

Chapter 2

To Shout or to Whisper? Strategies for Encoding Public and Private Information in Sound Signals



Ole Naesbye Larsen

Abstract To make sound communication public or private is a question of making the active space of the emitted sound signals large or small. A sender can only encode the sound signals within the parameter space defined by its own anatomy and physiology but, in addition, it may choose acoustic behaviors that will help to increase or decrease the active space. Both signal encoding and behavioral choices are limited by the acoustical properties of the noisy environment that changes the propagating sound signal. To make the sound signals public by increasing the size of the active space, the sender must try to overcome the limitations of the environment, whereas to make the sound signals private the sender could make use of these limitations to reduce the size of the active space. Signal encoding is also limited by the auditory physiology of the receiver whose auditory sensitivity and critical ratio relative to the ambient sound level determine the distance, over which a sound signal can be received. The best documented and most important parameter for changing the size of the active space is the source level of the emitted sound, which may be divided into high-amplitude broadcast sounds and low-amplitude soft sounds. In addition, sound signal frequency parameters may help to improve reception of public sound signals and to reduce reception of private signals, whereas other potential active space regulating parameters such as signal duration only follow predictions for some species.

2.1 Introduction

Our own experience and common sense tell us that there are good reasons for keeping some conversation private whereas other types of vocal communication such as warning signals must be public. A vocalizing male songbird may also face conflicting demands as loud public singing on one hand may give away its position

O. N. Larsen (✉)

Department of Biology, University of Southern Denmark, Odense, Denmark

e-mail: onl@biology.sdu.dk

© Springer Nature Switzerland AG 2020

T. Aubin, N. Mathevon (eds.), *Coding Strategies in Vertebrate Acoustic Communication*, Animal Signals and Communication 7,

https://doi.org/10.1007/978-3-030-39200-0_2

to listening predators and parasites but on the other hand, in the fitness context, loud signals are worth the risk by attracting willing females and keeping away conspecific competitors from its territory. Once the male is face to face with a soliciting female or an aggressive competitor, however, loud singing or calling may no more be the best communication strategy.

Classic studies on avian sound communication have focused on adaptations evolved to maximize the area or space, over which a song or call can be heard and interpreted by conspecific listeners above the ambient noise of their habitat (Chappuis 1971; Morton 1975; Marten and Marler 1977; Henwood and Fabrick 1979; Dooling 1982; Brenowitz 1982; Wiley and Richards 1978; Ryan and Brenowitz 1985; Dabelsteen et al. 1993; Klump 1996; Aubin and Jouventin 1998). Especially the “acoustic adaptation hypothesis” proposed by Morton (1975, 1986) has received much attention (Boncoraglio and Saino 2007; Ey and Fischer 2009). It postulates that animals’ acoustic signals have been shaped by selection pressures exerted by the acoustic properties of their habitats leading to microevolutionary changes. The acoustic signals of a given species consequently are confined within a certain parameter space or “room for variation” that can only change over evolutionary time (Dabelsteen 1985). Such classic studies have suggested, for instance, that male songbirds’ territorial proclamation song, the broadcast song, in general may be detectable by conspecifics located up to two average territory diameters away from the singer (e.g., Brenowitz 1982; Dabelsteen et al. 1993). In addition, it has become clear that focusing on the sender–receiver dyad often gives a wrong impression of sound communication in nature, where acoustic communication is better described by a network of senders and both conspecific and hetero-specific receivers (McGregor and Dabelsteen 1996).

More recently scientists have started to investigate the occurrence and function of unobtrusive low-amplitude vocalizations (McGregor and Dabelsteen 1996; Dabelsteen et al. 1998; Titus 1998; Dabelsteen 2005; Searcy and Yasukawa 2017; Vargas-Castro et al. 2017; Niederhauser et al. 2018). Whereas the former vocalizations definitely are “public,” the latter may be loosely categorized as “private.” According to the Oxford English Dictionary (Hornby et al. 1970) the adjective “private” is opposed to “public” and in general means “belonging to or for the use of one particular person or group of people only.” In the present context, “private” may then be defined as “sound communication involving only a particular pair or group of individuals and dealing with matters that are not to be disclosed to others.”

In theory there are at least two ways for a sender to produce a private sound signal: (1) to “encrypt the message” of the sound signal such that, although many neighboring animals will be able to hear the sound signal, only receivers who possess the encryption key can decode its message; (2) to ensure that the message is impossible to detect and decode beyond a certain distance from the sender. The former strategy is problematic for a vocalizing animal, since receivers in many cases will be able to extract information to at least localize the position of, or direction to, the sender, which may be detrimental in case of predator and parasite listeners. However, special sound signals with faint or no directional cues may overcome this problem (Marler 1955). The second strategy is more robust as no listeners beyond a

certain distance from the sender will be able to retrieve any information from the sound signal. This certain distance defines the absolute outer boundary of the so-called “active acoustic space” of a sound signal (Marten and Marler 1977; Brenowitz 1982; Wiley and Richards 1982; Ryan and Brenowitz 1985; Lohr et al. 2003).

Who are the receivers? In his famous paper, Peter Marler (1955) proposed to distinguish between intended and unintended receivers. He further proposed that sound signals have evolved not only to facilitate communication with intended receivers but also in many cases to impede information transfer to unintended receivers. First, there are the intended receivers, those with high fitness value to the sender—mate, offspring, group/family—and those who carry low or negative fitness values: known predators and conspecific competitors to resources (for mates, food, or shelter) who should be avoided or scared away. Secondly, there are the unintended receivers, most of which should not be alerted by the vocalization because of negative effects on signaler fitness such as hetero-specific predators and parasites (Zuk and Kulluru 1998) but also concealed conspecific competitors who might use the information obtained by eavesdropping on the communication between the sender and intended receivers to their own advantage in future encounters (McGregor and Dabelsteen 1996). Eavesdropping by unintended receivers, however, does not always have negative fitness value for the sender. Eavesdropping on the alarm calls of other species subjected to the same predators, for instance, may be beneficial to the sender (Marler 1955; Magrath et al. 2015).

If the sender wishes to avoid the unintended receivers, a safe strategy is somehow to reduce the active space. The “Eavesdropping Avoidance Hypothesis” states that animals actively reduce their active space to avoid unintended receivers (McGregor and Dabelsteen 1996; Searcy and Yasukawa 2017; Niederhauser et al. 2018). A small active space excludes most unintended receivers and maximizes communication with closely located intended receivers. As we shall see, animals do in fact under certain circumstances reduce their active space but so far there has been little support for the eavesdropping avoidance hypothesis as a general explanation for this behavior (Searcy and Yasukawa 2017), at least in the predator context (Akçay et al. 2016; Niederhauser et al. 2018).

In this chapter we will investigate the concept of active space and attempt to predict by which signal encoding and behavioral mechanisms a vocalizing bird could vary its active space and thus make its vocalizations public or private. We will elaborate on the properties and constraints of the three components of the communication chain: the sender, the sound signal propagating through the noisy environment, and the receivers, the network of listening individuals. Finally, we will compare the predicted coding strategies with observed coding strategies exemplified in a few case studies on presumed private and public acoustic communication.

The general findings presented here may apply to any taxon of sound communicating animals, but we limit ourselves to birds, since the subject of private–public sound communication has been discussed especially in relation to birds (for recent reviews see Dabelsteen 2005; Mathevon et al. 2008; Akçay et al. 2015; Reichard and Welklin 2015; Zollinger and Brumm 2015; Searcy and Yasukawa 2017). However,

a number of similar studies have also been performed in terrestrial mammals (for a recent review see Gustison and Townsend 2015) and a change from high-amplitude public sound signals to low-amplitude private sound signals has also been observed in fishes (e.g., “purring sounds” of croaking gourami (*Trichopsis vittata*) females; Ladich 2007), in frogs (e.g., close-range courtship calls of male golden rocket frogs (*Colostethus beebei*); Bourne et al. 2001), and in insects (e.g., courtship songs of male field crickets (*Gryllus campestris*); e.g., Huber 1955).

2.2 The Active Space of a Propagating Sound Signal

When a bird sender vocalizes in a natural noisy environment, its sound signals propagate away from the source and become softer with distance as the sound energy is distributed over a larger and larger spherical surface and reduced by additional mechanisms. A conspecific receiver located very far from the sender is not able to hear the emitted sound signal, since the signal amplitude here is below the bird’s absolute hearing threshold (and below the ambient noise level). At progressively shorter distances from the sender, the signal amplitude may be above the receiver’s absolute hearing threshold but the signal-to-noise ratio (SNR) may still be too low for detection by the listener. Only at even shorter distances will both the signal amplitude and SNR be sufficiently large for the listening bird to extract relevant information from the sender’s vocalization (Lohr et al. 2003; Dooling et al. 2009; Dooling and Blumenrath 2013; Dooling and Leek 2018).

The active space of a sound signal could then be defined in general as “the physical space surrounding a sender, within which a listening individual can extract relevant information from the sender’s sound signals and act adaptively.” As suggested by Lohr et al. (2003) it seems reasonable to expect that as a conspecific receiver approaches the sender in the natural habitat, it may be able to extract progressively more information from the sound signals. At the farthest distance, where the sound signal is just *detectable*, the receiver may be able to determine the direction to the sender but not much more. At shorter distances, the receiver may be able to *discriminate* hetero-specific from conspecific calls and discriminate between conspecific song or call types (Lohr et al. 2003) or to determine if the sound signals are produced by two or more different senders that require different responses (Wiley 2013). At progressively shorter distances, the receiver may extract more information from the signal on, for instance, the sender’s sex, identity, the messages, and the communication context (*recognition*). At the closest ranges, receivers may be able to engage in what in humans is referred to as *comfortable conversation* (Dooling et al. 2009; Dooling and Blumenrath 2013; Dooling and Leek 2018) and extract even more detailed information, for instance, on the motivational state of the sender. These four broad perceptual categories of detection, discrimination, recognition, and comfortable conversation are based on psychoacoustical measurements in the laboratory on both humans and birds and may also apply to the natural environment, where they may be interpreted as geographical “information zones”

surrounding the sender (Lohr et al. 2003; Dooling and Blumenrath 2013; Dooling and Leek 2018).

Hetero-specific receivers with different hearing ranges and sensitivities will experience different extents of the active space (measured, e.g., by its radius if circular) of a given sender's vocalization. A Eurasian sparrowhawk (*Accipiter nisus*), for instance, experiences a much smaller active space of the 8-kHz seat-alarm call of the great tit (*Parus major*) than listening great tits, which can detect the call at much longer distances than the predator (Klump et al. 1986). In general, larger birds like the sparrowhawk are less sensitive to high frequencies (have lower high-frequency cut-off in their audiograms) than smaller birds (Dooling 1992). This means that the extent of the active space is an ambiguous entity depending not only on the sender but also on the individual receiver's hearing physiology.

However, no matter what definition of active space extent is used, by varying its size a sender can potentially vary the number of possible receivers in the acoustic communication network. A very small active space with only one or a few possible receivers defines "private" communication, whereas a large active space with many potential receivers defines "public" communication. The interplay between sender, environment, and receivers constantly and dynamically determines the size and shape of the active space. The extent of the active space may then be modeled by a simple equation:

$$SL - A = RL \quad (2.1)$$

where SL is the source level at the sender, defined as the sound pressure level measured in front of the vocalizing bird on its beak's length axis and at a distance of 1 m. A is the attenuation of the signal from sender to receiver caused by geometrical and environmental factors. RL is the received level, defined as the sound pressure level of the arriving signal measured at the ears of the receiver. The receiver can only detect the signal, if RL exceeds the thresholds defined by the auditory system of the receiver, which we here refer to as "the required RL_{Det} " (see Sect. 2.3.4), relative to the ambient noise level in the frequency band of the signal.

2.3 Coding Constraints and Possibilities

How can a sound signal producing animal, a sender, then vary the size of the active space of its songs or calls? Before answering the question, we must realize that there are coding constraints imposed on the sender by its biological characteristics, by properties of the environment, through which the sound signal propagates, and by characteristics of the receiver's auditory system. So, the sender can only maximize its active space within certain limits to make it public. However, theoretically it may also take advantage of these limitations to minimize its sound signals' active space to make it private.

