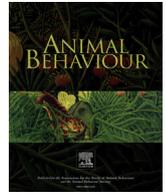




Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Whispered Communication

Stridulated soft song by singing insects

Susan L. Balenger*

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

ARTICLE INFO

Article history:

Received 6 January 2015
 Initial acceptance 30 January 2015
 Final acceptance 4 March 2015
 Available online xxx
 MS. number: SI-15-00008

Keywords:

acoustic communication
 courtship song
 eavesdropping avoidance
 field cricket
 tympanate moth

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.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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.

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 adaptations 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

not know whether sounds are produced at all, and when they are, we do not know how and/or why in many cases (Nakano, Takanashi, Surlykke, Skals, & Ishikawa, 2013).

At first glance, acoustic signalling by moths might not appear to add much to our understanding of soft song if we utilize the working definition that is typically used with respect to avian vocal communication. Moths produce either loud or soft sounds, and species are not known to produce both types. In some cases, loud sounds have evolved to interfere with or 'jam' bat signals by mimicking the echos and altering the bat's perception of the distance to its prey (Fullard et al., 1979). When the signal's function is to interfere with bat echolocation, both male and female moths produce the loud signal (Fullard et al., 1979). Loud sounds also function in intraspecific sexual communication in moths. When used in sexual communication, only males produce ultrasonic high-amplitude songs (approximately 90–100 dB SPL at 10 cm). These songs function as advertisement in mid-range sexual communication with females (i.e. closer than sex pheromones can be detected; Nakano et al., 2014). Loud sounds that do not interfere with bat echolocation, however, can be risky to produce by increasing the likelihood of predator eavesdropping. Quiet sound production, on the other hand, may be a relatively underappreciated mode of sexual signalling that has evolved repeatedly in moths.

A series of studies over the last decade from researchers in Japan and Denmark have greatly added to our understanding of the evolution and function of acoustic communication in moths. These studies suggest that sexual sound communication may be more common in moths than generally believed because many species may be using low-amplitude high-frequency channels (Nakano et al., 2013, 2014). Beginning with studies of the Asian corn borer moth, *Ostrinia furnacalis*, researchers identified extremely quiet ultrasonic sounds produced by the stridulation of specialized wing and thorax scales found only on males (Nakano et al., 2006, 2008). These 'whispered courtship songs' are produced when females are in extremely close proximity, and are not detected by females that are more than 3 cm away (Nakano et al., 2008). In *O. furnacalis*, these whispered songs by males cause females in the immediate vicinity to behave as though they have just heard a bat in the distance; females freeze in place to avoid bat detection and predation, and males exploit this behavioural response to mate with stationary females (Nakano, Takanashi, Skals, Surlykke, & Ishikawa, 2010, Nakano et al., 2013). This led the researchers to hypothesize that whispering might be a widespread form of courtship song among moths attempting to simultaneously avoid bat detection and obtain copulations (Nakano et al., 2008, Nakano, Ishikawa, et al., 2009). To test this idea, Nakano, Takanashi, et al. (2009b) looked for low-amplitude whispered courtship songs in 13 tympanate moth species across four families. Of the species that did produce ultrasonic signals when near females, all nine species produced ultrasonic signals at a relatively low amplitude (43–76 dB SPL at 1 cm), suggesting that quiet courtship may in fact be a relatively common phenomenon among singing moths (Nakano, Takanashi, et al., 2009b).

Nakano et al. (2014) refer to the quiet ultrasonic communication used by some male moths as both 'whispers' and 'soft song'. In a recent review of acoustic communication in nocturnal Lepidoptera, Greenfield (2014) used the term 'soft song' to discuss this phenomenon. It, therefore, appears that some researchers studying quiet ultrasonic signals produced by moths are embracing a connection with the field of soft song.

A great deal of research is still needed to determine both the extent of soft song in moths and its function. Moth acoustic communication promises to be a particularly compelling example for studying the evolution of soft song since acoustic communication evolved independently multiple times within this group.

