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Stridulated soft song by singing insects

Susan L. Balenger*

Department of Ecology, Evolution and Behavior, University of Minnesota, Twin Cities, MN, U.S.A.

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The study of low-amplitude or 'soft' songs and calls has largely been limited to organisms that produce multiple call types that fall neatly into a bimodal distribution with respect to amplitude. The soft vocalizations of many of these animals, including birds and mammals, have proven to be extremely difficult to collect data on due to difficulty in hearing and recording such songs in the wild, the lack of production of these sounds in captivity, and the difficulty in standardizing measurements of the amplitude produced by free-moving animals. Here I suggest we consistently expand the working definition of soft song to allow for the inclusion of insects and other organisms whose calls do not easily fit into a 'high-amplitude' versus 'low-amplitude' signal paradigm. For instance, some species of moths produce extremely quiet ultrasonic courtship songs without also producing a high-amplitude song, and field crickets sing courtship songs that contain both relatively loud and quiet elements within the same song. Soft-singing moths and crickets may not only prove more practical to work with, but may also provide answers to heretofore untestable hypotheses about the function and evolution of soft song.

Study of acoustic communication has historically focused most attention on signals that are easily identified and observed by humans (i.e. sounds produced within the range of human hearing and produced often enough to be noticed; Bradbury & Vehrencamp, 2011). Over the last century, the study of acoustic communication and signalling has benefited greatly from extensive observation of wild animals under natural conditions as well as the development of technology for recording and measuring sounds that fall outside of the human hearing range (Ghose & Moss, 2003; Griffin, 1950; Noyes & Pierce, 1938). Such advances have enabled the documentation of elements of acoustic signals that might otherwise have gone unnoticed and unconfirmed (Griffin, 1946; Thorpe & Griffin, 1962).

Resulting in part from these technical advances, enormous progress has been made in understanding, for instance, the coevolution of ultrasonic signalling by bats and moths, as well as a more general understanding of predator–prey influences on signal evolution (Conner & Corcoran, 2012; Greenfield, 2014). In addition to our interest in sounds outside of the human frequency range, researchers have variously paid attention to sounds produced at relatively low amplitudes. Such sounds can be difficult to detect when studying wild animals that are reticent to behave normally when human observers are close by, but the sounds are of such low amplitude that humans have a difficult time hearing them from more than a few metres away. As a further complication, recent discoveries in moths have found that many species produce extremely low-amplitude courtship signals within the ultrasonic frequency range (Nakano et al., 2008, Nakano, Takanashi, & Surlykke, 2014).

Low-amplitude signalling, variably called 'quiet song', 'soft song' or 'whisper communication', is an easily overlooked form of conspecific acoustic signal when more easily studied high-amplitude signals exist (Dabelsteen, McGregor, Lampe, Langmore, & Holland, 1998). Although much of the research with respect to quiet acoustic signals has dealt with songbirds, soft song still has seen limited study (Dabelsteen, 2005). In a recent survey of low-amplitude vocalizations across North American birds, Reichard and Welklin (2015) found descriptions of soft songs, soft calls or whispers performed by more than half of the species described in the *Birds of North America* online archive (Poole & Gill, 2005). This result strongly suggests that quiet acoustic signalling is a prevalent phenomenon among birds and that greater attention should be given to understanding its evolution, function and structural variation from louder, more obvious songs and calls.

In birds, soft intraspecific communication has been associated with both aggression (Akçay, Tom, Campbell, & Beecher, 2011; Ballentine, Searcy, & Nowicki, 2008) and courtship (Dabelsteen et al., 1998; Reichard, Rice, Vanderbilt, & Ketterson, 2011), and

* S. L. Balenger, Department of Ecology, Evolution and Behavior, University of Minnesota, Twin Cities, MN 55108, U.S.A.
E-mail address: sbalenge@umn.edu.

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there are multiple hypotheses regarding the role of 'quietness' per se, most notably the ability to convey private information while avoiding eavesdropping by unintended receivers (Dabelsteen et al., 1998; Nakano et al., 2014). These unintended receivers likely include conspecific rivals for mates, predators and acoustically orienting parasitoids (Conner, 2014; Dabelsteen et al., 1998; Searcy & Nowicki, 2006). Avian soft song is generally characterized as falling into one of two categories: a low-amplitude version of a species-typical, long-range song or a low-amplitude song that varies considerably in temporal characteristics from the typical long-range song (Anderson, Nowicki, & Searcy, 2007, Anderson, Searcy, Peters, & Nowicki, 2008; Reichard et al., 2011).

In singing insects, however, the best examples of low-amplitude signalling do not fit the above categories of soft song. In this paper, I first ask whether this is a phenomenon that is likely to be limited to sophisticated vocal communicators with complex vocal and social structures, or whether greater attention should also be given to quiet acoustic signalling performed by insects, in particular those that produce sound via stridulation. I then provide a simple but crucial expansion of the definition of soft song, under the assumption that singing insects are to be included in the study of soft song. Finally, I explore the structure, significance and function of low-amplitude courtship song of two types of insect: moths (Lepidoptera: Pyralidae, Crambidae and Noctuidae) and field crickets (Orthoptera: Gryllidae, Gryllinae). The songs of field crickets have a long history of study, and their courtship songs loosely share certain characteristics with the soft songs produced by songbirds. Low-amplitude moth songs, on the other hand, do not easily fit widely used definitions of soft song, even though the quietness of their songs appears to be integral to their mating function.