2.3.1 *Constraints Imposed by Sender Anatomy and Vocal Physiology*

The sender cannot vary the output volume of its vocalizations arbitrarily because it is limited by its body size, anatomy, and physiology. A vocalizing songbird, for instance, cannot increase the sound pressure amplitude beyond a certain limit, even in its peak frequency band as there is an upper limit to the subsyringeal pressure that it can produce by muscular control when forcing an airflow through the specialized valves of the syrinx (e.g., Zollinger et al. 2011; Elemans et al. 2015; Srivastava et al. 2015; Mencio et al. 2017). On the other hand, there also may be a lower limit to the SL that a bird can produce for a given song element, since the syringeal mechanism needs a certain subsyringeal air pressure to produce the self-sustained oscillation that generate the radiated sound (Goller and Larsen 1997; Jensen et al. 2007). However, to my knowledge such quantitative information on a lower limit to SL is not available in the literature.

Besides the sender's ability to produce high subsyringeal pressures within a certain frequency range, its body size sets a lower limit to the sound frequencies that it can efficiently radiate. Generally, sounds with wavelengths much longer than the head and body dimensions cannot be broadcast efficiently (for a discussion of this constraint see, e.g., Larsen and Wahlberg 2017). For many birds therefore, the vocalization frequency interval correlates negatively with body mass (and therefore with body size) on a double logarithmic scale such that larger body mass correlates with lower vocalization frequency (Fletcher 2004). A 58-kg cassowary (*Casuarius casuarius*), for instance, produces intense booming sounds with a fundamental frequency down to about 30 Hz (e.g., Mack and Jones 2003), whereas an 8-g blue-throated hummingbird (*Lampornis clemenciae*) does not produce loud sounds below about 3 kHz but its songs may contain strong harmonic components up to about 30 kHz (Pytte et al. 2004).

Within songbirds, however, there is little evidence for such an unambiguous relation between body size (or body mass) and maximum song amplitude, at least for nightingales (*Luscinia megarhynchos*) and zebra finches (Brumm 2009). However, other song parameters than amplitude may correlate with body size, for instance in tanagers (*Thraupidae*) where 9 out of 10 song parameters, especially frequency parameters, correlated with body mass (Mason and Burns 2015). Generally, birds sing their broadcast songs with higher amplitude when using higher frequency (HF) song elements than low frequency (LF) ones. This has been shown experimentally in European blackbirds (*Turdus merula*) and great tits, which increase their territorial public song amplitude in response to increase in ambient noise by switching to higher frequency song types (Nemeth et al. 2013). On the other hand, birds could theoretically use sounds with wavelengths longer than their head and body dimensions to produce soft private signals, since LF signals would not be emitted efficiently.

The sender's head size also determines the directionality of emitted sounds and can be modified by body postures as observed in the red-winged blackbird (*Agelaius*

phoeniceus) (Patricelli et al. 2008). When the head and body dimensions become large relative to the wavelength of the emitted sound, the radiation pattern (and thereby the active space) indicated by iso-pressure curves changes from circular (or omnidirectional) to more elongated (or directional) as the relative sound pressure is reduced behind the bird but remains in its frontal field (Larsen and Dabelsteen 1990; Brumm 2002; Patricelli et al. 2007, 2008). For a given HF sound signal emitted by a nonmoving bird, the active space therefore is directionally elongated but the bird may increase the size of its operational active space by frequently changing its beak direction. There is evidence that some bird species even use elongation of the active space to specifically address known predator receivers, by adjusting the directionality of their public antipredator calls with higher frequencies (Yorzinski and Patricelli 2010).

There are further limitations regarding to what extent birds can vary their active space. In the time domain birds can only vary sound signal envelopes (amplitude modulation) and frequencies (frequency modulation) up to a certain pace—even by superfast muscles, which have an inherent upper contraction “speed limit” of about 250 Hz (Mead et al. 2017). Most of these limitations are either dictated by physical laws or can only be changed over evolutionary time by anatomical or physiological adaptations.

In addition, vocalizing birds have a sometimes very large but always limited signal “library” (MacDougall-Shackleton 1997), i.e., memory of inherited or learned vocalizations, from which to choose calls or song elements with specific characteristics (e.g., LF or HF, narrow frequency band or broadband, simple or complex sounds). Finally, very complex songs require appropriate motor control skills (Podos 1997) that vary between but also within species depending on individual cognitive skills and conditions experienced during individual development (Naguib and Riebel 2014).

2.3.2 *Potential Active Space Regulation by Sender Behavior*

Over the past 20 years much research has been aimed at elucidating the effects of ambient noise on animal sound communication, especially the possible detrimental effects of man-made noise (Slabbekoorn et al. 2018). Territorial songbird songs are public and broadcast with high sound levels that seem energetically optimized (Ward et al. 2004; Zollinger et al. 2011). Studies also suggest that songbirds seek out song posts at specific heights above ground to optimize the transmission range (e.g., Lemon et al. 1981; Dabelsteen et al. 1993). So, it seems reasonable to expect that a territorial bird singing a public song should try to maintain its active space when conditions change, e.g., with increase in ambient sound. Both correlational and experimental studies suggest that birds singing such songs do in fact attempt to maintain the size of their active space by regulating their sound output in response to changes in ambient noise through different mechanisms. For instance, if the

ambient noise level increases naturally or experimentally, an avian sender automatically increases its source level.

Part of this increase is caused by a feedback mechanism, the so-called Lombard response that occurs when there is spectral overlap between signal and noise (Manabe et al. 1998; Brumm and Todt 2002; Pytte et al. 2003; Brumm and Zollinger 2011, 2013; Zollinger et al. 2011). This response does not compensate 1:1 for increased noise levels. In many cases, the Lombard response only compensates by an increase of sound pressure amplitude of 0.1–0.7 dB per dB increase in ambient noise level (Osmanski and Dooling 2009). A physiological consequence of increased signal amplitude above the normal level, however, is an increase in the emitted sound frequency pushing the song to frequency bands with less ambient noise and consequently partly compensating for “inefficient” Lombard responses (for a thorough discussion see Zollinger et al. 2012 and the abovementioned example of city-dwelling blackbirds and great tits by Nemeth et al. 2013).

Other sender responses serving to keep the size of the active space of a public song in response to temporary increases in certain frequency bands of ambient noise, includes switching to other song types that are louder and contain higher frequencies than the normal proclamation song (for a comprehensive review of these responses see Brumm and Zollinger 2013). Finally, the sender may help to keep the size of the active space by repeating its song over and over, i.e., making the sound signals highly redundant, which according to signal detection theory (so-called error correcting coding) improves detectability (Lengagne et al. 1999; Price 2013; Wiley 2013).

In the here-and-now, the sound emitting bird can also choose what, when, and where to sing or call, unless an immediate reaction is called upon by, for instance, intruders, group movements, or roosting. By carefully selecting its song posts (or singing during flight) the sender can—at least theoretically—vary (maximize or minimize) its active space as a function of habitat characteristics, such as singing height above ground in forest environments, or in response to meteorological conditions, such as wind direction in open environments (Henwood and Fabrick 1979; Dabelsteen et al. 1993; Mathevon et al. 1996, 2005; Halfwerk et al. 2012, 2018).

The sender may also vary the extent of its active space by choosing time of day and season when sound propagation characteristics differ, for instance, before or after leaf fall in deciduous forests (Blumenrath and Dabelsteen 2004), or in relation to daily variation in ambient sound levels (e.g., Henwood and Fabrick 1979; Brenowitz 1982; Brumm 2004; Fuller et al. 2007; McLaughlin and Kunc 2013), or by trying to avoid overlapping songs of simultaneously vocalizing nearby senders (Brumm and Todt 2004; Goodwin and Podos 2013; Yang et al. 2014).

Such active choices by the sender to optimize its active space are theoretically possible and have been demonstrated convincingly in many cases but mainly for keeping the signals public. However, whether singing birds on a regular basis do make behavioral choices for making their vocalizations private still needs to be determined by many more careful and comparative studies in the field.

2.3.3 Coding Constraints and Possibilities by Sound Propagation Through the Noisy Environment

The sound signal radiated from the sender is inevitably subject to change by several mechanisms during propagation through the environment. Therefore, the signal is no longer in its original form when it reaches receivers in the communication network, even after short distance propagation (Richards and Wiley 1980; Wiley and Richards 1978; Dabelsteen et al. 1993).

The most important environmental coding constraint on propagating sound signals is geometric attenuation caused by spherical spreading (see, e.g., Wahlberg and Larsen 2017; Larsen and Radford 2018). Geometric attenuation acts equally on all sound frequencies and is omnipresent. It dominates sound signal attenuation within a radius of up to about 100 m from the sender in most terrestrial environments (Fig. 2.1). Spherical attenuation in general attenuates the emitted sound as a function of distance from the sender and is measured as sound pressure level (or peak pressure) calculated from the expression $20\log_{10}(\text{distance}/\text{reference distance})$ decibel (dB) (for derivation of the expression see, e.g., Wahlberg and Larsen 2017). From this expression it is obvious that the received level (RL) at a distance r of, for instance, 100 m from a sender is 40 dB lower than the sender's SL (Fig. 2.1). From 100 m to 200 m the spherical attenuation increases by only 6 dB and at further 100-m steps by even less.

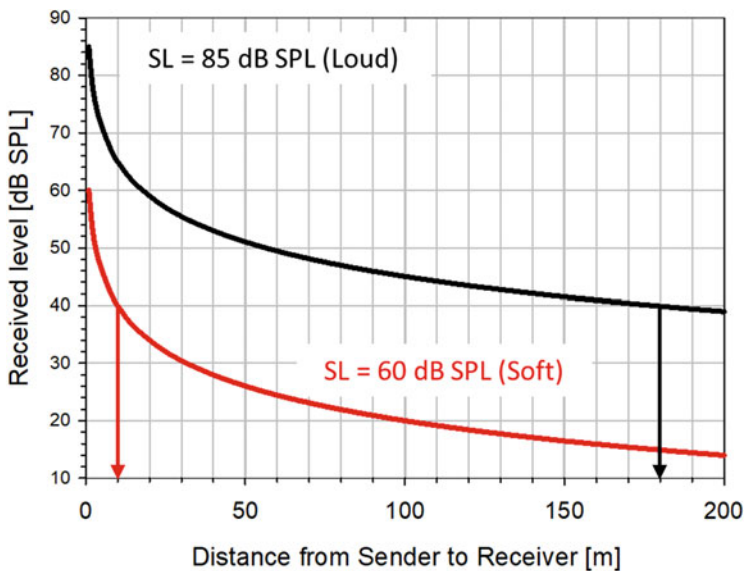


Fig. 2.1 Received level (RL) as a function of distance from a sender emitting songs or calls at two different source levels (SL), when only geometric attenuation from a point source is taken into consideration. If the receiver needs a sound level of 40 dB SPL to be able to detect the vocalization ($RL_{\text{Det}} = 40$ dB SPL), then a source level of 85 dB SPL will give a maximum detection range of 178 m, whereas a source level of 60 dB SPL gives a maximum detection range of only 10 m

Theoretically, a bird can then vary the size of the active space of its calls or songs simply by varying SL of a given sound signal. Rearranging Eq. 2.1, the relationship between SL and RL to a first approximation including only spherical attenuation in A is then:

$$RL = SL - 20 \log_{10} r/r_{\text{ref}} \quad (2.2)$$

where r is the distance from sender to the ears of the receiver and r_{ref} is the 1-m reference distance at the sender. From this equation it is easy to see that by far the most efficient way for the sender of reducing the active space to avoid unintended receivers is to lower the signal volume, i.e., reducing SL. Using Eq. 2.2 we can get a first impression of the space reduction based on geometric attenuation alone. For instance, if the sender sings or calls out with a SL of 85 dB SPL (Fig. 2.1) and if the receiver's required detection threshold is at $RL_{\text{Det}} = 40$ dB SPL in the same frequency range, then this will produce an active "detection" space with a radius of about 178 m (that covers an area of 100,000 m², if the active space to a first approximation is spherical and consequently circular on the ground). However, if the sender lowers its SL by 25 dB to 60 dB SPL, then the active space radius is reduced to 10 m (area 314 m²) at ground level. Note that the active space measured as horizontal area is reduced by a factor of about 300. These values of active space radii should be compared with recent comprehensive field studies taking into consideration all relevant factors for active spaces of broadcast song such as the study of Gall et al. (2012) reporting an active space radius range of 88–101 m for brown-headed cowbird (*Molothrus ater*) song.