Therefore, if we consider soft song to include animals that do not also produce a louder song, we will likely gain greater insight into its evolution and function.

FIELD CRICKET COURTSHIP SONG

In most field crickets (Orthoptera, Gryllidae, Gryllinae), males produce three distinct songs or signals by scraping or pulsing their two forewings together. By far the most commonly studied song is the calling song, a loud, long-distance song that males use to announce their location to females (Alexander, 1961, 1962). Aggressive songs are loud, sharp signals used during male–male conflicts over territory and dominance (Alexander, 1961, 1962). Courtship songs are produced when members of a pair are in physical contact with one another, allowing for quiet acoustic communication as well as simultaneous chemical signalling via cuticular hydrocarbon profiles (Alexander, 1961, 1962; Simmons, Thomas, Simmons, & Zuk, 2013; Thomas & Simmons, 2009). Species vary in whether and to what extent they modulate the amplitude of elements within each of these songs. Although courtship song is used by both moths and crickets to increase a male's likelihood of mating, there are crucial differences, most notably female choice, suggesting that courtship song in crickets may be related to male quality or condition. Plainly put, female crickets control male mating opportunities. For copulation to occur, a female must choose to mount a male and participate in spermatophore transfer (Alexander, 1961; Burk, 1983). Studies examining the relationship between courtship song and body size and condition (*Gryllus lineaticeps*: Wagner & Reiser, 2000; *Gryllus texensis*: Gray & Eckhardt, 2001, *Gryllus pennsylvanicus*: Harrison, Thomson, Grant, & Bertram, 2013), sperm quality (*Teleogryllus oceanicus*: Simmons, Tinghitella, & Zuk, 2010), immune function (*Gryllus bimaculatus*: Rantala & Kortet, 2003; *T. oceanicus*: Simmons et al., 2010; Tregenza, Simmons, Wedell, & Zuk, 2006) and energetic expenditure (*Acheta domesticus*: Hack, 1998; *G. bimaculatus*: Mowles, 2014) have produced variable support for a relationship between a male's courtship song and his quality or condition. Clearly more work is necessary to elucidate what, if any, information females gain through listening to the courtship song of a prospective mate.

Field crickets are an attractive target for researchers of soft song for several practical reasons. It is generally simple and straightforward to observe and record both the calling and courtship songs produced by male crickets in a laboratory setting. Generally, darkness and a reasonable temperature will induce calling in a male; all he needs to begin courting is the close physical presence of a female. It is easy to simulate appropriate conditions in the laboratory, allowing for repeated observation of single individuals and the recording of song parameters of many individuals. Field crickets also provide the opportunity to study female responsiveness to amplitude variation utilizing synthesized songs and playback. Essentially, many of the difficulties associated with studying soft song in birds and mammals (e.g. its rarity of detection and the difficulty in standardizing amplitude from recordings) are essentially irrelevant when it comes to studying crickets in the laboratory. Unfortunately, many of the difficulties associated with field studies remain. Few studies have examined amplitude of field cricket song in the wild (Nandi & Balakrishnan, 2013). In the future it will also be important to record song amplitudes under field conditions to determine how the distribution of this trait in the wild corresponds to that in captivity.

The courtship songs produced by the various North American *Gryllus* species have all been found to characteristically include two distinct types of pulses: 'ticks', which are short and sharp and have a relatively high fundamental frequency (generally ~14–17 kHz),

and 'chirps', which are less intense and have a fundamental frequency similar to that of *Gryllus* calling songs (~3.5–5 kHz; Alexander, 1961; Fitzpatrick & Gray, 2001; Walker, 1974; see Fig. 1). Vedenina and Pollack (2012) quantified among- and within-male variability in courtship song parameters of *Gryllus assimilis*, including temporal aspects of pulses, number of pulses, frequency characteristics and the ratio of chirp to tick amplitude. The most variable of all the measured song characteristics was the ratio of chirp to tick amplitude, with the among-male coefficient of variation (CV) for 21 males being 93% and the within-male being 58% (Vedenina & Pollack, 2012). When among-male variability is greater than within-male variability, a trait may represent a good target for sexual selection (Gerhardt, 1991). In the case of *G. assimilis*, although within-male variability in the ratio of chirp to tick amplitude is lower than among-male variability, it is still so variable that females are unlikely to be able to base a preference on the characteristics of any individual male's amplitude ratio (Vedenina & Pollack, 2012). It still remains to be tested, however, whether this ratio is important in *G. assimilis*, or in any other species of field cricket, since the authors used constant amplitudes for both chirp and tick pulses when assessing female responsiveness to structural and sound properties of courtship song (Vedenina & Pollack, 2012).

