & Hazlett, 2010; Reichard, Rice, Vanderbilt, & Ketterson, 2011; Reichard & Welklin, 2015; Rek, 2013; Vargas-Castro, 2015; Xia et al., 2013). Quantitative data comparing the structural differences between high- and low-amplitude signals are rare, which highlights an important area for future research.

Data collected from dark-eyed juncos (*Junco hyemalis*; Titus 1998), European blackbirds (*Turdus merula*; Dabelsteen 1984), and song sparrows (Anderson et al., 2008) indicate that within each species, songs produced only at low amplitude have a broader frequency bandwidth

than the broadcast songs that are produced at both high and low amplitudes. In addition to a broader frequency range, the structurally distinct low-amplitude songs of dark-eyed juncos and song sparrows also exhibit an increase in note variability in that certain note types are unique to the low-amplitude song repertoire and never observed in a high-amplitude song (Anderson et al., 2008; Titus, 1998; Figure 1). A similar increase in note variability associated with low-amplitude signals has also been observed in male Pacific field crickets (*Teleogryllus oceanicus*; Zuk et al. 2008; Figure 1), sac-winged bats (*Saccopteryx bilineata*; Behr and von Helversen 2004), and multiple species of cicadas (genus *Tibicina*; Sueur and Aubin 2004), which produce a structurally distinct and variable low-amplitude signal in close proximity to receptive females. Collectively, these data emphasize the structural differences present in some low-amplitude signals and suggest that these signals belong to a unique signal class.

Up to this point, we have focused on the structure of low-amplitude signals in species and interactions where longer, more variable signals are common. There are also numerous examples of simple low-amplitude signals, often consisting of only one or a few note types. Examples of these signals include the begging calls of offspring (Horn & Leonard, 2002), contact calls produced by members of a pair or social group (Elfström, 1992; Sharp & Hatchwell, 2005; Townsend et al., 2010), and certain types of alarm calls produced in response to predators (Morrison & Reiss, 2013; Wilson & Hare, 2004). Similar to the trends observed with longer, more variable signals, some simpler signals are produced over a range of amplitudes (e.g., Horn & Leonard, 2002; Morrison & Reiss, 2013), while others are produced only at low amplitudes (e.g., Wilson & Hare, 2004).

FUNCTIONS

138 *Mating displays: courtship and competition*

139 Low-amplitude signals are commonly used in close range mating displays. In croaking
140 gouramis (*Trichopsis vittata*), females produce low amplitude “purring sounds” in the presence
141 of courting males (Ladich, 2007). In the mandarin vole (*Lasiopodomys mandarinus*), both males
142 and females produce “quiet squeals” during sexual behaviour and also during intrasexual
143 affiliative interactions (Rutovskaya, 2011). Male golden rocket frogs (*Colostethus beebei*)
144 produce a high-amplitude, advertisement call to attract females from a distance, and transition to
145 a rapidly delivered, low-amplitude call after a female approaches (Bourne et al. 2001). Similarly,
146 many species of singing insects produce a high-amplitude calling song for mate attraction and a
147 low amplitude courtship song when a female contacts a male (crickets: Alexander, 1961; cicadas:
148 Sueur & Aubin, 2004). Multiple species of moths (Nakano et al. 2009) and at least one species of
149 beetle (*Dendroctonus ponderosae*; Fleming et al. 2013) produce a low amplitude courtship signal
150 but rely on chemical signals for long-distance mate attraction.

151 In birds, high-amplitude “broadcast” songs function in both territorial defense and
152 courtship contexts. Low-amplitude songs function in either or both contexts in many species
153 (Reichard & Welklin, 2015). Eurasian blackbirds (*Turdus merula*) and redwings (*Turdus iliacus*)
154 sing long-range songs composed of loud “motifs” and quiet “twitters.” This strategy effectively
155 combines both a high- and low-amplitude signal into a single vocalization, as is also observed in
156 other songbirds (e.g., Collins, 2004; Collins, de Kort, Perez-Tris, & Telleria, 2009) and some
157 crickets (e.g., Zuk et al., 2008; Figure 1). Both blackbird and redwing males also produce quiet
158 twitter song (referred to as “strangled song”) during close-range interactions; males are
159 threatened with twitter song and females are courted with this same song (Dabelsteen, 1984;
160 Dabelsteen & Pedersen, 1988; Dabelsteen & Pedersen, 1990). Similarly, in the corn crake (*Crex*

161 *crex*), males produce soft calls during both sexual displays and agonistic interactions (reviewed
162 in Ręk & Osiejuk, 2011). Dark-eyed juncos sing two types of low-amplitude song: (1) a low
163 amplitude version of the junco's high amplitude broadcast song (referred to as "soft, long-range
164 song") that is produced during both intersexual and intrasexual contexts, and thus appears to be a
165 dual-function signal, and (2) a structurally distinct low-amplitude song (referred to as "short-
166 range song") that appears to function in a female-directed context (Figure 1; Reichard et al.,
167 2013; Reichard et al., 2011; Titus, 1998).

168 In other avian species, low-amplitude song is restricted to either courtship or aggressive
169 contexts. For example, the low amplitude "diving song" of male common whitethroats (*Sylvia*
170 *communis*; Balsby 2000, Balsby and Dabelsteen 2003), the "low-volume" song of male common
171 yellowthroats (*Geothlypis trichasi*; Ritchison 1995), and the "whisper song" of house wrens
172 (*Troglodytes aedon*; Johnson and Kermott 1991) are directed exclusively to females during the
173 breeding season. In contrast, low-amplitude songs function only in intrasexual agonistic
174 interactions between males in at least one songbird, the song sparrow (Searcy et al. 2006).
175 Broadcast song types serve both intra- and intersexual functions, but low-amplitude "soft songs"
176 appear to function only in aggressive competition between males (Figure 1). The available data
177 suggest that soft songs are not effective as courtship signals (Anderson et al., 2007) but are true
178 aggressive signals in the sense that they predict physical aggression (see below, also Akçay,
179 Anderson, Nowicki, Beecher, & Searcy, 2015 in this issue).