Behavioral experiments in the laboratory on birds like budgerigars (*Melopsittacus undulatus*) and zebra finches (*Taeniopygia guttata*) suggest that a receiving bird needs a sound level that is 2–5 dB higher for *discrimination* than that for *detection* and a sound level that is 2–3 dB even higher for *recognition* (Lohr et al. 2003). By comparison with humans it can also be argued that *comfortable conversation* may occur at sound levels about 15 dB higher than for recognition (Dooling and Leek 2018). So, a detection threshold of, for instance, 40 dB sound pressure level (SPL), means a discrimination threshold of 42–45 dB SPL, a recognition threshold of typically 44–48 dB SPL, and a level of comfortable conversation of 59–63 dB SPL. Therefore, researchers should specify what kind of obtainable information defines the border of the active space they investigate; i.e., if the active space is defined by detection, by discrimination, by recognition, or when comfortable communication is possible. Unfortunately, this is rarely stated in the literature, where mainly detection and recognition ranges are mentioned (e.g., Brenowitz 1982; Klump 1996; Gall et al. 2012).

Since the "discrimination" threshold (RL_{Dis}) as measured in the laboratory is 2–5 dB higher than the "detection" threshold, then the "discrimination" space (Fig. 2.2) for a discrimination threshold of, e.g., 43 dB, compared to the detection threshold at 40 dB, reduces the radius of the active space from 178 m to 126 m (and covers an area of about 50,000 m²) for a source level of 85 dB SPL but to a radius of

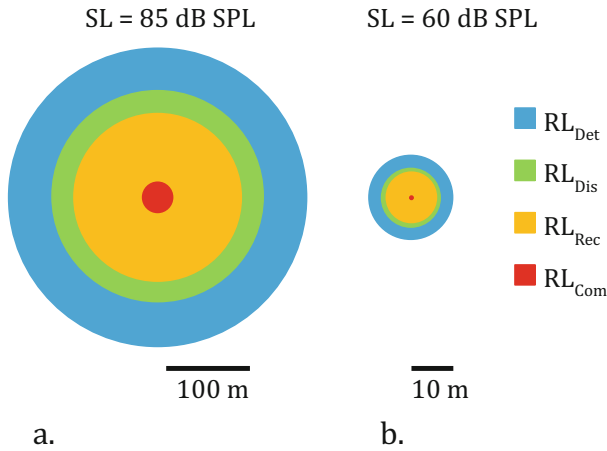


Fig. 2.2 Size of active spaces for two senders with different source levels and taking into consideration only geometric attenuation. The active space can be subdivided in four different “information zones” depending on the sound level required by the receiver for detection ($RL_{Det} = 40$ dB SPL—blue), the sound level required for discrimination ($RL_{Dis} = 43$ dB SPL—green), the sound level required for recognition ($RL_{Rec} = 45$ dB SPL—orange) and the sound level required for comfortable conversation ($RL_{Com} = 60$ dB SPL—red). (a) Sender’s source level is 85 dB SPL. (b) Sender’s source level is 60 dB SPL. Note different distance scales in (a) and (b)

7 m (area now about 160 m^2) for a source level of 60 dB corresponding to an area reduction by a factor of about 300 (Fig. 2.2).

Geometric attenuation always attenuates a propagating sound wave predictably. At longer distances, however, the measured attenuation typically deviates from the one predicted by geometric attenuation. In most environments the sound pressure level of a song or call measured at a certain distance from the sender is lower than predicted by spherical attenuation. The extra attenuation component is called Excess Attenuation (EA) and is traditionally measured in dB/m (Marten and Marler 1977). Please note, however, that some studies suggest that EA might also be measured on a logarithmic length scale, i.e., in dB/log(distance) (Dabelsteen et al. 1993) or develop in a more complicated fashion (Rek 2013).

In contrast to spherical attenuation the magnitude of EA is highly frequency (f) dependent and varies with time of day and year (t), with environment (e), and meteorological conditions (m), i.e., it could be expressed as $EA(f, t, e, m)$. After rearranging RL and SL in Eq. 2.2 and setting $r_{ref} = 1$, a second approximation of the relationship between SL and RL at a distance r (in meter) from a point source sender therefore is:

$$SL - RL = 20 \log_{10}(r) + rEA(f, t, e, m) \quad (2.3)$$

When the difference (SL – RL) is small because of SL is low or because the “required RL” is high, then the corresponding distance r and consequently the active space becomes small. In a similar fashion, when the difference (SL – RL) is large, r and the active space becomes large. It is important to point out that in contrast to geometric attenuation, which varies with distance on a logarithmic scale, EA is usually supposed to vary with distance on a linear scale (Marten and Marler 1977; Lohr et al. 2003; Langemann and Klump 2005). Knowing SL and EA and using Eq. 2.3 it is easy to calculate RL at any distance from the source. However, in the present context it is more relevant to ask at what distance r the RL has dropped to the level required for discrimination (RL_{Dis}) or recognition (RL_{Rec}). Unfortunately, there is no analytical solution for solving Eq. 2.3, but it can be solved computationally, e.g., by using the Newton–Raphson method as suggested and used by Nemeth and Brumm (2010) to calculate maximum communication distances for European blackbird and great tit songs in urban and forest habitats. The magnitude of EA as judged from transmission experiments in different environments and based on values at several distances is of the order of 0.16 dB/m for many types of bird sounds (Morton 1975; Dabelsteen et al. 1993; Holland et al. 1998; Nemeth et al. 2001; Mathevon et al. 2005; Nemeth et al. 2006) but some more recent measurements suggest EA values on the order of 0.3 dB/m (Barker et al. 2009; Sandoval et al. 2015; Piza and Sandoval 2016) or even about 0.8 dB/m (Niederhauser et al. 2018).

Excess attenuation is an umbrella term for a number of habitat-induced effects, the most predictable being frequency dependent atmospheric absorption (e.g., Attenborough 2007). Absorption is directly proportional to distance from the sender and depends not only on sound frequency but also on temperature, atmospheric pressure, and relative humidity (ISO 1993). For instance, at 20 °C and 1 atm, the atmospheric absorption attenuation varies from about 0.0002 dB/m at 100 Hz to about 0.005 dB/m at 1 kHz, whereas from 1 kHz it increases up to about 0.2 dB/m at 10 kHz (e.g., Bass et al. 1995). So, under these atmospheric conditions and at distances of up to 100 m from the sender, the absorption attenuation hardly influences sound at low frequencies (from 0.1 to 1 kHz between 0.02 and 0.5 dB) whereas at higher frequencies the attenuation becomes appreciable (between 1 and 10 kHz up to about 20 dB)—in addition to the 40 dB caused by spherical attenuation at 100 m. In general, the frequency dependence of atmospheric absorption means that sound propagation acts as a low-pass filter (Fig. 2.3), such that LF components of any sound signal dominate when received at distances far from the sender, since HF harmonics attenuate rapidly with distance (Meyer 2015).

Theoretically, a sender can vary its active space further by singing or calling when ambient temperature and humidity produce high EA (more private) or low EA (more public) and/or by using mainly HF or LF sound signals, respectively. Again, more field experiments are needed to test if birds actually do make use of these mechanisms for varying their active space.

Another mechanism of frequency-dependent attenuation that may influence the size and shape of active space is refraction. Phenomena like air turbulence, reflection, and diffraction from the ground and obstacles in the propagation path mainly

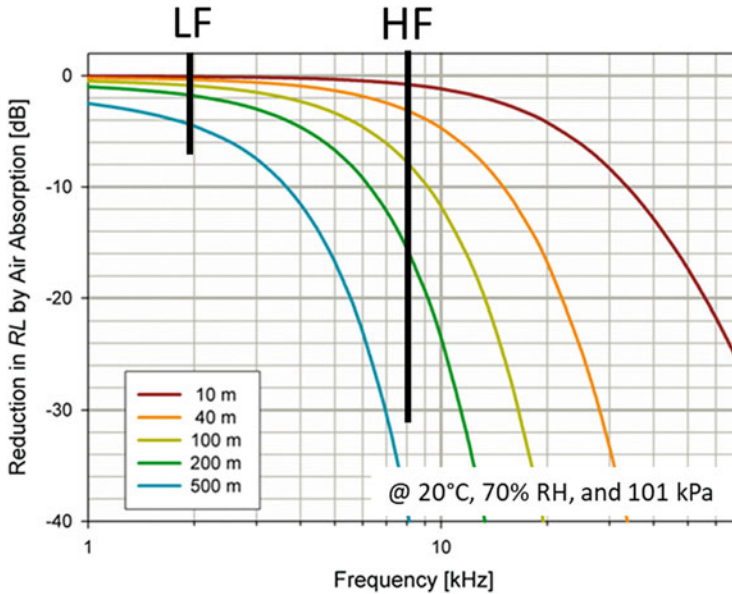


Fig. 2.3 Reduction in received level (*RL*) produced by atmospheric attenuation as a function of frequency at different distances from the sender (point source) showing the lowpass filtering caused by atmospheric absorption. This attenuation adds to the geometric attenuation at the same distances. The level of low frequency (*LF*) sound signals only get a few dB additional attenuation even at 200 m, whereas high frequency (*HF*) sound signals get a marked additional attenuation by atmospheric absorption even at 40 m. The attenuation curves were calculated for 20 °C, 101 kPa, and 70% relative humidity, using absorption values from the Web calculator at the National Physical Laboratory, UK (<http://resource.npl.co.uk/acoustics/techguides/absorption/>)

distort the envelope of the sound signals by extending their duration from echoes, filtering out certain frequency bands, or introducing variations in their amplitudes (Wiley and Richards 1978; Richards and Wiley 1980; Attenborough 2007; Wahlberg and Larsen 2017; Larsen and Radford 2018). Refraction means that the propagating sound changes direction toward regions of air with lower sound velocity and away from regions with higher sound velocity (Wiley and Richards 1978). The speed of sound (c) is mainly determined by temperature and increases with increasing temperature. Daytime air temperature is often highest close to the ground and decreases with height when the air is still, i.e., a temperature gradient is established, the so-called temperature lapse. This means that a wave front of sound propagating parallel to ground will bend skywards. In this situation, a receiver located close to the ground at a given distance from the sender will hear a fainter sound signal than when the air is more turbulent and no temperature gradient can exist. So, under these conditions the active space of the sender is reduced in the horizontal direction but increased in the vertical one. The opposite situation can occur on windless nights when the air temperature becomes lowest close to the ground and increases up to a given height above ground from where it decreases again with height; this is called

temperature inversion. Here, upwards directed wave fronts will bend back toward the ground and add by linear superposition to the sound propagating parallel to ground. During a nightly temperature inversion, which extends well into the morning, a receiver located at a given distance from the sender will consequently hear a stronger sound signal than when the sender emits the same signal at noon or in the afternoon. This means that the sender increases its horizontal active space but decreases its vertical active space if it vocalizes during nightly temperature inversions relative to the active space produced in daytime. Temperature gradients are vertical, which means that they influence sound signals equally in all horizontal directions and a circular active space remains circular when temperature gradients change.

Not only temperature gradients but also wind can produce refraction that will change the size and shape of the active space (Morton 1975; Wiley and Richards 1978, 1982; Wiley 1991; Lengagne et al. 1999). Upwind refraction induces additional attenuation and will decrease the size of the active space in the same way as during daytime temperature lapses. Downwind refraction induces reduced attenuation and will increase the active space as during nighttime temperature inversions (see also Larsen and Radford 2018). Wind by definition is directional, which means that the active space is reduced in size upwind but extended in size downwind. So, a circular active space in quiet air becomes “flatter” upwind and more elongated downwind under windy conditions (Henwood and Fabrick 1979).

Finally, the often neglected “ground effect” may comb-filter the propagating sound signal and enhance low frequency sound but attenuate higher frequencies. Including it in calculations of outdoor sound propagation predicts changes in propagating sound signals in open environments quite well (for a general introduction see Wahlberg and Larsen (2017); for a specific study on hooded crows (*Corvus corone cornix*) see Jensen et al. (2008)).