SOFT SOUND PRODUCTION BY NONVOCALIZING ANIMALS?

Animals that produce sound through contractions of their respiratory system are said to vocalize. All terrestrial vertebrates possess a vocal tract, but sounds are also commonly produced by these and other animals through nonvocal means (Fitch & Hauser, 2003). Nonvocal acoustic communication, however, has informed little of our current understanding of soft song perhaps due at least in part to the different terminology used and the importance placed on amplitude by researchers who study various taxonomic groups (Reichard et al., 2011).

According to Ewing (1989), 'there is no entirely satisfactory classification of the diverse methods of the sound production in arthropods' (page 16). Acoustic signalling by insects and other arthropods, however, typically involves using the exoskeleton in conjunction with muscle contraction of body parts to achieve sound production (Ewing, 1989). While sounds produced by insects through moving two body parts across one another (i.e. stridulation) or through vibrating the exoskeleton in response to muscle contraction–expansion (i.e. tymbal vibrations) are generally not as structurally complex as those produced by some birds and mammals, many singing insects do have additional morphological or behavioural adaptions that allow for the modulation of amplitude. For example, field crickets lower their wings during the quieter trill portion of courtship song, which may have the effect of dampening the sound, although I am not aware of any study having been performed to test this hypothesis. Many other crickets utilize burrows (mole crickets: Grylloptalpidae) or foliage (tree crickets: Gryllidae, Oecanthinae) for sound amplification (Bennet-Clark, 1970, 1989). Furthermore, some organisms that utilize nonvocal means of acoustic communication strictly produce quiet sounds and do not have the ability to modulate amplitude.

DEFINING SOFT SONG

Dabelsteen et al. (1998) defined quiet singing by songbirds as 'low volume singing with a probable social function during the breeding season' (page 101). Soft song is also described as a song that is produced at a relatively lower amplitude than that of a species-typical broadcast or full song (Reichard, Rice, Schultz, & Schrock, 2013; Reichard et al., 2011). By incorporating the relative amplitude of the signal into the definition, one can avoid the issue of the receiver's sensory abilities (Dabelsteen et al., 1998). Subtypes of soft song have been described as those that are quiet versions of their normal long-range song (soft long-range song) and those that are quiet and distinct spectrally and temporally from the species-typical long-range song (short-range song; Reichard et al., 2013, 2011; Titus, 1998). By limiting our definition of soft song to such relative characterizations, though, we will exclude many organisms that produce only quiet acoustic sounds, perhaps most notably among singing insects.

In the case of singing insects, two of the most studied types of low-amplitude signals are (1) courtship songs that are quiet but are produced by species that do not produce a louder, long-range calling song, and (2) courtship songs that are temporally distinct from long-range calling songs and that contain both high- and low-amplitude elements. Our understanding of soft song will be facilitated by a more inclusive definition that encourages dialogue between researchers studying diverse taxonomic groups that produce soft song in different ways potentially for different reasons. I will focus on moths and field crickets as examples of (1) and (2), respectively, because these types of low-amplitude courtship songs have been most thoroughly studied in these groups of insects.

Recent investigations into the function of the absolute quietness of the courtship songs of some moths have found that amplitude appears crucial to the existence of a private communication channel used by males to ensure mating success (Nakano et al., 2014). In the case of field crickets, however, the function of the amplitude of song elements has been little studied (but see Balakrishnan & Pollack, 1996; Mhatre & Balakrishnan, 2006; Nandi & Balakrishnan, 2013; Vedenina & Pollack, 2012). I argue that our understanding of soft song will benefit if we broaden its definition to include any intraspecific acoustic form of communication in which relative or absolute quietness is a dominant and consistent element of the signal (Reichard & Welklin, 2015). Recently, Reichard and Welklin (2015) defined low-amplitude signals as 'any acoustic signal produced at a low volume such that the signal's effective transmission distance is limited to a close-proximity interaction between the sender and receiver' (page 156). Definitions such as this are more taxonomically inclusive by removing the need for relative comparisons to louder signals but require that researchers also attend to the sensory abilities of receivers.

ULTRASONIC COURTSHIP WHISPERING BY MOTHS

It is generally accepted that ultrasonic hearing evolved in moths as a defence mechanism allowing avoidance of predation by bats (Conner & Corcoran, 2012). Subsequently, inter- and intraspecific ultrasonic communication evolved repeatedly in this lineage via sensory bias, utilizing a variety of sound-producing mechanisms (Conner & Corcoran, 2012). The repeated evolution of singing in moths has produced a variety of behavioural and mechanistic solutions to the need for ultrasonic communication, including (but not limited to) drumming (percussion), tymbal vibrations and stridulation of a multitude of specialized scales and body parts (Conner, 1999; Nakano et al., 2013). Therefore, moths represent a fascinating group in which to study acoustic signalling from a comparative perspective. In the majority of families, though, we do

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