181 *Contact and group cohesion*

182 Group-living species often utilize high-amplitude contact calls to coordinate group
183 movements and other social behaviour over large distances. However, low amplitude 'close'

calls, which are typically shorter in duration and acoustically more variable than loud contact calls, are often the most frequent call type given and yet are relatively understudied (Snowdon, 1988). Close calls serve a variety of functions including contact maintenance among group members, sharing of information about food quality and location, and regulation of individual spacing during foraging (reviewed in Radford & Ridley, 2008).

In primates, a group cohesion function has often been ascribed to close calls (e.g., Palombit, 1992), but studies have found evidence supporting additional functions such as reduction of competition within foraging patches (Boinski & Campbell, 1996), facilitation of affiliative social interactions among group members (Cheney, Seyfarth, & Silk, 1995), and mediation of aggressive interactions among males (Bolt, 2014). Meerkats (*Suricata suricatta*) utilize loud calls as part of a functionally referential alarm call system and to coordinate whole-group behaviour (Manser, 1998). Meerkats also produce close calls, which are relatively brief, pulsatile vocalizations that typically travel no farther than 20 m. Close calls are the most common call type produced by this species and probably function to maintain group cohesion and regulate spacing among individuals foraging together at close range (Townsend et al., 2010). A similar signaling strategy is utilized by killer whales (*Orcinus orca*), and it has been hypothesized that their low-amplitude calls not only maintain contact but also function in coordinating group hunting (Saulitis et al., 2005). See Gustison and Townsend (2015) in this Special Issue for a review of low-amplitude vocalizations in mammals. Although we have focused on mammalian species here, close calls are also common in many social avian species (e.g., Radford & Ridley, 2008; Sharp & Hatchwell, 2005).

207 *Alarm calls and predation*

208 High-amplitude alarm calls can function both as a warning to conspecifics that a predator
209 is nearby and also as a potential signal to predators that they have been detected. One frequently
210 cited cost for alarm signaling is revealing one's location to a nearby predator, but some species
211 may limit this cost by producing low amplitude alarm calls in certain contexts. The functional
212 limitation of low amplitude alarm signaling is that the signal's reduced active space will limit its
213 transmission to close-proximity conspecifics, but many species of birds (Reichard & Welklin,
214 2015) and mammals (Cheney & Seyfarth, 1992; Morrison & Reiss, 2013; Wilson & Hare, 2004)
215 are known to produce low amplitude alarm signals. In some cases these alarm calls are not only
216 low amplitude, but also ultrasonic in frequency, which further limits the signal's active space
217 (Wilson & Hare, 2004). There is also evidence that some low amplitude alarm calls can be
218 referential to specific types of predators (Greene & Meagher, 1998; Seyfarth, Cheney, & Marler,
219 1980; but see Digweed & Rendall, 2009), as is also true of some loud alarm calls (Kalan,
220 Mundry, & Boesch, 2015; Templeton, Greene, & Davis, 2005).

221
222 *Parent-offspring communication*

223 Given that parents and offspring are often in close proximity to one another, it is not
224 surprising that their interactions often include low amplitude acoustic signals. Many of these
225 signals are produced during feeding behaviour. The begging calls of altricial songbirds, for
226 example, signal information relating to offspring quality and level of need (Horn & Leonard,
227 2002; Soler & Aviles, 2010). The parents of some bird species produce low amplitude feeding
228 calls that may serve to signal the arrival of food to the offspring and/or as a sign of nest relief to
229 the other parent (Ishizuka, 2009). Female superb fairy-wrens (*Malurus cyaneus*) are also known

to produce a vocalization during incubation, which the offspring appear to learn in the egg and produce after hatching thereby allowing the parents to distinguish their own offspring from the offspring of brood parasites (Colombelli-Négrel et al., 2012). Independent of nesting contexts, parents may also rely on low-amplitude signals to maintain contact with their offspring in large groups and to differentiate their own offspring from others. Evidence in cattle, for example, has indicated that the contact calls of both cows and calves have individually distinct acoustic structures that may facilitate individual recognition (Padilla de la Torre, Briefer, Reader, & McElligott, 2015).

WHY SIGNAL SOFTLY?

Audience and third party effects

One of the most widely cited explanations for the occurrence of low-amplitude signaling is the “eavesdropping avoidance hypothesis.” This hypothesis argues that signalers produce signals at reduced amplitudes due to the costs associated with attracting unwanted eavesdroppers such as conspecific competitors or heterospecific predators (Dabelsteen, 2005; Dabelsteen et al., 1998).

Three major predictions can be derived from this hypothesis: (1) signalers incur costs from eavesdroppers, (2) low-amplitude signals should be more difficult for eavesdroppers to detect than high-amplitude signals, and (3) low-amplitude signaling should occur more often when conditions increase the likelihood of eavesdropping. Eavesdropping pressure is likely to be density-dependent, and signalers may either maintain a plastic response by varying their

amplitude according to the perceived eavesdropping pressure, or they may become canalized and always produces certain signals at low amplitudes.

