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Why birds sing loud songs and why they sometimes don't

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In birdsong, and in most commonly studied acoustic communication systems, research has often focused on temporal and frequency-related signal parameters. However, although variations in amplitude are often overlooked and seldom measured, they are just as critical in communication. Recent studies have demonstrated that vocal amplitude plays an important role in both territorial behaviours and mate choice in birds. Several songbird species have been shown to produce low-amplitude songs, used primarily in aggressive encounters between males. On the other hand, loud songs may be an honest signal of current condition in males and recent studies have shown that females may prefer high-amplitude songs. Although it is generally assumed that louder song is more costly to produce, there is little empirical evidence to support this assumption. Here we review data on the metabolic costs of singing at different vocal amplitudes, and discuss recent studies from our laboratory showing that louder songs elicit stronger aggressive responses from territorial males. Together, these findings suggest that while the energetic costs of singing loudly are negligibly small, social aggression may be a key constraint that limits the upper amplitude of vocal signals. Finally we discuss future directions that can increase our understanding of the role that amplitude plays in acoustic communication in animals.

AMPLITUDE MATTERS

Acoustic signalling, while not the most common mode of communication in animals, is one of the most studied by biologists. In large part, the study of acoustic signals in all taxa has focused on spectral parameters and temporal patterns. Relatively little attention, however, has been paid to signal amplitude, but nevertheless amplitude, the intensity of the signal, is a critically important component of any acoustic signal. The most obvious significance may be that louder signals can be heard over longer distances and can be detected more easily in noise. Indeed, there is a wealth of perceptual studies demonstrating that signal amplitude at the position of the receiver (or more accurately, the signal-to-noise ratio) is crucial for the detection and recognition of acoustic signals (Brumm, 2013). Thus, amplitude is one of the decisive parameters for successful song transmission in birds (Dooling & Blumenrath, 2013). Moreover, as we will show in this paper, the amplitude of birdsong may also encode important information that is relevant for mating and reproduction.

One of the reasons why signal amplitude is often neglected in animal communication studies is that it is not straightforward to measure accurately. By way of example, consider a researcher attempting to measure the song amplitude of a bird singing in a nearby tree. The amplitude of the signal at the position of the observer and her sound pressure level (SPL) meter or calibrated microphone, depends on several factors: (1) the distance from the singing bird, (2) the orientation of the singer (Brumm, 2002; Larsen & Dabelsteen, 1990; Nelson, Beckers, & Suthers, 2005; Patricelli, Dantzker, & Bradbury, 2007), and (3) the environmental acoustics (e.g. Harris, 1966; Nelson, 2003; Wiley & Richards, 1982). Signal transmission is influenced by environmental acoustics due to absorption of and scattering by vegetation and others reflective surfaces in the habitat, air temperature and humidity, and fluctuations of signal amplitude induced by wind. Therefore, the researcher must take all these variables into account when trying to measure sound amplitude. This can be done by measuring the distance to the singing bird, standardizing the orientation of the singing bird relative to the microphone (e.g. by only using recordings made while the bird is facing in one direction), recording the temperature, humidity and weather conditions, minimizing the distance

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between the bird and microphone, and trying to find unobstructed lines of sight between the microphone and singer.

In the laboratory, measuring song amplitude is a bit more straightforward since environmental conditions can be controlled and the distance between the vocalizing animal and the microphone can be fixed. In addition, problems of directional sound radiation patterns can be circumvented by measuring from directly above the bird rather than from the side or the front (Brumm & Todt, 2002). When birds regularly choose the same song perches, this method can even be used in field studies by fixing the recording microphone directly above the perch where the bird sings (Nemeth, Kempenaers, Matessi, & Brumm, 2012). But although the accurate measurement of amplitude requires these extra considerations, it is important to go to the trouble if one really wants to understand the role of song amplitude in bird communication. This is particularly the case for the study of the so-called ‘soft songs’, which by their nature ought to be defined by their amplitude. However, the category of ‘soft’ or ‘low-amplitude’ song in a given species can comprise different types of song that differ in their structure but which cannot be distinguished based on amplitude alone (Anderson, Searcy, Peters, & Nowicki, 2008).

Although we present this paper as part of a special issue devoted to low-amplitude signalling, we will discuss primarily the costs and constraints surrounding the production of high-amplitude signals. At first glance, one might wonder what relevance this has to the understanding of the usage of soft or quiet signals by animals, but it is essential to define what physiological, physical and behavioural limitations constrain the amplitude of acoustic signals if we are to discover why animals produce signals at different amplitudes in the first place. Low-amplitude signals are used by species across a range of taxa and in a number of different contexts and there are several hypotheses about why they do so. Many songbirds produce quiet songs during moments when they are aggressively or sexually aroused, for example during escalated territorial disputes or during courtship (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998; Searcy & Nowicki, 2006). Explanations for why animals use soft signals tend to be two-fold: first, that low-amplitude signals prevent eavesdropping by predators or competitors (Dabelsteen et al., 1998; Searcy, Akçay, Nowicki, & Beecher, 2014), and second, that soft signals are less costly to produce than loud signals (Gil & Gahr, 2002; Searcy et al., 2014). These hypotheses hint at fitness-related costs for the production of loud songs, which in turn raises the possibility that song amplitude may be linked to sexual selection.