In a study designed to evaluate whether courtship song might be involved in reproductive isolation between the cryptic sister species *G. texensis* and *Gryllus rubens*, Fitzpatrick and Gray (2001) found that amplitude was the same on average (79.8 dB at 19 cm) for the high-frequency ticks, but significantly different between the two species for the low-frequency chirps (65.9 dB for *G. texensis*, 71.9 dB for *G. rubens* at 19 cm). The within-species CV for the amplitudes of both ticks and chirps were relatively low (4.4–8.2%), but it remains unclear whether amplitude in this case would be more

likely to indicate species identity than male quality because there was no information regarding within-male variability. Subsequent studies of these two species have evaluated both within-species and within-individual song properties, but have focused on calling song and ignored amplitude (Higgins & Waugaman, 2004).

The courtship song of *T. oceanicus* also contains two distinct elements of pulses, but in contrast to *Gryllus* species, the elements are referred to as 'chirps' and 'trills'. Both chirps and trills of this species utilize a similar fundamental frequency (4.5 kHz), and it is the chirp portion that is relatively more intense than the trill portion. The chirp consists of a series of seven to nine pulses, which increase in intensity with each pulse (Fig. 1). The trill, on the other hand, contains a long series of pulses at a constant intensity (Fig. 1).

Balakrishnan and Pollack (1996) performed the most comprehensive study to date of the role of amplitude modulation of courtship song on female recognition and preference using *T. oceanicus*. The authors found clear evidence that amplitude modulation of the chirp portion (first chirp: ~88 dB SPL, last chirp: ~100 dB SPL at 46 cm) is unnecessary for female acceptance and mounting. In all song manipulations, however, the trill component (i.e. the soft pulses) were held constant at 90 dB SPL. Therefore, the role, if any, of the relative quietness of the trill portion of this field cricket's courtship song remains unstudied. The crucial findings of this study were that females of this species require a fundamental chirp frequency of 4.5 kHz and a species-typical temporal pattern of the chirp. When played only the trill pulses of the song, female responsiveness decreased, even when the amplitude was manipulated to mimic that of a song containing both the chirp and trill portions. Perhaps most interesting from the perspective of soft song was the finding that reducing the amplitude of the chirp so the amplitude of the entire song matched the 'quiet' 90 dB SPL of the trill resulted in no change in female responsiveness when compared to a normal courtship song.

Courtship song amplitude modulation by at least some species of field crickets appears unlikely to function in avoiding eavesdropping by parasitoids and predators for two primary reasons. Calling song is loud and, of species where this has been studied, male field crickets spend several hours, on average, each night producing this song, but they spend only a few brief seconds to minutes courting any given female (Alexander, 1961). The protective value of reducing amplitude while courting seems trivial when compared to the amount of time males spend calling loudly in ways that increase their exposure to parasitoids and predators. Furthermore, in some species, courtship songs contain elements that are at least as loud if not louder than the calling song (e.g. *T. oceanicus*: Balakrishnan & Pollack, 1996). While such loud elements in courtship song are often brief, suggesting they may be less likely to be heard, on average, one would expect selection against these loud elements entirely if they increase predation.

It is still unknown whether acoustically orienting parasitoids like *Ormia ochracea* use courtship song to find their cricket hosts. It does seem probable, though, since *O. ochracea* is widely distributed with many host species across North America. Gray, Banelos, Walker, Cade, and Zuk (2007) found that gravid female flies are preferentially attracted to the calling song of their local host species, but many still recognize other species as hosts.