Costs incurred from eavesdroppers

Focusing first on potential costs incurred from eavesdropping by predators, evidence from multiple species of songbirds has indicated that a direct cost is incurred from eavesdropping predators when offspring in the nest call to their parents at higher rates (Haff & Magrath, 2011; Haskell, 1994). In addition, the offspring of species that experience higher predation rates produce begging calls at lower amplitudes and higher frequencies (Briskie, Martin, & Martin, 1999). A similar dynamic occurs in multiple species of moths, which produce ultrasonic courtship songs and are preyed upon by bats that have the ability to perceive ultrasonic signals (Nakano et al., 2009). In many of these species, males produce courtship songs at very low amplitudes, which limits the signal's active space to a few centimeters (Nakano et al., 2008; Nakano et al., 2009). These data suggest that predation pressure of a sufficient magnitude can drive the evolution of low-amplitude signaling, and can even lead to the total loss of acoustic signals (Zuk, Rotenberry, & Tinghitella, 2006).

Although predation pressure appears to select for the production of low-amplitude signals under certain conditions, the presence of predators alone is insufficient to explain low-amplitude signaling across all behavioural contexts. For example, the production of low-amplitude signals during aggressive interactions may decrease the likelihood that a predator will be attracted to the area during a period of decreased vigilance, but the only study to empirically test this hypothesis failed to find any relationship between a perceived predator presence and the production of low-amplitude signals: male song sparrows that heard conspecific alarm calls during a territorial

intrusion actually sang fewer low-amplitude songs than they did during intrusions that lacked any simulated risk of predation (Searcy & Nowicki, 2006). More research is needed to determine the role of predation pressure in modulating signaling strategies during social interactions when vigilance is reduced, and future studies would benefit from employing more sophisticated predator stimuli such as taxidermic mounts in addition to conspecific alarm signals.

The potential fitness cost associated with attracting an eavesdropping predator is obvious (i.e., death), but the costs incurred from conspecific eavesdroppers can be more complicated. In some dyadic interactions such as courtship, the cost of producing high-amplitude signals appears to be clear as attracting other male competitors can directly result in reduced mating success (Balsby & Dabelsteen, 2005; Stoltz & Andrade, 2010). However, in dyadic agonistic interactions, individuals may actually increase their fitness by broadly advertising the interaction if they are dominant over their competitor (Mennill, Ratcliffe, & Boag, 2002; Otter et al., 1999; Zuk & Simmons, 1997). At the same time, the individual may also pay a fitness cost by broadly advertising a temporary decrease in vigilance over their mate or territory (Naguib, Amrhein, & Kunc, 2004) or by transmitting information that competitors may use in future interactions (Mennill & Ratcliffe, 2004; Naguib & Todt, 1997; Peake, Matessi, McGregor, & Dabelsteen, 2005). Whether these potential costs of conspecific eavesdroppers are strong enough to select for low-amplitude signaling has largely remained untested, and these costs are likely to vary according to species, population density, mating system, sex ratio, and other factors (Reichard et al., 2011). For example, in species where the population density is high and signalers actively engage in mate guarding, we would predict increased production of low-amplitude signals during both courtship and aggressive interactions.

Two studies in songbirds have empirically tested the responses and potential costs of conspecific eavesdroppers across different social contexts where low-amplitude signals are produced. In one study, free-living male whitethroats, which produce a low amplitude courtship song, were induced to court a decoy female and then separately respond to a song playback simulating an intruding male (Balsby & Dabelsteen, 2005). Neighbors of the focal males intruded onto the focal male's territory only during the simulated courtship interaction, never during the simulated aggressive interaction, which supports a cost from eavesdroppers of broadly advertising a courtship interaction. The second study, in free-living song sparrows, compared the number of neighboring males that intruded onto a focal male's territory in response to a simulated aggressive vocal interaction consisting of only loud songs and an interaction consisting of both soft and loud songs (Searcy & Nowicki, 2006). Contrary to the predictions of the eavesdropping avoidance hypothesis, neighboring males intruded more frequently in response to the interactions that contained soft songs, suggesting that low-amplitude signaling may actually promote intrusions from eavesdroppers under certain conditions rather than deter them.

Collectively, pressure from eavesdroppers fails to explain low-amplitude signaling in all contexts. There is currently greater empirical support for the role of eavesdropping predators than for that of eavesdropping conspecifics in driving the evolution of low-amplitude signals. However, empirical tests have thus far been limited to a few types of social interactions and more research is needed, particularly in non-avian taxa. It is also important to note that eavesdropping by predators and conspecifics are not mutually exclusive selective pressures, as signalers will frequently experience pressure from both types of eavesdroppers simultaneously. For example, when courting females, male moths likely benefit from producing low-amplitude songs by limiting their interactions with both predatory and conspecific eavesdroppers (Nakano

et al., 2009). Future tests of the eavesdropping avoidance hypothesis would benefit from considering both of these alternatives.

Are low-amplitude signals more difficult to detect?

To avoid costs associated with unwanted eavesdroppers, signalers should produce signals that are difficult for eavesdroppers to detect, but are still detectable by their intended receivers. Thus, signalers are constrained in their signal design by the perceptual abilities and behaviors of both types of receivers. Evidence from signal detection theory has shown that signalers can reduce the detectability of their signals by (1) decreasing the amplitude, (2) decreasing the signal's contrast with other sounds in the environment (e.g., noise), (3) decreasing the signal's stereotypy or redundancy, and (4) decreasing the likelihood that the receiver will encounter the signal (e.g., by signaling unpredictably from a variety of locations; Wiley 1983; 1994). As noted above, we find many examples of low-amplitude signals that are more variable and less stereotyped than the high-amplitude signals in a species' repertoire, consistent with the predictions for decreased detectability. In addition, most low-amplitude signals are not repeatedly produced at reliable times or locations like the high-amplitude broadcast songs of territorial species (Wiley 1994), which will further limit detectability.