AMPLITUDE IN BIRDSONGS AS A SEXUALLY SELECTED TRAIT?

In their influential review on the costs of birdsong, Gil and Gahr (2002) listed a number of song traits that may be important in sexual selection, and in particular they hypothesized that performance-related traits like song rate, repertoire size, length of songs or bouts, and song amplitude may potentially function as honest signals.

If song amplitude is sexually selected, it would mean that birds with loud songs have a mating advantage that ultimately leads to increased fitness. Unfortunately, studies showing such a link are still lacking. Until future studies resolve the question of whether song amplitude plays a role in sexual selection, by directly correlating variations in amplitude with variations in reproductive success (Nemeth et al., 2012), we can learn from studies that look for indirect evidence, such as proximate constraints that may limit song performance. Along these lines, Gil and Gahr (2002) postulated that the costs acting on sexually selected song traits may stem from energetic needs, developmental constraints, neural constraints, social aggression, predation and immunocompetence.

Compelling initial evidence suggesting that song amplitude may play a role in sexual selection comes from studies on female song preferences for high-amplitude song. When presented with male songs at two different amplitudes, female red-winged blackbirds, *Agelaius phoeniceus*, responded with a higher number of copulation solicitation displays to the higher-amplitude song (Searcy, 1996). Similarly, female zebra finches, *Taeniopygia guttata*, in an operant task showed a preference for louder songs, even when accounting for changes in amplitude with distance (Ritschard, Riebel, & Brumm, 2010). These results suggest that high-amplitude songs may indeed lead to mating advantages. But why would females show this preference? What information does a high-amplitude song communicate? The first step to understanding preferences is to understand degrees and sources of variation in the trait, and indeed male songbirds, at least those species for which amplitude has been measured, differ markedly in their song amplitude (Fig. 1). Several laboratory and field studies found song amplitude differences as high as 5–15 dB between male birds within a given population (Brumm, 2009; Brumm & Ritschard, 2012; Dabelsteen, 1981; Nemeth et al., 2012; Ritschard, Laucht, Dale, & Brumm, 2011). An increase of 6 dB equals a doubling in sound pressure; thus, a bird needs to increase its vocal sound pressure more than 5.6 times to achieve the 15 dB difference found in some species. If this variation in song amplitude is linked to some fitness-related trait in males, females could use amplitude to assess the quality of potential mates. But which trait is reflected in the amplitude of a male's song? Several potential candidates have been investigated to date but undoubtedly there may be more.

The observation that females may prefer louder songs, may lead to the assumption that larger individuals produce higher sound amplitudes, as is the case in some other taxa, such as arthropods and anurans (Gerhardt & Huber, 2002), and that females are using amplitude as an index signal of male size. While it has been hypothesized in the literature that larger bird species may be able to produce louder sounds (Brackenbury, 1979), a study on captive and free-ranging songbirds (Brumm, 2009) did not find any evidence that this is true within species. The notion of no association between body size and song amplitude in songbirds is corroborated

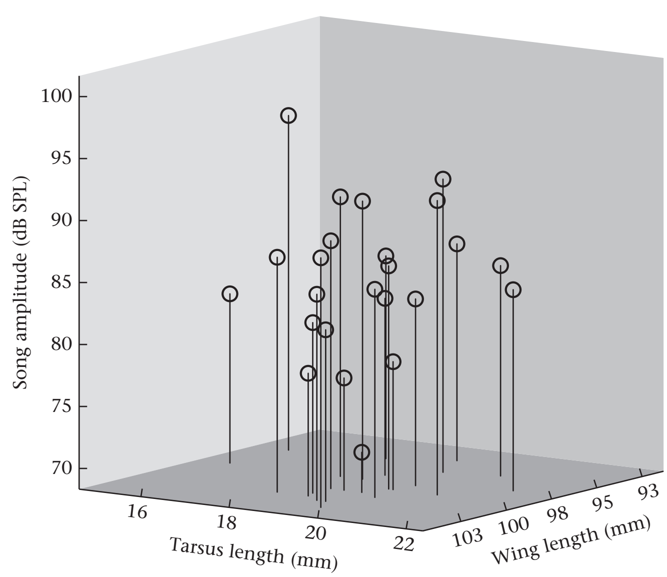

Figure 1. Vocal amplitude is not a reliable index signal of body size in rock sparrows, *P. petronia*. Each data point gives measures of one individual male ($N = 24$): amplitude/tarsus length (Spearman rank correlation: $r_S = -0.56$, $P = 0.794$); amplitude/wing length ($r_S = 0.257$, $P = 0.226$). Data were collected by Erwin Nemeth, Henrik Brumm, and Giuliano Matessi (for details see Nemeth et al., 2012).

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