Sound signals virtually always propagate in a “sea” of ambient environmental sound consisting of well-defined localizable biotic sound sources such as roaring mammals or singing birds and an abiotic and biotic background “hum” of non-localizable distributed sources. The latter sources are, for instance, wind-induced rattling of grass in the open, where a light breeze of 4 m/s produces an ambient sound level of about 35 dB(A) (Boersma 1997) or of rattling canopy leaves in closed environments, where the same breeze may produce sound levels of 45–55 dB (A) (Fegeant 1999). Rainy conditions may produce sound levels of 50 dB(A) in forests (Miller 1978) and reduce the active space area of tawny owls (*Strix aluco*) by a factor 69 compared to dry conditions (Lengagne and Slater 2002). Chorusing frogs or insects will also increase the ambient sound level (Brumm and Slabbekoorn 2005). Especially in tropical environments intense insect sounds can totally “drown” or mask all other sounds in a frequency band of typically 5–7 kHz, which may be the reason that bird species in tropical forests sing at lower frequencies than species in open habitats such as grasslands (Ryan and Brenowitz 1985; Weir et al. 2012). In addition to natural biotic and abiotic sound sources there is nowadays in most environments also appreciable sound components generated by human activities that interfere with the abilities of animals to detect important sound signals

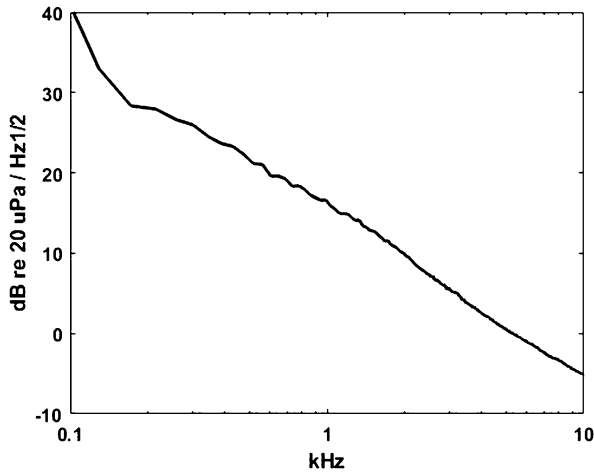


Fig. 2.4 Example of spectrum level of ambient sound as a function of frequency. Ambient sound was recorded close to a puffin rookery on Tjörnes in northern Iceland (Mooney et al. 2019). Note how the spectrum level increases markedly with lower frequencies, especially below 200 Hz and that in a dB-log(frequency) diagram the spectrum level falls off toward higher frequencies, almost as a straight line. So, spectrum levels of ambient sound are very different from the flat (horizontal) spectrum levels of white noise traditionally used in psychoacoustical studies of avian hearing. Courtesy of Adam Smith and Magnus Wahlberg

(Slabbekoorn and Ripmeester 2008; Barber et al. 2010; Francis and Barber 2013; Shannon et al. 2016; Slabbekoorn et al. 2018).

A spectral analysis of ambient sound recorded far from localized sources and where distributed sources prevail often reveals a power spectrum dominated by low frequencies and leveling off toward higher frequencies (Fig. 2.4). This is a direct consequence of the low-pass filtering by atmospheric absorption described above: at the position of the receiver LF sounds are collected and added by linear superposition from a much larger area than HF sounds. So, although LF sound signals propagate much further than HF sounds, since they are not subject to as much low-pass filtering by atmospheric absorption, they may be masked by the omnipresent LF ambient sound, which tends to decrease their active space.

Ambient sound of both biotic and abiotic origin is often referred to as “background noise” or “ambient noise.” One should note, however, that the term “noise” is a relative term and used from somebody’s perspective: what is noise to one individual may be valuable sound information to another individual. Therefore, “ambient sound” is the neutral term that should be used in most contexts. However, when dealing with the physiological mechanisms producing receiver perception the term “noise” is traditionally used to signify ambient sounds that reduce the receiver’s possibility of decoding sound signals carrying relevant information and will consequently be used here.

2.3.4 Coding Constraints Imposed by Receiver Auditory Physiology

The active space of a sound signal is determined not only by sender and the environment, through which it propagates, but also by the properties of the avian receiver's auditory physiology (Gall et al. 2012) that changes only over evolutionary time. In the absolute quiet of a laboratory sound insulated booth the so-called audiogram of a bird can be determined by psychoacoustical or by physiological methods (Dooling 1982). For each of a number of frequencies the lowest sound pressure level, the threshold value, required by the receiver to produce a statistically significant response to indicate that it has detected the test tone, is determined. For birds in general, the result is a U-shaped curve of threshold in the quiet as a function of frequency, which at threshold values below, for instance, 40 dB SPL typically extends from about 300 Hz to about 8 kHz with the lowest threshold of about 10 dB SPL at a best frequency (BF) of about 2 kHz (Dooling and Leek 2018). Big birds tend to have BF at lower frequencies, whereas small birds have BF at higher frequencies and owls are special with much lower thresholds than other birds (cf. the sparrowhawk example in Sect. 2.2).

Knowledge of the audiogram in the quiet, however, will not help much when trying to estimate functional active spaces in the noisy environment of the real world, where sound communication takes place (Klump 1996). First, we need to introduce an important aspect of animal auditory physiology, the so-called critical masking ratio or just critical ratio (CR) (for a comprehensive introduction see, e.g., Klump 1996, Dooling et al. 2000, or Dooling and Leek 2018). In hearing vertebrates, the peripheral auditory system can be perceived as a series of overlapping bandpass filters, each of which lets a certain band of sound frequencies pass for further analysis in the central auditory system but rejects lower and higher frequencies (Fletcher 1940). Whereas the audiogram in the quiet remains constant for an individual bird and species, an audiogram measured in the presence of ambient noise depends on the composition of the noise (frequency, amplitude), which may also fluctuate over time and vary with environment, i.e., the noise level can be expressed as a function $N(f,t,e)$. Audiograms measured in the presence of ambient noise are “masked audiograms” with higher thresholds than in the quiet but are the only ones relevant for sound communication and determination of active spaces.

In the presence of a given noise level, CR can be measured in the laboratory by presenting a pure tone (i.e., a single frequency) at progressively lower sound levels and recording the sound level, for which the receiving bird can no longer detect the tone above the noise, i.e., for which the tone is just masked. The power of the test tone at this threshold (measured in watt) divided by the power (in watt) of $N(f,t,e)$ in the 1-Hz band of the tone is the critical ratio, CR, often expressed in dB (if for instance the power of the test tone at threshold is 10 times larger than that of the noise in the corresponding 1-Hz band, then $CR = 20\log_{10}(10) = 20$ dB). The noise power in each 1-Hz band is called the spectrum level of the noise at that frequency. It is assumed that the noise power is flat in a frequency band centered at the signal

frequency and with a bandwidth of at least one-third of an octave (or 23% of the center frequency).

As pointed out in Fig. 2.4, the spectrum level of the ambient noise in natural environments decreases with frequency. In contrast, the critical ratio of the avian auditory system increases with frequency and should be denoted $CR(f)$. The approximate median $CR(f)$ for the 14 bird species tested so far with ambient white noise is 19 dB at 250 Hz, 22 dB at 500 Hz, 24 dB at 1 kHz, 26 dB at 2 kHz, 30 dB at 4 kHz, and 38 dB at 8 kHz (Dooling and Blumenrath 2013; Dooling and Leek 2018). $CR(f)$ in many bird species therefore almost, but not quite, increases by about 3 dB/octave (i.e., 3 dB per doubling of frequency) as observed in humans and other animals. So, to detect a sound signal a bird receiver will need a larger signal-to-noise ratio (SNR) of the sound signal if it is composed of high frequencies than of low frequencies.

In contrast to cricket song, birdsong is seldom composed of single frequency tones, but each song varies in a certain frequency band, for instance from 2 to 7 kHz in great tits (McGregor and Krebs 1982), but often has a prominent peak frequency. Fortunately, it turns out that the CR values measured with pure tones by psychoacoustical methods in the laboratory predicts the responses of receiving birds to the peak frequencies of the sender's song quite well (Dooling and Leek 2018). So, if the spectrum level of wind-generated masking noise, $N(f,t,e)$, in a deciduous forest varies from 10 dB re. 20 $\mu\text{Pa Hz}^{-1/2}$ at 2 kHz to 5 dB re. 20 $\mu\text{Pa Hz}^{-1/2}$ at 4 kHz (Klump 1996), then the "median bird" mentioned above with CR's varying from 26 dB at 2 kHz to 30 dB at 4 kHz will require a received level, RL_{Det} , of more than 36 dB at 2 kHz and more than 35 dB at 4 kHz to detect a song dominated by frequencies in this range. So, in this example the received level required for detection, RL_{Det} , remains rather constant in this frequency range.

In general, the RL (in Eq. 2.3 above) required by a certain bird species for detecting a call or song, RL_{Det} , should then be larger than the sum of the bird's $CR(f)$ in the relevant frequency range and the spectrum level of the ambient noise, $N(f,t,e)$, in the same frequency range. If the extra dB values mentioned in Sect. 2.3.3 required for discrimination, recognition, and comfortable conversation applies to birds in general, then for instance $RL_{\text{Rec}} = RL_{\text{Det}} + 6$ dB (between 4 and 8 dB extra; Lohr et al. 2003) should be used in Eq. 2.3. (For a most educational introduction to calculating communication distances based on realistic source levels, received levels, noise levels, and critical ratios, see Nemeth and Brumm (2010)).

Other properties of the avian auditory system should be taken into consideration when estimating the required RL, for instance, the relation between signal-to-noise ratio at threshold and amplitude (AM) or frequency modulation (FM) of the songs or calls. Unfortunately, to my knowledge, no systematic study of this relation has been reported but Lohr et al. (2003) showed that in budgerigar, zebra finch, and canary (*Serinus canaria*) receivers, high AM of a 2860 Hz pure tone decreased the detection threshold in broadband noise by about 5 dB relative to that of an unmodulated pure tone of 2860 Hz. In contrast, sinusoidal FM did not change the detection threshold. So, an avian sender may conceivably increase the range of its sound signals in

ambient noise by changing from unmodulated to AM song and call elements. A 5-dB decrease in threshold may increase the detection range by a factor 1.8, i.e., making the song more public by extending the range from, e.g., 10 to 18 m in Fig. 2.2b. However, we cannot generalize until more systematic studies have been performed. A study on human speech reception (Zeng et al. 2005) found that AM is important for speech recognition in the quiet, but that FM significantly enhances speech recognition in noise. Whether AM and FM have similar roles in avian song recognition remains unknown.

We know much more regarding the relation between auditory threshold and duration of calls or song elements. Traditionally, the peripheral auditory system has been modeled as a leaky-energy detector with a certain integration time, T_i (Plomp and Bouman 1959). In this model, thresholds will remain constant for stimulus tone durations longer than T_i but increase when stimulus duration is progressively shorter than T_i . Such a relation was seemingly found by testing the budgerigar with different duration tones at the best frequency of the audiogram, where T_i was estimated to be 230 ms and where the threshold at a stimulus duration of, for instance, 10 ms was about 15 dB higher than at 230 ms (Dooling and Searcy 1985). This should be compared with average budgerigar contact call durations of about 190 ms (Farabaugh et al. 1998). Later studies examining more frequencies in the European starling (*Sturnus vulgaris*) found a marked frequency dependence of integration times that varied such that at midfrequencies 1–2 kHz T_i was about 550 ms, whereas at lower (500 Hz) and higher (4 kHz) frequencies it was about 200 ms (Klump and Maier 1990). In starlings, the average duration of, for instance, starling motif song is 640 ms (Eens et al. 1989). More recently, careful behavioral studies of threshold level duration (TLD) functions in great tits (Pohl et al. 2013) found time constants of 132 ms in the quiet and 85 ms in noise, which should be compared with an average song element duration of 100 ms (Pohl et al. 2009). So, the relation between duration of song elements and integration times seems rather complicated. Consequently, the validity of the leaky-energy detector model has been questioned and a physiologically more likely probabilistic model has been proposed (for a detailed introduction and discussion, see Pohl et al. 2013). What remains certain though, is the general trend of the threshold level duration (TLD) curves, which for all the mentioned studies show increasing thresholds of 5–15 dB when stimulus sounds are shortened from 1000 ms to 10 ms, which is the duration range of most bird calls and song elements. In the present context this means that the required RL for detection, RL_{Det} , should include not only the $CR(f)$ of the bird and $N(f, t, e)$ but also the threshold increase depending vocalization duration from the TLD-curves, which may be denoted $TLD(\Delta t)$. If the sender shortens the element durations, the RL_{Det} increases; this decreases the size of the active space and consequently makes the signals more private. Note however that the call or song element duration at the receiver is often longer than that at the sender, especially in closed environments where reverberation tends to increase the duration with distance (Mathevon et al. 1996). In summary, for detection of a sound signal embedded in the ambient sound

of the natural world the receiver's auditory system requires an RL_{Det} that is larger than the sum of (at least) the following parameters:

$$RL_{\text{Det}} \geq CR(f) + N(f, t, e) + TLD(\Delta t) \quad (2.4)$$

where $CR(f)$ is the critical ratio of the receiver as a function of frequency and $N(f, t, e)$ is the spectrum level of the ambient noise as a function of frequency, time, and environment.