Producing sounds that attenuate more rapidly will decrease a signal's active space making detectability challenging for distant receivers but still possible for those in close proximity. How rapidly signals attenuate is the result of a complex process that involves energy loss due to spherical spreading, atmospheric absorption, scattering, and interactions with the ground (Naguib and Wiley 2001; Wiley 1994; Wiley and Richards 1982). Signals produced at ground level, for example, will result in a rapid attenuation of all frequencies above 500 Hz

(Embleton et al. 1976). When signaling above the ground (i.e., > 1 m), higher frequencies will attenuate faster than most low frequencies (Wiley and Richards 1982), and high frequencies are also more directional such that they can be beamed to a specific receiver (Larsen and Dabelsteen, 1990; Patricelli et al. 2007). There are many examples of low-amplitude signals that consist only of high frequency elements, such as nestling begging calls, adult contact calls, and the ultrasonic frequencies produced by some insects and mammals. In these cases, the higher frequency elements are predicted to attenuate more rapidly, thereby further decreasing the signal's active space and likelihood of detection beyond a nearby receiver.

To date, three studies have empirically tested the transmission efficacy of both the high- and low amplitude vocalizations of three different avian species that each exhibit discrete structural differences among the two signal classes (Balsby, Dabelsteen, & Pedersen, 2003; Dabelsteen, Larsen, & Pedersen, 1993; Røk, 2013). In all cases, there was some evidence that the low-amplitude vocalizations, which had equal or greater note variability, degraded more rapidly than the high-amplitude vocalizations. However, these tests are limited in interpretive power because they relied on the ability of a microphone to record each signal at varying distances rather than directly testing the abilities of receivers to perceive and respond to each signal. Direct tests of the auditory capabilities of receivers are essential for determining a signal's active space. In addition, comparisons of the responses of potential eavesdroppers to both high and low-amplitude signals would offer a strong test of whether low-amplitude signals are indeed less likely to attract eavesdroppers.

Does eavesdropping pressure predict low-amplitude signaling?

Our third prediction that the occurrence of low-amplitude signaling should relate to the amount of pressure from eavesdroppers is largely untested and relies on the assumption that low-amplitude signaling is a facultative response. To test this prediction, certain study systems may be more amenable to direct experimental manipulations of eavesdropping pressure than others. Crickets and other insect systems that can be easily maintained in captivity at different densities represent ideal systems for testing whether individuals modulate signal amplitude according to population density, sex ratio, or other ecological variables. Manipulations of predator presence could also be performed either with captive populations or in the field during natural or simulated behavioural interactions through the introduction of live predators or predator cues.

Direct comparisons of species that vary in both production of low-amplitude signals and eavesdropping pressure represent another promising avenue for future research. As an example, some avian species produce low-amplitude songs during male-male aggressive interactions, during courtship, or in both contexts. One might predict that species with low-amplitude courtship would exhibit denser breeding populations and higher extra-pair paternity, which implies greater selective pressure to avoid eavesdropping by neighboring males, especially when females are fertile. Future comparative tests with more accurate data quantifying song output, population densities, risk of paternity loss, density of predators, and the predation risk associated with acoustic signaling will serve as valuable tests of the eavesdropping avoidance hypothesis.

Reliability of low-amplitude signals

A reliable signal is one that accurately represents the intrinsic quality or state being advertised by the signaler (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). Reliable signals present a puzzle whenever there is a conflict of interest between signaler and receiver, for

example, rivals contesting a resource, or siblings competing for parental care. Such conflicts lead to selection that favors signalers that cheat or bluff in order to manipulate receivers to their own advantage (Dawkins & Krebs, 1978). Despite this expected selection for dishonesty in signaling, signals are reliable enough of the time that both signalers and receivers benefit from the communication system (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005).

Two general mechanisms hypothesized to explain reliability in acoustic signals are production costs and physical constraints (reviewed in Hurd & Enquist, 2005; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Vehrencamp, 2000). Production costs act as “handicaps” that make bluffing too costly for lower-quality signalers. Under this mechanism all individuals are physically able to produce the signal, but only those of higher quality can bear the associated costs (Zahavi 1975, 1977; Grafen 1990). Physical constraints arise from a link between some signal feature and some physical characteristic of the signaler. These “index” signals cannot be faked or exaggerated by lower-quality individuals because they are physically constrained from doing so (Maynard Smith and Harper 2003).

In addition to the costs imposed by eavesdroppers as previously discussed, high-amplitude signals can impose energetic costs, such as the advertisement calls of insects and anurans (Prestwich 1994), or developmental costs, such as those involved with bird song learning (Nowicki et al. 2002). Many low-amplitude signals appear to escape these costs, especially when the low-amplitude signal is structurally similar to a high-amplitude signal. For example, it is unlikely that these signals are more energetically costly to produce. To generate variation in amplitude, organisms must change the amount of pressure applied by muscle contractions near the sound source, lungs, or air sacs (Ewing, 1989; Fletcher, 1992; Suthers, Goller, & Pytte, 1999). Consequently, reducing a signal’s amplitude will require weaker muscle

contractions and should be less energetically costly for the signaler. In songbirds, the metabolic costs associated with vocal production are thought to be minimal even at high amplitudes (Oberweger & Goller, 2001; Zollinger, Goller, & Brumm, 2011), but it seems clear that reducing a signal's amplitude will reduce its production cost somewhat (Zollinger & Brumm, 2015; Zollinger et al., 2011).