It appears more likely that the low-amplitude components of cricket courtship songs would be involved in avoiding eavesdropping by conspecific males rather than predators. It is generally accepted that the intended receiver of a cricket courtship song is a female in close physical proximity to the caller. Depending on the distance between neighbouring males, a caller might limit the likelihood of courtship interference from competitors if those competitors are not capable of detecting the quiet song. As described earlier, however, some crickets also have high-amplitude

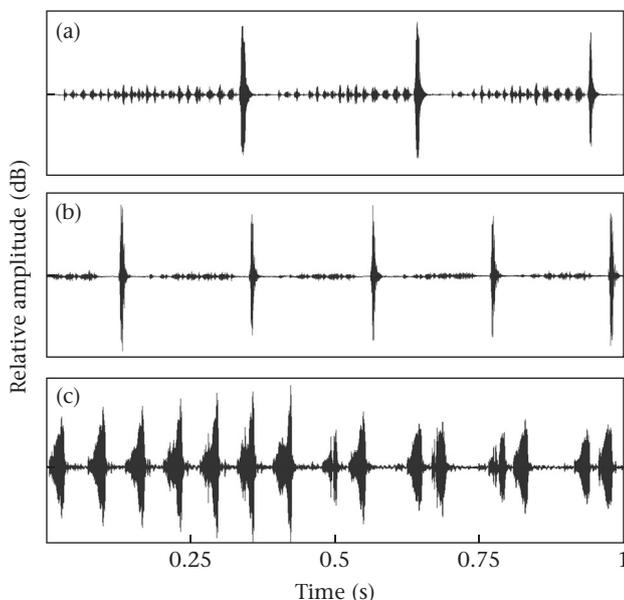


Figure 1. Examples of field cricket courtship songs. Oscillograms of stereotypical, loud high-amplitude 'ticks' and softer lower-amplitude 'chirps' of (a) *Gryllus texensis* and (b) *G. ovisopsis*. (c) Oscillogram of courtship song of *Teleogryllus oceanicus* showing stereotypical high-amplitude 'chirps', followed by lower-amplitude pulses, which make up the 'trill'. These examples are not indicative of the relative differences in absolute amplitude between these individuals or species. (a) Entire recording available at <http://macaulaylibrary.org/audio/130070>. Recording made by T. J. Walker, Arkansas, August 1973. (b) Entire recording available at <http://macaulaylibrary.org/audio/129871>. Recording made by T. J. Walker, Florida, September 1972. (c) Entire recording available upon request. Recording made by S. L. Balenger, Minnesota, March 2013.

elements in their courtship songs (Fig. 1), which could notify neighbouring males of the presence of a female (unintended receivers) or provide a warning to those males to stay away (intended receivers). Studies that measure or manipulate courtship song amplitude and evaluate the response of nearby males would be useful in disentangling this issue.

One extremely effective way to avoid acoustic eavesdroppers is to exercise adaptive silence (Conner, 2014). Males of many species of field cricket behave as satellite males, which forgo singing the loud, long-distance calling song and instead attempt to intercept females attracted to other calling males (Cade, 1975). One advantage to this behaviour is that it results in some savings of energy, particularly when competition is high. However, satellite behaviour is also beneficial for males from the many populations of field crickets that are subject to acoustically orienting predators and parasitoids (Cade, 1975; Zuk & Kolluru, 1998). The greater variability of courtship song over calling song by *T. oceanicus* supports the hypotheses that calling song is used as a species identifier and courtship song is more important in mate choice (Rebar et al., 2009; Zuk, Rebar, & Scott, 2008). Furthermore, the relatively common satellite behaviour by males makes courtship song a reliable signal for females that may not be absolutely certain that the male they are interacting with is the original calling male (Zuk et al., 2008). If the amplitude of courtship song does make eavesdropping by parasitoids like *O. ochracea* more difficult, then males that behave as satellites and only sing courtship song would be capable of both reducing detection by predators/parasitoids, while still managing to communicate with prospective mates.