2.3.5 *Potential Active Space Regulation by Receiver Behavior*

The receiver may behaviorally change the extent of the active space of a sound signal emitted from a sender by moving in real time, e.g., in closed environments by flying up in or above vegetation, which may reduce the local $EA(f, t, e, m)$ by several dB (Lemon et al. 1981; Dabelsteen et al. 1993; Mathevon et al. 2005). A European blackbird receiver, for instance, located in the forest undergrowth 3 m above ground and close to the border of the active space, where it can just detect the song of a conspecific sender, may gain about 5 dB by flying up to a perch 9 m above ground and thus enter the discrimination (or perhaps even the recognition) zone (Dabelsteen et al. 1993). So, for birds "active spaces" actually are 3D spaces and not just horizontal areas as for many mammals.

Receivers may also extend the range of their active space by different mechanisms of "release from masking." If the receiver is located near a localized masking noise source, such as a vocalizing hetero-specific animal or group of animals, it may experience up to 10 dB release from masking, the so-called spatial release from masking, by placing itself such that the angle between a conspecific sender and the noise source is about 90° as has been observed in budgerigars (Dent et al. 1997). Another mechanism for release from masking is the so-called "co-modulation masking release" (CMR). Birds and other animals often (perhaps almost always) experience masking sounds with slow amplitude fluctuations caused by wind gusts or turbulence in the air. If broadband maskers, covering several of the previously mentioned overlapping bandpass filters in the auditory periphery, are coherently and slowly amplitude modulated, then signal detection is improved considerably. CMR in European starlings, for instance, has been studied intensively and release from masking with impressive median values of 28 dB has been reported (for a comprehensive introduction and discussion see Langemann and Klump 2001). These mechanisms of release from masking cannot be used by the sender for encoding public or private information but do emphasize the fact that the extent of the functional active space is much more complicated than predicted by Eq. 2.3.

2.4 Predictions on Encoding of Public and Private Sound Signals

We can now try to answer the introductory question in Sect. 2.3 on how the sender can encode private and public information by varying the size of the active space of its vocalizations. First, we will predict sender actions, each of which would encode for *public* signals, which maximize the active space (Table 2.1). Public calls or song elements should first and foremost be loud, that is, have a high source level (SL). The signals should predominately be concentrated at low frequencies to minimize the effect of atmospheric absorption and other types of excess attenuation ($EA(f,t,e,m)$) at longer distances. However, signals with frequencies much lower than 1 kHz might be masked by ambient sound, the spectrum level of which in many environments increases at lower frequencies (Fig. 2.4). By concentrating the sound signal energy in a narrow frequency band, the sender would further enhance the active space by increasing the SNR, i.e., $(SL - N(f,t,e))$, in one or only a few auditory bandpass filters of the receiver. High amplitude modulation (AM) of narrow band signals would enhance detection, but AM might be masked by fluctuations caused by reverberation and atmospheric turbulence (Wiley and Richards 1978). Duration of calls or song elements (Δt) should be relatively long, at least as long as the integration time of the receiver's auditory system, if the leaky-energy detector model is used; signal durations longer than a few hundred ms would optimize detectability, since the TLD(Δt) curve would approach a constant low value. Directionality should be close to omnidirectionality to reach as many visually concealed receivers as possible. This would require emitting sounds with wavelengths longer than the body dimensions, such that the sender could be described as a point source (see, e.g., Larsen and Wahlberg 2017), i.e., also argue for using LF signals. In case the bird for other reasons was confined to using directional high-frequency sounds, it could enhance omnidirectionality by frequently turning its head. Each of these parameter choices for encoding the signals mentioned above would help to make the sound signals public. However, different birds may have been adapted by selection to using only a subset of these choices as they are limited by their sound signals' parameter space or "room for

Table 2.1 Overview of possible encoding of signal parameters that a vocalizing bird could use to make calls or song elements public or private by increasing or decreasing the extent of the signal's active space

Parameter of sound signal	Public	Private
Source level (SPL or peak pressure)	High	Low
Frequency (dominant band)	Low	High (or very low)
Bandwidth	Narrow	Broad
Frequency modulation	Low	High (sweeps)
Amplitude modulation	High	Low (or none)
Duration of elements or calls	Long (>about 500 ms)	Short (<about 500 ms)
Directionality	Omnidirectional	Directional

Table 2.2 Overview of possible behavioral choices that a vocalizing bird could make to increase or decrease the extent of its active space by making it easier (public) or more difficult (private) for a receiver to hear and interpret the sender's calls or songs

Behavior	Public	Private
Time of day for calling or singing relative to ambient noise, N	When ambient noise is low (morning, evening, or night)	When ambient noise is high (midday)
Time of day for calling or singing relative to excess attenuation, EA	When temperature and humidity minimize EA	When temperature, humidity, and wind maximize EA
Song post choice	High above ground with few intervening objects	Close to ground or intervening objects
Repetition of sound signals	Highly redundant (many repetitions)	Single signal or great variability of signals
Duration of social interactions	Long	Short

variation" (Dabelsteen 1985). So, they could not choose any combination of parameters for enhancing the active space, especially if some combinations changed the signals' information such that, for instance, a blackbird no longer sounded like a blackbird.

In addition to encoding sound parameters for making the signals public, the sender could maximize the range of broadcast signals by some behavioral choices (Table 2.2). The sender should sing or call predominantly when ambient noise, $N(f, t, e)$ was low, and temperature and wind gradients enhanced transmission distance by reducing $EA(f, t, e, m)$. The sender should emit the sound signals from song posts located far away from ground or when flying to avoid attenuation by the ground effect and intervening objects. To make sure that the message got across through the noisy habitat, the sender should finally, like the Eurasian skylark (*Alauda arvensis*), repeat the sound signal over and over, i.e., the sound signal should be highly redundant, since this would increase the receivers' probability of both detecting, discriminating, and recognizing the signal (Price 2013; Wiley 2013). Finally, social communication interactions could be of long duration as this would emphasize, for instance, territory ownership to all receivers.

Secondly, to encode for small *private* active spaces, the sender should use the opposite strategy (Table 2.1). The source level (SL) of calls and song elements should be low, i.e., the signals quiet or soft. As we saw in Fig. 2.2, a source level reduction of just 25 dB would lead to a dramatic reduction in the active space. Soft signals should predominantly contain high frequencies to take advantage of the components of $EA(f, t, e, m)$ (e.g., atmospheric attenuation) that increase with frequency, but they could also be very low frequency, since LF signals cannot be emitted efficiently from small animals and in addition they would be masked by LF ambient noise. In contrast to a narrow band signal of a certain SL, a broadband signal of the same SL would be more private, since it would have its energy smeared out over many auditory bandpass filters of the receiver, which means that the required RL_{Det} might not be reached in any filter (i.e., be below $CR(f) + N(f, t, e)$), unless the receiver came much closer to the sender. Low or no amplitude modulation would further decrease the active space, if the findings regarding AM of Lohr et al. (2003)

apply to birds in general (see Sect. 2.3.4). Calls or song elements with durations much shorter than the integration time of the auditory system should be preferred, since the $TLD(\Delta t)$ curves add extra dB to RL_{Det} (Eq. 2.4) and thereby reduce the active space further. Highly directional calls could address a specific receiver such as a competitor but be less obvious to potential receivers located in other directions.

Also for soft vocalizations, the sender would have some behavioral choices of when and where to signal (Table 2.2). In the middle of day, the ambient noise level is often rather high and the SNR consequently rather low, which reduces the size of the active space by masking. Signaling when the wind is high will further reduce the active space by increasing the ambient noise in general and enhance attenuation upwind but reduce attenuation downwind. Optimal locations will be close to the intended receivers and on or close to ground. In addition, there is the possibility to combine close quarter sound signals with visual gestures or vibrational signals that work only at close distances. Redundancy of private signals should be low since single messages or great variability in song elements need a high signal-to-noise level to get across to receivers. Finally, vocal interactions should be short duration to reduce probability of catching the attention of unintended receivers.

2.5 Observed Soft Private and Loud Public Calls and Songs

Do vocalizing birds actually encode private and public information in their calls and songs as predicted above? Earlier transmission studies in deciduous forest habitats of European blackbird broadcast song consisting of introductory loud, unmodulated about 2-kHz song elements (whistles) and terminal softer, highly modulated 2–8 kHz elements (twitter), for instance, found that the whistle elements transmitted much further than the twitter elements (Dabelsteen et al. 1993). The structure of the soft twitter elements, sometimes used as “strangled song” for private communication was much in accordance with the predictions listed above including low amplitude, broadband sweeps or harmonics, and high note variability (Dabelsteen et al. 1998). However, this was just one species and we did not take into consideration the auditory physiology of the receiver and overestimated the size of active space of the broadcast song. Later studies, however, have corrected the extent of the active space of blackbird broadcast song (for a comprehensive discussion see Nemeth and Brumm 2010).

2.5.1 Observed Soft and Loud Vocalizations

There is now a substantial literature on low-amplitude private versus high-amplitude public calls and songs. Here, we will use the term “soft” to indicate low-amplitude vocalizations, whereas other terms have been used in the past, such as “strangled song” (Snow 1958), “quiet song” (Dabelsteen et al. 1998), “short-range song” (Titus

1998; Reichard et al. 2013), “whisper song” (Morton 2000; Ishizuka 2009), “quiet call” (Gorissen and Eens 2004), and “low-amplitude song” (Reichard et al. 2011).

The literature mainly discusses the *function* of soft songs or calls, i.e., their correlation with subsequent receiver behavior, where for example the use of soft songs by passerines seems to reliably predict attacks (Hof and Hazlett 2010); for a clear and comprehensive recent review on soft signaling see Reichard and Anderson (2015). In addition, spectrographic parameters of the songs are often reported, whereas quantitative source levels are not. Soft vocalizations have been observed in several types of social interaction, which include, for instance, aggressive interactions (e.g., Searcy and Nowicki 2006; Anderson et al. 2007; Ballentine et al. 2008; Searcy and Beecher 2009; Hof and Hazlett 2010; Akçay et al. 2011, 2015; Zollinger and Brumm 2015; Krieg and Burnett 2017), courtship (e.g., Balsby and Dabelsteen 2005; Reichard et al. 2011, 2013), nest relief when feeding the chicks (e.g., Ishizuka 2009; Elie et al. 2010), and coordination of group movement (e.g., Radford and Ridley 2008). But apart from the coding by change of (mainly qualitatively estimated) amplitude, it is difficult to find enough information to test, if birds in general follow the other six predictions on how to encode their calls and songs with public or private information (Table 2.1).

A recent literature review (Reichard and Welklin 2015) shows that soft vocalizations have been reported from 433 (58%) out of a total of 749 species of North American breeding birds divided in 22 taxonomic orders, out of which 743 species (99%) also sing loud broadcast song. High-amplitude calls are present in twice as many species as high-amplitude songs. Soft calls occur in 2.6 times as many species as soft song, which occur mainly in the context of courtship and territoriality, whereas soft calls mainly occur in the context of contact and courtship but less in aggression and alarm. However, in the literature analyzed, the distinction between loud and soft sound signals was based mainly on qualitative human assessment such as: soft calls are “inaudible at more than 15 m from the bird.” Seldom was the evaluation based on quantitative dB measurements.

In about 60% of the species, the reported soft calls or songs were judged to be softer versions of the loud song (Reichard and Welklin 2015). If these numbers are representative, it suggests that 60% of the species code for privacy only by amplitude reduction. But there is a problem: The maximum song amplitude may vary appreciably within a population of conspecific songbirds. In a population of nightingales, for instance, Brumm and Todt (2002) found differences in median vocal sound pressure levels of up to 10 dB between six identified males; differences in median song amplitude of up to 14 dB were reported from 11 zebra finches (Brumm and Slater 2006), Kobayashi and Okanoya (2003) found average amplitude differences of 6 dB among six Bengalese finches (*Lonchura striata*), Brumm and Ritschard (2011) found 9 dB differences in chaffinches, and Nemeth et al. (2012) reported a 12 dB maximum difference in song amplitude between rock sparrows (*Petronia petronia*). So, without quantitative measurements of dB values and without making sure that the same individual sings both a high amplitude and a low amplitude version of the broadcast song, the observed variability in broadcast song amplitude

may just be an expression of population variability—not an active choice of reducing the active space to obtain privacy.