A well-studied example of low-amplitude signals for which production costs seem not to apply is the soft songs and calls given in agonistic contexts in birds (see Akçay et al., 2015, in this issue). In song sparrows (Akçay, Tom, Holmes, Campbell, & Beecher, 2011; Searcy et al., 2006; Templeton, Akçay, Campbell, & Beecher, 2012), swamp sparrows (*Melospiza georgiana*; Ballentine et al. 2008), black-throated blue warblers (*Setophaga caerulescens*; Hof & Hazlett 2010), brownish-flanked bush warblers (*Cettia fortipes*; Xia, Liu, Alström, Wu, & Zhang 2013), and corn crakes (Ręk & Osiejuk, 2011), the number of soft songs/calls given by the signaler reliably signals the likelihood that the signaler will attack its opponent. Production and developmental costs seem unlikely to apply to aggressive soft song; instead, the evidence to date supports the idea that reliability is maintained by a receiver-dependent social cost (Anderson, Searcy, Hughes, & Nowicki, 2012; Molles & Vehrencamp, 2001; Ręk & Osiejuk, 2011; Templeton et al., 2012; Xia, Liu, Alström, Wu, & Zhang, 2013). The use of soft song as a bluff is inhibited by the possibility that the signal will elicit a strong aggressive response from receivers, a response that is particularly costly to weak signalers (Enquist, 1985; Hurd, 1997; Maynard Smith & Harper, 1988). Beyond songbirds, receiver-dependent costs could apply broadly to low-amplitude signals, especially those used during aggressive interactions.

As previously noted, the low-amplitude signals of many species contain broader frequency ranges and greater note variability than the species' high-amplitude signals. Increases

in signal complexity may impose additional developmental, maintenance and energetic costs. In support of this hypothesis, some cricket species have exhibited increased metabolic costs when producing a more variable, low-amplitude signal. For example, male Mediterranean field crickets (*Gryllus bimaculatus*) exhibit higher levels of haemolymph lactate, a product of costly anaerobic respiration, after producing a low-amplitude courtship song (Mowles, 2014). These data suggest that there is an energetic cost associated with the low-amplitude song, but this study lacks a comparison to the high-amplitude calling song. In the house cricket (*Acheta domestica*), a male's oxygen consumption is 2.5 times higher when producing low-amplitude courtship song than when producing high-amplitude calling song (Hack, 1998). However, males also produce a visual courtship display (i.e., rocking back and forth in place) that may account for some of the increased respiration. Despite a potential increased energetic cost of low-amplitude signaling in crickets, studies that have tried to link courtship song production to metrics of male quality such as body condition (Gray & Eckhardt, 2001; Wagner & Reiser, 2000) or immunity (Simmons, Tinghitella, & Zuk, 2010) have largely yielded mixed results (see Balenger, 2015 in this issue for a review), so more research is needed.

Finally, the increased complexity of many low-amplitude signals raises the possibility that these are index signals that reveal the physical qualities of the signaler. For example, producing complex signals requires more sophisticated muscle control (Suthers et al., 1999), which could make some low-amplitude signals more challenging to produce. Thus, acoustically complex low-amplitude signals may provide reliable indicators of the signaler's fighting ability or quality as a potential mate, as is seen with some high-amplitude signals (e.g., Ballentine 2009). In addition, low-amplitude signals can encompass a wider frequency range than the species' high-amplitude signals (e.g., Anderson et al. 2008; Titus 1998), thus some animals are

capable of producing sounds at higher and lower frequencies than is revealed by their high-amplitude repertoire. These broader frequency ranges may more accurately reflect each individual's physical limit, making some low-amplitude signals a more reliable indicator of body size or some other physical trait. For example, in oscine songbirds, the link between body size and minimum frequency of high-amplitude songs has been inconsistent within species, but strong across species where larger differences in body size exist (reviewed in Cardoso et al. 2008). Examining the minimum frequencies of low-amplitude songs might reveal a more reliable relationship within species between body size and song frequency. In general, more research is needed across taxa to further elucidate the production costs and constraints underlying acoustic signaling at different amplitudes, and the relationships between low-amplitude signal production and aspects of signaler quality.

Autocommunication

Under certain conditions, the function of low-amplitude signals may be autocommunication or self-stimulation rather than true communication with another individual (Cheng, 1992). A well established example of this phenomenon occurs in female ring doves (*Streptopelia risoria*), which produce a “coo” vocalization that is more effective at altering the singing female’s circulating hormone levels and promoting follicle development than male courtship displays (Cheng, 1992; Cheng, 1986). Domestic cats (*Felis catus*) produce a low amplitude purr during certain stressful situations such as after an injury, which may act to soothe the signaler (Peters, 2002). There is also evidence that male song production in birds may feedback positively on an individual’s endocrine system (Brockway, 1967; reviewed in Cheng, 1992), which raises the possibility that the low-amplitude signals produced during aggressive

interactions, for example, may facilitate the signaler's physiological response to the aggressive interaction (Wingfield, Hegner, Dufty, & Ball, 1990). In general, autocommunication represents an intriguing but often overlooked explanation for why animals produce acoustic signals, particularly when those signals are low amplitude and only heard by the signaler and a small number of potential receivers.

CONCLUSIONS AND FUTURE DIRECTIONS

Our primary aim for this review has been to demonstrate that low-amplitude signaling is a common method of communication across a broad taxonomic scale and that low-amplitude signals are produced in a variety of social contexts directly related to fitness. In some cases, these signals are simply whispered versions of typical high-amplitude signals, but there are also many examples of low-amplitude signals that differ in structure from any high-amplitude signal. Clearly, considering only the conspicuous, high-amplitude signals in a species' acoustic repertoire presents an incomplete picture of the signaling strategies present in the system.