In the remaining 40% of species their soft songs were reported to have a structure different from the broadcast songs, such as broader bandwidth and greater note variability (Reichard and Welklin 2015). This is in accordance with predictions of Table 2.1. The soft songs or calls were observed to be emitted in close proximity to receivers and in the contexts of aggression, courtship, contact, and alarm. So, soft songs and calls seem common in vocalizing birds in North America but at this stage we cannot be certain of how common the occurrence is across the whole avian class.

2.5.2 Observed Source Levels of Soft and Loud Vocalizations

Studies of marine mammal sound communication and echolocation always report source levels (SL) or even apparent source levels (ASL) of their experimental animals (e.g., Møhl et al. 2000). ASL is the source level back-calculated from recordings at a distance of the animal without knowledge of the direction of the vocalizing mammal's head or body axis. Back-calculated ASL could also be used for estimating SL in bird species with visually hidden vocalizing individuals. It is therefore rather surprising that quantitative source levels of birdsong are still seldom reported in the literature. This means that for many bird species we are left with only qualitative impressions of their active spaces—and therefore of their possible coding for privacy versus publicity.

Perusing the literature, we find that the broadcast loud songs or calls generally have source levels ranging from 80 to 95 dB SPL (Table 2.3). Sometimes, SL is reported in dB(A), where “(A)” indicates that the sound was high-pass filtered before measuring the sound level, i.e., rejecting the power of low frequencies. Brackenbury (1979) found that the maximum total radiated power varied from 10 mW/(kg body weight) to 870 mW/(kg body weight) in 17 different European songbird species. This corresponded to maximum source levels (SL) ranging from 74 dB SPL in the whitethroat (*Sylvia communis*) to 100 dB SPL in the song thrush (*Turdus philomelos*) (Brackenbury 1979). Later model calculations suggest that avian peak acoustic power is of the order of 200 mW (Fletcher 1988) but this constraint on maximum SL needs further investigation. An outlier regarding avian source levels is the screaming piha (*Lipaugus vociferans*) from Brazilian rain forests with source levels of 110 dB(A) (Nemeth 2004). In contrast, source levels of soft songs and calls are seldom reported but seem to be in the range 50–77 dB SPL (Table 2.4).

Fortunately, there are examples of quantitative studies reporting source levels for both broadcast and soft vocalizations in the same bird species. One study on song sparrows (*Melospiza melodia*; Anderson et al. 2008), found that the SL of their loud broadcast songs ranged from 78 to 85 dB SPL, whereas their soft song SL was reported to vary continuously in the range 55–77 dB SPL with a median difference to their broadcast song levels of 14 dB, corresponding to a reduction of active space radius with a factor five when changing from broadcast to soft vocalizations.

Table 2.3 Broadcast song

Species	SL mean	SL range	References
Song sparrow (<i>Melospiza melodia</i>)	80	78–85	Anderson et al. (2008)
Eurasian wren (<i>Troglodytes troglodytes</i>)	91	–	Armstrong and Whitehouse (1977)
King penguin (<i>Aptenodytes patagonicus</i>)	95	–	Aubin and Jouventin (1998)
Great tit (<i>Parus major</i>)	89	–	Blumenrath and Dabelsteen (2004)
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	91	88–94	Brenowitz (1982)
Nightingale (<i>Luscinia megarhynchos</i>)	85	76–92	Brumm (2004, 2009)
Chaffinch (<i>Fringilla coelebs</i>)	82	78–87	Brumm and Ritschard (2011)
Zebra finch (<i>Taeniopygia guttata</i>)	80	60–90	Cynx et al. (1998)
Zebra finch (<i>Taeniopygia guttata</i>)	72	68–78	Ritschard and Brumm (2011) (in anechoic chamber)
European blackbird (<i>Turdus merula</i>)	85	–	Dabelsteen (1981)
Screaming piha (<i>Lipaugus vociferans</i>)	110	–	Nemeth (2004)
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	83	79–94	Patricelli et al. (2007, 2008)
Corncrake (<i>Crex crex</i>)	96	80–101	Ręk and Osiejuk (2011)

Examples of source level (SL) of loud broadcast songs and calls of various bird species measured as sound pressure level (dB SPL, i.e., root-mean-square sound pressure re. 20 μ Pa)

Table 2.4 Soft song and calls

Species	Mean or median	SL range	References
Song sparrow (<i>Melospiza melodia</i>)	65	54–77	Anderson et al. (2008)
House wren (<i>Troglodytes aedon</i>)	–	25–33 dB softer than broadcast	Krieg and Burnett (2017)
Corncrake (<i>Crex crex</i>)	71	65–76	Ręk and Osiejuk (2011)
Brown-flanked bush warbler (<i>Cettia fortipes</i>)	13 dB softer than broadcast	–	Xia et al. (2013)

Examples of source levels (SL) of soft song of various bird species measured as dB SPL. Note that in some studies, soft song levels are given only relative to the SPL of the broadcast song, which has not been quantified

However, the difference between the loudest broadcast song and the softest song was 36 dB corresponding to a space radius reduction of a factor 63. In addition, the authors divided soft songs into “crystallized soft songs,” whose structure was much

the same as the broadcast songs, and very soft “warbled songs” whose was very different from that of broadcast songs.

Other informative studies concerned corncrakes (*Crex crex*) that belong to quite another order (*Gruiformes*) than songbirds (Ręk and Osiejuk 2011; Ręk 2013). Nevertheless, the corncrakes expressed the same pattern as the song sparrows producing loud calls with median SL of 96 dB SPL (range 80–101 dB SPL) and low-amplitude aggressive gurgling–mewing calls with median SL of 70 dB SPL (range 65–76 dB SPL); i.e., with a median difference of 25 dB between high- and low-amplitude calls corresponding to a reduction of active space radius by a factor 18, when changing from loud to soft vocalizations (cf. Figs. 2.1 and 2.2). When measuring soft call transmission and taking the receiver’s presumed $CR(f)$ into consideration, this suggests a maximum active space radius of 20–40 m (Ręk 2013).

These two examples raise the question whether the intuitive division by human observers of songs and calls into only two categories, soft and loud, really reflects reality to the birds. Perhaps more amplitude ranges should be included or perhaps the change in amplitude actually is a continuum? In addition, some authors suggest that using peak pressures to calculate active spaces and not only RMS pressures will give a better estimate of the functional active spaces as bird receivers may not need to identify the complete song but only its most intense components.

2.5.3 Other Coding Parameters Observed in Soft and Loud Vocalizations

We predicted that broadcast loud calls and song elements should be of longer duration than soft ones. But in the two quantitative studies just mentioned this is not the case. In song sparrows there was no difference in song element duration (Anderson et al. 2008)—and in the corncrakes the duration of soft calls was actually about four times longer than that of broadcast calls (Ręk 2013). However, Xia et al. (2013) found significantly shorter duration elements in the soft song (40–80 ms) than in the broadcast song (>200 ms) of the brownish-flanked bush warbler (*Cettia fortipes*).

The song sparrow and corncrake examples show two very different frequency ranges of soft vocalizations relative to the broadcast ones. In song sparrows the two versions of soft song had a wider frequency range than broadcast songs—but not much (Anderson et al. 2008). The broadcast song varied in the range 2.0–8.0 kHz, whereas the two versions of the soft song varied in the range 1.7–8.1 kHz (crystalized soft song) and 1.5–9.1 kHz (warbled song). This follows the predictions of Table 2.1.

In corncrakes, on the other hand, the soft call elements were much lower frequency range than the broadcast calls (Ręk 2013); broadcast call frequency range was 0.5–5.0 kHz opposed to soft call ranges of less than 1 kHz (gurgling note) and 1–2 kHz (mewing note). This is the opposite of the predictions of

Table 2.1. This deviation illustrates that other parameters than frequency content and duration should be included to understand detectability of sound signals. Corncrake song is special consisting of sweeps of transients, which are super easy to recognize for humans even at long distances, although the signals' frequency content is broadband. So, this is a good example of a "weird exemption" from most songbird songs, which generally are tonal.

Other studies show marked differences between broadcast and soft songs following all the predictions of Table 2.1. Vargas-Castro (2015), for instance, showed that soft song elements in the white-throated thrush (*Turdus assimilis*) are much more broadband, at higher frequencies, and with much longer frequency sweeps (FM) than broadcast song elements and therefore follow the same pattern as other *Turdus* species such as the European blackbird (Dabelsteen et al. 1993). Finally, greater variability in soft song elements than in broadcast song seems widespread, as recently documented by Vargas-Castro (2015) and Xia et al. (2013).

2.5.4 Observed Behavioral Choices of Soft and Loud Calls and Songs

Behavioral choices for extending the size of the active space by optimizing song post height above ground have been reported for some species, e.g., in rainforest antbirds (Nemeth et al. 2001). However, behavioral choices for reducing the active space seem inadequately reported in the literature to make any strong conclusions about exploitation of environmental properties such as those predicted in Table 2.3 for encoding private information in avian calls or song elements.

2.6 Conclusions

Functionally, birds encode private and public information in their vocalizations. The main mechanism is regulation of the size of the active space. Active space reduction by lowering the voice makes the vocalizations more private and seems common in birds. But we need more quantitative studies to be able to generalize on privacy coding. We also need more quantitative source level measurements of known individuals to investigate whether there are more relevant amplitude categories than just the two, broadcast and soft, perhaps even a continuum. Coding for privacy by frequency parameters can be enhanced either by using broadband high frequency sounds, limited by atmospheric attenuation, or low frequency sounds potentially masked by low frequency ambient noise. Coding of public or private information by sound signal duration follows predictions in some studies but not in other, so to generalize we need more experimental works. Finally, social behavior of vocalizing birds is carefully reported in the literature but behavioral choices concerning where

and when to vocalize relative to environment, time, and meteorological conditions are generally not. So, there is still much to do before we can make strong conclusions about the strategies for encoding public and private information in sound signals.

Acknowledgments I am grateful to the editors for inviting me to write this chapter and to Magnus Wahlberg for his comments to improve the manuscript.

References

- Akçay Ç, Tom ME, Holmes D, Campbell E, Beecher MD (2011) Sing softly and carry a big stick: signals of aggressive intent in the song sparrow. *Anim Behav* 82:377–382
- Akçay Ç, Anderson RC, Nowicki S, Beecher MD, Searcy WA (2015) Quiet threats: soft song as an aggressive signal in birds. *Anim Behav* 105:267–274
- Akçay Ç, Clay A, Campbell E, Beecher MD (2016) The sparrow and the hawk: aggressive signalling under the risk of predation. *Behav Ecol* 27(2):601–607
- Anderson RC, Nowicki S, Searcy WA (2007) Soft song in song sparrows: response of males and females to an enigmatic signal. *Behav Ecol Sociobiol* 61:1267–1274
- Anderson RC, Searcy WA, Peters S, Nowicki S (2008) Soft song in song sparrows: acoustic structure and implications for signal function. *Ethology* 114:662–676
- Armstrong EA, Whitehouse HLK (1977) Behavioural adaptations of the wren (*Troglodytes troglodytes*). *Biol Rev* 52:235–294
- Attenborough K (2007) Sound propagation in the atmosphere. In: Rossing TD (ed) *Handbook of acoustics*. Springer, New York, pp 113–147
- Aubin T, Jouventin P (1998) Cocktail-party effect in king penguin colonies. *Proc R Soc B* 265:1665–1673
- Ballentine B, Searcy WA, Nowicki S (2008) Reliable aggressive signalling in swamp sparrows. *Anim Behav* 75:693–703
- Balsby TJS, Dabelsteen T (2005) Simulated courtship interactions elicit neighbour intrusions in the whitethroat, *Sylvia communis*. *Anim Behav* 69(1):161–168
- Barber JB, Crooks KR, Fristrup KM (2010) The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol Evol* 25(3):180–189
- Barker NKS, Dabelsteen T, Mennill DJ (2009) Degradation of male and female rufous-and-white wren songs in a tropical forest: effects of sex, perch height, and habitat. *Behaviour* 146:1093–1122
- Bass HE, Sutherland LC, Zuckerwar AJ, Blackstock DT, Hester DM (1995) Atmospheric absorption of sound: further developments. *J Acoust Soc Am* 97(1):680–683
- Blumenrath SH, Dabelsteen T (2004) Degradation of great tit *Parus major* song before and after foliation: implications for vocal communication in deciduous forests. *Behaviour* 8:935–958
- Boersma HF (1997) Characterization of the natural ambient sound environment: measurements in open agricultural grassland. *J Acoust Soc Am* 101(4):2104–2110
- Boncoraglio G, Saino N (2007) Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Funct Ecol* 21:134–142
- Bourne GR, Collins AC, Holder AM, McCarthy CL (2001) Vocal communication and reproductive behavior of the frog *Colostethus beebei* in Guyana. *J Herpetol* 35:272–281
- Brackenbury JH (1979) Power capabilities of the avian sound-producing system. *J Exp Biol* 78:163–166
- Brenowitz EA (1982) The active space of red-winged blackbird song. *J Comp Physiol A* 147:511–522
- Brumm H (2002) Sound radiation patterns in nightingale (*Luscinia megarhynchos*) songs. *J Ornithol* 143:468–471