To date, studies of low-amplitude signals in songbirds and insects have provided a strong foundation for research on low-amplitude signaling as a whole. More studies documenting the production, perception and function of these signals in other taxonomic groups are now essential. Amphibians and fish produce acoustic signals during courtship and competition, but the few studies on low-amplitude signaling in these groups have been purely descriptive (Table 1). These groups are also intriguing because they inhabit aquatic environments, which introduce different transmission constraints and ecological variables that are typically not considered when studying terrestrial species.

A persistent barrier to research on low-amplitude signals has been challenges associated with observing and recording these signals. The small active space of low-amplitude signals requires the microphone to be in close proximity to the signaler in order to collect data, and some of these signals are produced at ultrasonic frequencies, which are inaudible to humans. However, recent advances in recording technology and methodological approaches have made these signals more accessible than ever before. Researchers have begun simulating social interactions near a stationary shotgun or omnidirectional microphone to collect high-quality recordings of low-amplitude signals (Anderson et al. 2008, Nakano et al. 2006, Reichard et al. 2011, Zuk et al. 2008; Table 1). In addition, radio-transmitters containing tiny, on-board microphones have been developed and attached to songbirds (Illes, 2015). The transmitter method is potentially powerful in that the microphone will remain in close proximity to the signaler while allowing us to observe and record the production of low-amplitude signals under free-living conditions. Finally, microphone array networks have proven effective at remote sensing, and this technology is becoming increasingly portable and affordable (Mennill, Battiston, Wilson, Foote, & Doucet, 2012). Microphone arrays of sufficient density and sensitivity hold promise as a method for recording low-amplitude signals in the field.

Low-amplitude signal structure

Despite advances in recording technology, there are still very few quantitative studies of differences in the acoustic structure between high- and low-amplitude songs. There are also limited studies that include measures of absolute amplitude, so we often lack essential data for calculating the active space of these signals. Quantifying amplitude is particularly challenging because measurements will change anytime the distance between the subject and the microphone

shifts, and objects between the signaler and microphone can introduce frequency-dependent attenuation (Cardoso & Atwell, 2012; Zollinger, Podos, Nemeth, Goller, & Brumm, 2012). In addition, the accurate measurement of absolute amplitudes also requires the use of a properly calibrated microphone. Researchers have overcome these constraints by collecting recordings from captive animals under controlled conditions (e.g., Brumm 2009) or enticing animals to signal from a specific location in the field (e.g., Nemeth, Kempenaers, Matessi, & Brumm, 2012; Patricelli, Dantzker, & Bradbury, 2007). There is also potential for radio-transmitters to provide a reliable source for amplitude measurements given that the microphone is at a fixed distance from the sound source.

Quantifying amplitude and other aspects of acoustic structure of both high- and low-amplitude signals has the potential to provide novel insights into the production tradeoffs associated with acoustic signaling. There are three major components of acoustic signals that signalers can vary: frequency (spectral complexity), tempo (rate), and amplitude. Thus far, researchers have focused almost exclusively on tradeoffs between spectral and temporal characteristics and how those constraints relate to signal content and fitness. A well-studied example of this tradeoff occurs between frequency bandwidth and trill rate in the trilled components of some bird songs (Podos 1997).

Amplitude is also known to tradeoff with aspects of acoustic structure, with a classic example being the positive relationship between frequency and amplitude associated with the Lombard Effect (Brumm and Zollinger 2011). Evidence from multiple species of songbirds also suggests that a tradeoff might exist between amplitude and other aspects of signal structure (Cardoso 2010). As an example, Cardoso and Mota (2009) found that across 19 bird species in the genus *Serinus*, composite syllables that contained more elements were consistently produced

at lower amplitudes, which suggests a potential tradeoff between syllable complexity and amplitude. Continuing this line of inquiry with additional species, particularly non-avian species, will provide deeper insights into the mechanistic explanations for the production of different types of sounds at high and low amplitudes and a clearer understanding of how these tradeoffs might act as reliable signals of quality. Direct comparisons between high- and low-amplitude signals in particular, which can vary widely in both amplitude and structural complexity, represent a promising model for investigating these questions.

Low-amplitude signal function

A complete test of the function of any signal must include documenting the social contexts in which the signal is produced to examine potential functions from the perspective of the signaler, and also testing the responses of potential receivers to verify the signal's saliency (Searcy & Beecher, 2009). However, most published examples of low-amplitude signals are composed solely of observations of the social context in which the signal was produced (Table 1). More complete studies of low-amplitude signal function that include tests of receiver response are essential to facilitate comparative analyses of the selective forces underlying the evolution of low-amplitude signals.

As an example of such an analysis, comparative studies investigating potential links between the acoustic repertoire size and fitness of songbirds have yielded somewhat mixed results (Byers and Kroodsma 2009; Seary and Nowicki 2005). However, these studies focused exclusively on high-amplitude songs that function in mate attraction, and did not consider low-amplitude songs that function in directed courtship. The inclusion of low-amplitude songs would provide a more complete analysis of the acoustic signals that function in mate choice, and likely

provide greater variation in repertoire size between individuals. For example, the high-amplitude repertoire size of male dark-eyed juncos ranges from 1-3 syllable types per male while the low-amplitude courtship song repertoire contains 17-27 syllable types per male (Titus 1998). Thus, there is clear potential for greater explanatory power with respect to how acoustic signals affect fitness when both high- and low-amplitude signals are considered.