- Brumm H (2004) The impact of environmental noise on song amplitude in a territorial bird. *J Anim Ecol* 73:434–440
- Brumm H (2009) Song amplitude and body size in birds. *Behav Ecol Sociobiol* 63:1157–1165
- Brumm H, Ritschard M (2011) Song amplitude affects territorial aggression of male receivers in chaffinches. *Behav Ecol* 22:310–316
- Brumm H, Slabbekoom H (2005) Acoustic communication in noise. *Adv Study Behav* 35:151–209
- Brumm H, Slater PJB (2006) Animals can vary signal amplitude with receiver distance: evidence from zebra finch song. *Anim Behav* 71:699–705
- Brumm H, Todt D (2002) Noise-dependent song amplitude regulation in a territorial songbird. *Anim Behav* 63:891–897
- Brumm H, Todt D (2004) Male-male vocal interactions and the adjustment of song amplitude in a territorial bird. *Anim Behav* 67:281–286
- Brumm H, Zollinger SA (2011) The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* 148:1173–1198
- Brumm H, Zollinger SA (2013) Avian vocal production in noise. In: Brumm H (ed) *Animal communication and noise*. Springer, Berlin
- Chappuis C (1971) Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: L'évolution des chants en forêt équatoriale. *Terre Vie* 118:183–202
- Cynx J, Lewis R, Tavel B, Tse H (1998) Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Anim Behav* 56:107–113
- Dabelsteen T (1981) The sound pressure level in the dawn song of the blackbird *Turdus merula* and a method for adjusting the level in experimental song to the level in natural song. *Z Tierpsychol* 56(2):137–149
- Dabelsteen T (1985) Messages and meanings of bird song with special reference to the blackbird (*Turdus merula*) and some methodology problems. *Biologiske Skrifter* 25:173–208
- Dabelsteen T (2005) Public, private or anonymous? Facilitating and countering eavesdropping. In: McGregor P (ed) *Animal communication networks*. Cambridge University Press, Cambridge, NY, pp 38–62
- Dabelsteen T, Larsen ON, Pedersen SB (1993) Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *J Acoust Soc Am* 93:2206–2220
- Dabelsteen T, McGregor PK, Lampe HM, Langmore NE, Holland J (1998) Quiet song in song birds: an overlooked phenomenon. *Bioacoustics* 9:89–105
- Dent ML, Larsen ON, Dooling RJ (1997) Free-field binaural unmasking in budgerigars (*Melopsittacus undulatus*). *Behav Neurosci* 111(3):590–598
- Dooling RJ (1982) Auditory perception in birds. In: Kroodsma DE, Miller EH (eds) *Acoustic communication in birds, vol 1*. Academic, New York, pp 95–130
- Dooling RJ (1992) Hearing in birds. In: Webster DB, Fay RR, Popper AN (eds) *The evolutionary biology of hearing*. Springer, New York, pp 545–559
- Dooling RJ, Blumenrath SH (2013) Avian sound perception in noise. In: Brumm H (ed) *Animal communication and noise, animal signals and communication, vol 2*. Springer, Berlin, pp 229–250
- Dooling RJ, Leek MR (2018) Communication masking by man-made noise. In: Slabbekoom H, Dooling RJ, Fay RR, Popper AN (eds) *Effects of anthropogenic noise on animals*. Springer, New York, pp 23–46
- Dooling RJ, Searcy MH (1985) Temporal integration of acoustic signals by the budgerigar (*Melopsittacus undulatus*). *J Acoust Soc Am* 77(5):1917–1920
- Dooling RJ, Lohr B, Dent ML (2000) Hearing in birds and reptiles. In: Dooling RJ, Fay RR, Popper AN (eds) *Comparative hearing: birds and reptiles*. Springer, New York, pp 308–359
- Dooling RJ, Leek MR, West E (2009) Predicting the effects of masking noise on communication distance in birds. *J Acoust Soc Am* 125(4):2517
- Eens M, Pinxten R, Verheyen RF (1989) Temporal and sequential organization of song bouts in the starling. *Ardea* 77:75–86

- Elemans CP, Rasmussen JH, Herbst CT, Düring DN, Zollinger SA, Brumm H, Srivastava K, Svane N, Ding M, Larsen ON, Sober SJ, Švec JG (2015) Universal mechanisms of sound production and control in birds and mammals. *Nat Commun* 6:8978
- Elie JE, Mariette MM, Soula HA, Griffith SC, Mathevon N, Vignal C (2010) Vocal communication at the nest between mates in wild zebra finches: a private vocal duet? *Anim Behav* 80:597–605
- Ey E, Fischer J (2009) The “acoustic adaptation hypothesis” – a review of the evidence from birds, anurans and mammals. *Bioacoustics* 19:21–48
- Farabaugh SM, Dent ML, Dooling RJ (1998) Hearing and vocalizations of wild-caught Australian budgerigars (*Melopsittacus undulatus*). *J Comp Psychol* 112:74–81
- Fegeant O (1999) Wind-induced vegetation noise. Part II: field measurements. *Acta Acust Acust* 85 (2):241–249
- Fletcher H (1940) Auditory patterns. *Rev Mod Phy* 12:47–65
- Fletcher NH (1988) Bird song – a quantitative acoustic model. *J Theor Biol* 135:455–481
- Fletcher NH (2004) A simple frequency-scaling rule for animal communication. *J Acoust Soc Am* 115(5):2334–2338
- Francis CD, Barber JR (2013) A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Front Ecol Environ* 11(6):305–313
- Fuller RA, Warren PH, Gaston KJ (2007) Daytime noise predicts nocturnal singing in urban robins. *Biol Lett* 3:368–370
- Gall MD, Ronald KL, Bestrom ES, Lucas JR (2012) Effects of habitat and urbanization on the active space of brown-headed cowbird song. *J Acoust Soc Am* 132(6):4053–4062
- Goller F, Larsen ON (1997) In situ biomechanics of the syrinx and sound generation in pigeons. *J Exp Biol* 200:2165–2176
- Goodwin SE, Podos J (2013) Shift of song frequencies in response to masking tones. *Anim Behav* 85:435–440
- Gorissen L, Eens M (2004) Interactive communication between male and female great tits (*Parus major*) during the dawn chorus. *Auk* 121(1):184–191
- Gustison ML, Townsend SW (2015) A survey of the context and structure of high- and low-amplitude calls in mammals. *Anim Behav* 105:281–288
- Halfwerk W, Bot S, Slabbekoorn H (2012) Male great tit song perch selection in response to noise-dependent female feedback. *Funct Ecol* 26:1339–1347
- Halfwerk W, Lohr B, Slabbekoorn H (2018) Impact of man-made sound on birds and their songs. In: Slabbekoorn H, Dooling RJ, Popper AN, Fay RR (eds) *Effects of anthropogenic noise on animals*, vol 66. Springer, New York, pp 209–242
- Henwood K, Fabrick A (1979) A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *Am Nat* 114(2):260–274
- Hof D, Hazlett N (2010) Low-amplitude song predicts attack in a North American wood warbler. *Anim Behav* 80:821–828
- Holland J, Dabelsteen T, Pedersen SB, Larsen ON (1998) Degradation of wren *Troglodytes troglodytes* song: implications for information transfer and ranging. *J Acoust Soc Am* 103 (4):2154–2166
- Hornby AS, Gatenby EV, Wakefield H (1970) *The advanced learner’s dictionary of current English*. Oxford University Press, London
- Huber F (1955) Sitz und Bedeutung nervöser Zentren für Instinkthandlungen beim Männchen von *Gryllus campestris* L. *Z Tierpsychol* 12:12–48
- Ishizuka T (2009) Whisper song in the grey thrush *Turdus cardis* immediately before and after feeding their young. *J Yamashina Instit Ornithol* 41:34–41
- ISO (1993) Attenuation of sound during propagation outdoors. 1. Calculation of the absorption of sound by the atmosphere. ISO 9613-1. International Organization for Standardization, New York
- Jensen KK, Cooper BG, Larsen ON, Goller F (2007) Songbirds use pulse tone register in two voices to generate low-frequency sound. *Proc R Soc B* 274:2703–2710

- Jensen KK, Larsen ON, Attenborough K (2008) Measurements and predictions of hooded crow (*Corvus corone cornix*) call propagation over open field habitats. *J Acoust Soc Am* 123 (1):507–518
- Klump GM (1996) Bird communication in a noisy world. In: Kroodsma DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, London, pp 321–338
- Klump GM, Maier EH (1990) Temporal summation in the European starling (*Sturnus vulgaris*). *J Comp Psychol* 104(1):94–100
- Klump GM, Kretschmar E, Curio E (1986) The hearing of an avian predator and its avian prey. *Behav Ecol Sociobiol* 18:317–323
- Kobayashi K, Okanoya K (2003) Context-dependent song amplitude control in Bengalese finches. *Neuroreport* 14(3):521–524
- Krieg CA, Burnett AD (2017) Female house wrens may use a low-amplitude call as an aggressive signal. *Ethology* 123:316–327
- Ladich F (2007) Females whisper briefly during sex: context- and sex-specific differences in sounds made by croaking gouramis. *Anim Behav* 73:379–387
- Langemann U, Klump GM (2001) Signal detection in amplitude-modulated maskers. I. Behavioural auditory thresholds in a songbird. *Eur J Neurosci* 13:1025–1032
- Langemann U, Klump GM (2005) Perception and acoustic communication networks. In: McGregor PK (ed) *Animal communication networks*. Cambridge University Press, Cambridge, pp 451–480
- Larsen ON, Dabelsteen T (1990) Directionality of blackbird vocalization: implications for vocal communication and its further study. *Ornis Scand* 21(1):37–45
- Larsen ON, Radford C (2018) Acoustic conditions affecting sound communication in air and underwater. In: Slabbekoorn H, Dooling RJ, Fay RR, Popper AN (eds) *Effects of anthropogenic noise on animals*, vol 66. Springer, New York, pp 109–144
- Larsen ON, Wahlberg M (2017) Sound and sound sources. In: Brown CH, Riede T (eds) *Comparative bioacoustics: an overview*. Bentham Science, Sharjah, pp 3–62
- Lemon RE, Struger J, Lechowicz MJ, Norman RF (1981) Song features and singing heights of American warblers: maximization or optimization of distance? *J Acoust Soc Am* 69:1169–1176
- Lengagne T, Slater PJB (2002) The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. *Proc R Soc B* 269:2121–2125
- Lengagne T, Aubin T, Lauga J, Jouventin P (1999) How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proc R Soc B* 266:1623–1628
- Lohr B, Wright TF, Dooling RJ (2003) Detection and discrimination of natural calls in masking noise by birds: estimating the active space signal. *Anim Behav* 65:763–777
- MacDougall-Shackleton SA (1997) Sexual selection and the evolution of song repertoires. *Curr Ornithol* 14:81–124
- Mack AL, Jones J (2003) Low-frequency vocalizations by cassowaries (*Casuaris* spp.). *Auk* 120 (4):1062–1068
- Magrath RD, Haff TM, Fallow PM, Radford AN (2015) Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol Rev* 90:560–586
- Manabe K, Sadr EI, Dooling RJ (1998) Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): differential reinforcement of vocal intensity and the Lombard effect. *J Acoust Soc Am* 103(2):1190–1198
- Marler P (1955) Characteristics of some animal calls. *Nature* 176:6–8
- Marten K, Marler P (1977) Sound transmission and its significance for animal vocalization: I. Temperate habitats. *Behav Ecol Sociobiol* 2:271–290
- Mason NA, Burns KJ (2015) The effect of habitat and body size on the evolution of vocal displays in *Thraupidae* (tanagers), the largest family of songbirds. *Biol J Linn Soc* 114(3):538–551
- Mathevon N, Aubin T, Dabelsteen T (1996) Song degradation during propagation: importance of song post for the wren *Troglodytes troglodytes*. *Ethology* 102:397–412