In the context of sexual selection, acoustic signals can be shaped by both inter- and intrasexual selection, which may not always act in the same direction (Price 2013). This potential conflict has two possible evolutionary outcomes: (1) individuals may produce a single signal that functions in both inter- and intrasexual contexts and may be suboptimal for both or (2) multiple signal types may evolve to serve a specific function in each context (Collins 2004). High-amplitude broadcast signals, which often serve a dual function in attracting mates and repelling rivals, make it challenging to separate the relative effects of inter- and intrasexual selection (Spector 1992; but see Beebee 2004). Some low-amplitude signals, however, appear to serve specific functions in either courtship or aggressive behavior, thereby facilitating a more direct analysis of how sexual selection affects the structure of acoustic signals in these different contexts. Such analyses may provide novel insights into why certain low-amplitude signals are divergent in structure from the high-amplitude signals in a species repertoire. A complete understanding of the function of all low-amplitude signals in a species' repertoire is essential for pursuing this line of inquiry.

Deception with low-amplitude signals?

Once the function of a low-amplitude signal is identified it then follows to ask: is the signal reliable? If so, what mechanism maintains signal reliability? In the case of aggressive low-amplitude signals the mechanism is often a receiver-dependent social cost, but other possibilities exist and are likely to differ in other social contexts. An important area of future work is to identify the mechanisms, whether they are costs or constraints, which establish reliable signaling with low-amplitude sounds. The greater complexity or variability of some species' low-amplitude signals suggests the possibility that they are costly to produce, or may be performance or index signals, but tests of this idea are lacking. In addition, possibilities for deception using low-amplitude signals could be explored using the patterns and predictions of signal detection theory and the use of acoustic features in judging distance to the signaler, referred to as ranging, by receivers (Wiley, 1994; Naguib & Wiley, 2001). In cases where signalers benefit from misrepresenting their proximity to a receiver, deceptive ranging signals may evolve. This possibility seems most relevant to evading eavesdroppers in which case it benefits a signaler to provide ambiguous information about its location to predators or to conspecifics with conflicting interests. It is less clear why selection would favor this form of deception in close-range courtship or agonistic interactions, especially when signaler and receiver are in visual range, which renders acoustic ranging cues less important (Naguib & Wiley 2001).

Final thoughts: why signal softly?

Collectively, we have made limited progress in understanding why selection has so often favored low-amplitude communication. In some respects, this lack of progress is unsurprising because there is unlikely to be a single selective force that explains the evolution of these signals

617 across social contexts, just as we do not find a cohesive framework to explain the phenomenon
618 of high-amplitude signaling. However, there is reason to expect that the selective pressures
619 favoring low-amplitude signals are not identical to those favoring high-amplitude signals, and
620 the eavesdropping avoidance hypothesis provides a promising framework for future research on
621 this topic.

622 For selection to favor low-amplitude signaling under the eavesdropping avoidance
623 hypothesis, the benefits of evading eavesdroppers must outweigh the costs of reduced
624 communication with conspecifics. The benefits associated with eavesdropping avoidance seem
625 clear, but the potential costs of reduced communication with mates, competitors, or group
626 members should be explored. An additional prediction of the eavesdropping avoidance
627 hypothesis is that low-amplitude signals should possess other acoustic features besides low
628 amplitude that are adapted for decreasing the active space of the signal (Dabelsteen et al. 2005).
629 A few tests in birds support this prediction, but additional tests are needed in more species. More
630 direct tests of the eavesdropping avoidance hypothesis would compare the responses of potential
631 eavesdroppers to both high and low-amplitude signals to test the prediction that low-amplitude
632 signals are indeed less likely to attract eavesdroppers. Ultimately, understanding how selection
633 has acted through the environment, predation, sexual selection, and/or physical constraints to
634 produce low-amplitude signaling systems provides an intriguing new arena for studying how
635 animal behaviour evolves.

636
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638

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1086

1087 Figure 1.

1088 Sonograms showing examples of high- and low-amplitude signals given by songbirds and

1089 crickets. The bottom panel for each species shows signals with acoustically distinct structure that

1090 are produced only at low amplitude. Note that axes are different between bird and cricket

1091 examples. Sonograms of low-amplitude signals have been darkened to make their acoustic

1092 structure more visible.

song sparrow *M. melodia*

dark-eyed junco *J. hyemalis*

Pacific field cricket *T. oceanicus*

California field cricket *G. integer*

Table 1. Selected examples of low-amplitude signaling across five taxonomic classes. Behavioural contexts were assigned according to data or observations in the associated citations. Low-amplitude signals may function in other contexts for each species but have yet to be documented. The behavioural context data do not reflect tests of signal function in most cases. This table is not exhaustive and represents only a small sample of the low-amplitude signaling that occurs in each of these classes.