- Mathevon N, Dabelsteen T, Blumenrath SH (2005) Are high perches in the blackcap *Sylvia atricapilla* song or listening posts? A sound transmission study. *J Acoust Soc Am* 117 (1):442–449
- Mathevon N, Aubin T, Vielliard J, Da Silva ML, Sebe F, Boscolo D (2008) Singing in the RainForest: how a tropical bird's song transmits information. *PLoS One* 3(2):e1580
- McGregor PK, Dabelsteen T (1996) Communication networks. In: Kroodsmas DE, Miller EH (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 409–425
- McGregor PK, Krebs JR (1982) Song types in a population of great tits (*Parus major*): their distribution, abundance and acquisition by individuals. *Anim Behav* 79:126–152
- McLaughlin KE, Kunc HP (2013) Experimentally increased noise levels change spatial and singing behaviour. *Biol Lett* 9:20120771
- Mead AF, Osinalde N, Ørtenblad N, Nielsen J, Brewer J, Vellema M, Adam I, Scharff C, Song Y, Frandsen U, Blagoev B, Kratchmarova I, Elemans CPH (2017) Fundamental constraints in synchronous muscle limit superfast motor control in vertebrates. *elife* 6:e29425. <https://doi.org/10.7554/eLife.29425>
- Mencio C, Huberman B, Goller F (2017) Contributions of rapid neuromuscular transmission to the fine control of acoustic parameters of birdsong. *J Neurophysiol* 117:637–645
- Meyer J (2015) Acoustic adaptation to natural environments. In: Meyer J (ed) *Whistled languages: a worldwide inquiry about human whistled speech*. Springer, Berlin, pp 91–103
- Miller LN (1978) Sound levels of rain and wind in the trees. *Noise Control Eng J* 11:101–115
- Mooney TA, Smith A, Larsen ON, Hansen KA, Wahlberg M, Rasmussen MH (2019) Field-based hearing measurements of two seabird species. *J Exp Biol* 222:jeb190710. <https://doi.org/10.1242/jeb.190710>
- Morton ES (1975) Ecological sources of selection on avian sounds. *Am Nat* 109(965):17–34
- Morton ES (1986) Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour* 99:65–86
- Morton ES (2000) An evolutionary view of the origins and functions of avian vocal communication. *Jpn J Ornithol* 49:69–78
- Møhl B, Wahlberg M, Madsen PT, Miller LA, Surlykke A (2000) Sperm whale clicks: directionality and source level revisited. *J Acoust Soc Am* 107(1):638–648
- Naguib M, Riebel K (2014) Singing in space and time: the biology of birdsong. In: Witzany G (ed) *Biocommunication of animals*. Springer, Dordrecht
- Nemeth E (2004) Measuring the sound pressure level of the song of the screaming piha *Lipaugus vociferans*: one of the loudest birds in the world? *Bioacoustics* 14:225–228
- Nemeth E, Brumm H (2010) Birds and anthropogenic noise: are urban songs adaptive? *Am Nat* 176 (4):465–475
- Nemeth E, Winkler H, Dabelsteen T (2001) Differential degradation of antbird songs in a neotropical rainforest: adaptation to perch height? *J Acoust Soc Am* 110:3263–3274
- Nemeth E, Dabelsteen T, Pedersen SB, Winkler H (2006) Rainforests as concert halls for birds: are reverberations improving sound transmission of long song elements. *J Acoust Soc Am* 119 (1):620–626
- Nemeth E, Kempnaers B, Matessi G, Brumm H (2012) Rock sparrow song reflects male age and reproductive success. *PLoS One* 7(8):e43259
- Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Miranda AC, Brumm H (2013) Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proc R Soc B* 280:20122798
- Niederhauser JM, DuBois AL, Searcy WA, Nowicki S, Anderson RC (2018) A test of the eavesdropping avoidance hypothesis as an explanation for the structure of low-amplitude aggressive signals in the song sparrow. *Behav Ecol Sociobiol* 72:47
- Osmanski MS, Dooling RJ (2009) The effects of altered feedback and control of vocal production in budgerigars (*Melopsittacus undulatus*). *J Acoust Soc Am* 126:911–919

- Patricelli GA, Dantzker MS, Bradbury JW (2007) Differences in acoustic directionality among vocalizations of the male red-winged blackbird (*Agelaius phoeniceus*) are related to function in communication. *Behav Ecol Sociobiol* 61:1099–1110
- Patricelli GA, Dantzker MS, Bradbury JW (2008) Acoustic directionality of red-winged blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviours. *Anim Behav* 76:1389–1401
- Piza P, Sandoval L (2016) The differences in transmission properties of two bird calls show relation to their specific functions. *J Acoust Soc Am* 140(6):4271–4275
- Plomp R, Bouman MA (1959) Relation between hearing threshold and duration of tone pulses. *J Acoust Soc Am* 31:749–758
- Podos J (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* 51:537–551
- Pohl NU, Slabbekoorn H, Klump GM, Langemann U (2009) Effects of signal features and environmental noise on signal detection in the great tit, *Parus major*. *Anim Behav* 78:1293–1300
- Pohl NU, Slabbekoorn H, Neubauer H, Heil P, Klump GM, Ulrike Langemann U (2013) Why longer song elements are easier to detect: threshold level-duration functions in the Great Tit and comparison with human data. *J Comp Physiol A* 199(3):239–252
- Price JJ (2013) Why is birdsong so repetitive? Signal detection and the evolution of avian singing modes. *Behaviour* 150:995–1013
- Pytte CL, Rush KM, Ficken MS (2003) Regulation of vocal amplitude by the blue-throated hummingbird, *Lampornis clemenciae*. *Anim Behav* 66:703–710
- Pytte CL, Ficken MS, Moiseff A (2004) Ultrasonic singing by the blue-throated hummingbird: a comparison between production and perception. *J Comp Physiol A* 190:665–673
- Radford AN, Ridley AR (2008) Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Anim Behav* 75:519–527
- Reichard DG, Anderson RC (2015) Why signal softly? The structure, function and evolutionary significance of low-amplitude signals. *Anim Behav* 105:253–265
- Reichard DG, Welklin JF (2015) On the existence and potential functions of low-amplitude vocalizations in North American birds. *Auk* 132:156–166
- Reichard DG, Rice RR, Vanderbilt CC, Ketterson ED (2011) Deciphering information encoded in birdsong: male songbirds with fertile mates respond most strongly to complex, low-amplitude songs used in courtship. *Am Nat* 178(4):478–487
- Reichard DG, Rice RR, Schultz EM, Schrock SE (2013) Low-amplitude songs produced by male dark-eyed juncos (*Junco hyemalis*) differ when sung during intra- and inter-sexual interactions. *Behaviour* 150:1183–1202
- Rek P (2013) Soft calls and broadcast calls in the corncrake as adaptations to short and long range communication. *Behav Process* 99:121–129
- Rek P, Osiejuk TS (2011) Nonpasserine bird produces soft calls and pays retaliation cost. *Behav Ecol* 22:657–662
- Richards DG, Wiley RH (1980) Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am Nat* 115(3):381–399
- Ritschard M, Brumm H (2011) Effects of vocal learning, phonetics and inheritance on song amplitude in zebra finches. *Anim Behav* 82:1415–1422
- Ryan MJ, Brenowitz EA (1985) The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am Nat* 126(1):87–100
- Sandoval L, Dabelsteen T, Mennill DJ (2015) Transmission characteristics of solo songs and duets in a neotropical thicket habitat specialist bird. *Bioacoustics* 24(3):289–306
- Searcy WA, Beecher MD (2009) Song as an aggressive signal in songbirds. *Anim Behav* 78:1281–1292
- Searcy WA, Nowicki S (2006) Signal interception and use of soft song in aggressive interactions. *Ethology* 112:865–872
- Searcy WA, Yasukawa K (2017) Eavesdropping and cue denial in avian acoustic signals. *Anim Behav* 124:273–282

- Shannon G, McKenna MF, Angeloni LM, Crooks KR, Fristrup KM, Brown E, Warner KA, Nelson MD, White C, Briggs J, McFarland S, Wittermyer G (2016) A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol Rev* 91:982–1005
- Slabbekoorn H, Ripmeester EAP (2008) Birdsong and anthropogenic noise: implications and applications for conservation. *Mol Ecol* 17:72–83
- Slabbekoorn H, Dooling RJ, Popper AR, Fay RR (eds) (2018) Effects of anthropogenic noise on animals. Springer, New York, p 309
- Snow DW (1958) A study of blackbirds. Allen and Unwin, London
- Srivastava KH, Elemans CPH, Sober SJ (2015) Multifunctional and context-dependent control of vocal acoustics by individual muscles. *J Neurosci* 35(42):14183–14194
- Titus RC (1998) Short-range and long-range songs: use of two acoustically distinct song classes by dark-eyed juncos. *Auk* 115(2):386–393
- Vargas-Castro LE (2015) Spatial pattern of syllable sharing in white-throated thrushes: implications for song learning and dispersal behaviours. *Behaviour* 152(6):775–795
- Vargas-Castro LE, Sandoval L, Searcy WA (2017) Eavesdropping avoidance and sound propagation: the acoustic structure of soft song. *Anim Behav* 134:113–121
- Wahlberg M, Larsen ON (2017) Propagation of sound. In: Brown CH, Riede T (eds) Comparative bioacoustics: an overview. Bentham Science, Sharjah, pp 63–121
- Ward S, Lampe HM, Slater PJB (2004) Singing is not energetically demanding for pied flycatchers, *Ficedula hypoleuca*. *Behav Ecol* 15(3):477–484
- Weir JT, Wheatcroft DJ, Price TD (2012) The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evolution* 66:2773–2783
- Wiley RH (1991) Associations of song properties with habitats for territorial oscine birds of Eastern North-America. *Am Nat* 138:973–993
- Wiley RH (2013) Signal detection, noise, and the evolution of communication. In: Brumm H (ed) Animal communication and noise, animal signals and communication, vol 2. Springer, Berlin, pp 7–30
- Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav Ecol Sociobiol* 3:69–94
- Wiley RH, Richards DG (1982) Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsmas DE, Miller EH (eds) Acoustic communication in birds. Academic, New York, pp 132–181
- Xia C, Liu J, Alström P, Wu Q, Zhang Y (2013) Is the soft song of the brownish-flanked bush warbler an aggressive signal? *Ethology* 119:653–661
- Yang XJ, Ma XR, Slabbekoorn H (2014) Timing vocal behaviour: experimental evidence for song overlap avoidance in Eurasian wrens. *Behav Process* 103:84–90
- Yorzinski JL, Patricelli GL (2010) Birds adjust acoustic directionality to beam their antipredator calls to predators and conspecifics. *Proc R Soc B* 277:923–932
- Zeng FG, Nie K, Stickney GS, Kong YY, Vongphoe M, Bhargava A, Wei C, Cao K (2005) Speech recognition with amplitude and frequency modulations. *Proc Natl Acad Sci USA* 102(7):2293–2298
- Zollinger SA, Brumm H (2015) Why birds sing loud songs and why they sometimes don't. *Anim Behav* 105:289–295
- Zollinger SA, Goller F, Brumm H (2011) Metabolic and respiratory costs of increasing song amplitude in zebra finches. *PLoS One* 6(9):e23198
- Zollinger SA, Podos J, Nemeth E, Goller F, Brumm H (2012) On the relationship between, and measurement of, amplitude and frequency in birdsong. *Anim Behav* 84(4):e1–e9
- Zuk M, Kolluru GR (1998) Exploitation of sexual signals by predators and parasitoids. *Q Rev Biol* 73:415–438