Class	Scientific Name	Behavioural Context					Citations
		Male-Male	Male-Female	Group	Parent-Offspring	Predation	
Actinopterygii	<i>Hippocampus reidi</i>		X				Oliveira et al. 2014
	<i>Porichthys notatus</i>		X				Brantley and Bass 1994
	<i>Parablennius parvicornis</i>		X				De Jong et al. 2007
	<i>Trichopsis vittata</i>		X				Ladich 2007
	<i>Pempheris adspersa</i>			X			Radford et al. 2015
	<i>Pomacentrus partitus</i>		X				Kenyon 1994
	<i>Macropodus opercularis</i>	X					Bishcof 1996
	<i>Astatotilapia burtoni</i>		X				Maruska et al 2012
	<i>Metriaclima zebra</i>	X					Bertucci et al. 2010
	<i>Pseudotropheus zebra</i>	X	X				Simões et al. 2008a, b
	<i>Pseudotropheus emmiltos</i>		X				Simões et al. 2008b
	<i>Pseudotropheus fainzilberi</i>		X				Simões et al. 2008b
Amphibia	<i>Leptopelis viridis</i>	X					Grafe et al. 2000
	<i>Rana italica</i> ¹						Razzetti et al. 2006
	<i>Colostethus beebei</i>		X				Bourne et al. 2001
	<i>Dendrobates speciosus</i>		X				Jungfer 1985
	<i>Nectophrynoides asperginis</i>	X	X				Arch et al. 2011
Aves ²	<i>Melospiza melodia</i>	X					Anderson et al. 2007
	<i>Melospiza georgiana</i>	X					Ballentine et al. 2008
	<i>Junco hyemalis</i>	X	X				Reichard et al. 2013; Titus 1998
	<i>Sylvia communis</i>		X				Balsby 2000
	<i>Sylvia atricapilla</i>	X	X				Collins et al. 2009
	<i>Turdus merula</i>	X	X				Dabelsteen 2005

	<i>Turdus cardis</i>		X		X	Ishizuka 2009
	<i>Catharus fuscescens</i>	X				Belinsky et al. 2015
	<i>Anthus petrosus</i>			X		Elfström 1992
	<i>Setophaga caerulescens</i>	X				Hof and Hazlett 2010
	<i>Geothlypis trichasi</i>		X			Ritchison 1995
	<i>Cettia fortipes</i>	X				Xia et al. 2013
	<i>Gerygone igata</i>				X	Anderson et al. 2010
	<i>Troglodytes aedon</i>		X			Johnson and Kermott 1991
	<i>Turdoides bicolor</i>			X		Radford and Ridley 2008
	<i>Aegithalos caudatus</i>			X		Sharp and Hatchwell 2005
	<i>Crex crex</i>	X	X			Ręk and Osiejuk, 2011
Insecta ³	<i>Acheta spp.</i>		X			Alexander 1961
	<i>Miogryllus spp.</i>		X			Alexander 1961
	<i>Gryllodes spp.</i>		X			Alexander 1961
	<i>Nemobius spp.</i>		X			Alexander 1961
	<i>Gryllus spp.</i>		X			Alexander 1961
	<i>Anurogryllus spp.</i>		X			Alexander 1961
	<i>Scapsipedus spp.</i>		X			Alexander 1961
	<i>Teleogryllus oceanius</i>		X			Zuk et al. 2008
	<i>Spodoptera litura</i>		X			Nakano et al. 2009
	<i>Herminia tarsicrinalis</i>		X			Nakano et al. 2009
	<i>Spilosoma punctarium</i>		X			Nakano et al. 2009
	<i>Eilema japonica</i>		X			Nakano et al. 2009
	<i>Ascotis selenaria</i>		X			Nakano et al. 2009
	<i>Chilo suppressalis</i>		X			Nakano et al. 2009
	<i>Glyphodes pyloalis</i>		X			Nakano et al. 2009
	<i>Palpita nigropunctalis</i>		X			Nakano et al. 2009
	<i>Spoladea recurvalis</i>		X			Nakano et al. 2009
	<i>Ostrinia furnacalis</i>		X			Nakano et al. 2006
	<i>Tibicina haematodes</i>		X			Sueur and Aubin 2004
	<i>Tibicina tomentosa</i>		X			Sueur and Aubin 2004

	<i>Tibicina corsica</i>		X			Sueur and Aubin 2004
	<i>Tibicina quadrisignata</i>		X			Sueur and Aubin 2004
	<i>Tibicina nigronervosa</i>		X			Sueur and Aubin 2004
	<i>Tibicina garricola</i>		X			Sueur and Aubin 2004
	<i>Dendroctonus ponderosae</i>	X	X			Fleming et al. 2013
	<i>Saccolaryx bilineata</i>		X			Behr and von Helverson 2004
	<i>Suricata suricatta</i>			X		Townsend et al. 2010
	<i>Bos taurus</i>				X	Padilla de la Torre et al. 2015
	<i>Orcinus orca</i>		X			Saulitis et al. 2005
	<i>Tamiasciurus hudsonicus</i>				X	Greene and Meagher 1998
	<i>Uroditellus richardsonii</i>				X	Wilson and Hare 2004
	<i>Eutamias sonomae</i>				X	Smith 1978
	<i>Lasiopodomys mandarinus</i>		X			Rutovskaya 2011
Mammalia ⁴	<i>Theropithecus gelada</i>		X	X	X	Gustison et al. 2012
	<i>Papio ursinus</i>			X	X	Gustison et al. 2012
	<i>Macaca fascicularis</i>			X		Palombit 1992
	<i>Chlorocebus pygerythrus</i>				X	Seyfarth et al. 1980
	<i>Callicebus nigrifrons</i>				X	Casar et al. 2012
	<i>Cebus capucinus</i>			X		Boinski and Campbell 1996
	<i>Lemur catta</i>	X		X		Bolt 2014
	<i>Saguinus oedipus</i>				X	Morrison and Reiss 2013
	<i>Gorilla beringei</i>		X	X	X	Hedwig et al. 2014
	<i>Gorilla gorilla</i>		X	X	X	Hedwig et al. 2014

¹The behavioural context is unknown for this species.

²See Reichard and Welklin (2015) for a review of the putative functions of low-amplitude signals in North American birds.

³See Balenger (2015, in this issue) for a review of low-amplitude signaling in crickets and moths.

⁴See Gustison and Townsend (2015, in this issue) for a review of low-amplitude signaling in mammals.