One wonders, though, if courtship song is truly meant to be quiet and allow for private communication with females that are physically very close by (i.e. within antennal touching distance), why do males of some species produce chirps that reach 100 dB at 46 cm distance (*T. oceanicus*; Balakrishnan & Pollack, 1996)? Of course, to date, such measurements have all been made in laboratory settings, which might be influencing energy reserves and perceived risk by courting males. Field-based studies measuring the amplitude of song elements under natural conditions are desperately needed, especially as there are no studies I am aware of that have done so for courtship song. Regardless, that field cricket courtship songs contain loud and soft elements does suggest that the change in amplitude between the various song elements might serve another function. For example, it remains to be determined whether the ratio between loud and soft elements or the absolute amplitude of either element influences mating success.

CONCLUSIONS

Many have postulated that soft song may provide protection from eavesdropping by predators and parasitoids. One way to avoid eavesdropping is to use a separate signalling modality that is not as easily detected by predators/parasitoids (e.g. substrate vibrations, chemosensory cues, visual displays). Olfactory cues are used by moths (pheromones) and by field crickets (cuticular hydrocarbons), but acoustic signals are still common in courtship. If acoustic signalling is under strong sexual selection, then another way to avoid eavesdropping is to get up close and whisper your message. Many moths appear to do this. Crickets, on the other hand, may vary the relative amplitudes of the two elements of their courtship songs for some other, as yet undetermined, reason.

To date, the quiet signals produced by insects have largely been excluded from conversations about the structure and function of soft song. The purpose of this paper is to support a more inclusive definition of low-amplitude signalling and to provide examples of research on acoustic communication in insects that fall into such a definition. Thus, I hope to encourage the integration of insects, as

well as other organisms not covered in detail here, into the soft song literature.

Acknowledgments

Thanks to R. C. Anderson and D. G. Reichard for the invitation to participate in the 2014 Animal Behavior Society Low-amplitude Signaling symposium. Thanks also to M. Zuk for comments on the manuscript, and the Behavior Group at the University of Minnesota for thoughts and feedback on the ideas presented in this manuscript. I am grateful to D. G. Reichard and two anonymous referees who provided excellent feedback, adding substantially to the quality of the paper. This work was supported by the University of Minnesota and a National Science Foundation grant to M. Zuk (IOS 1261575).

References

- Akçay, Ç., Tom, M. E., Campbell, S. E., & Beecher, M. D. (2011). Sing softly and carry a big stick: signals of aggressive intent in the song sparrow. *Animal Behaviour*, *82*, 377–382.
- Alexander, R. D. (1961). Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour*, *17*, 130–223.
- Alexander, R. D. (1962). Evolutionary change in cricket acoustical communication. *Evolution*, *16*, 443–467.
- Anderson, R. C., Nowicki, S., & Searcy, W. A. (2007). Soft song in song sparrows: response of males and females to an enigmatic signal. *Behavioral Ecology and Sociobiology*, *61*, 1267–1274.
- Anderson, R. C., Searcy, W. A., Peters, S., & Nowicki, S. (2008). Soft song in song sparrows: acoustic structure and implications for signal function. *Ethology*, *114*, 662–676.
- Balakrishnan, R., & Pollack, G. S. (1996). Recognition of courtship song in the field cricket, *Teleogryllus oceanicus*. *Animal Behaviour*, *51*, 353–366.
- Ballentine, B., Searcy, W. A., & Nowicki, S. (2008). Reliable aggressive signalling in swamp sparrows. *Animal Behaviour*, *75*, 693–703.
- Bennet-Clark, H. C. (1970). The mechanism and efficiency of sound production in mole crickets. *Journal of Experimental Biology*, *52*, 619–652.
- Bennet-Clark, H. C. (1989). Songs and the physics of sound production. In F. Huber, T. E. Moore, & W. Loher (Eds.), *Crickets: behavior and neurobiology* (pp. 227–261). Ithaca, NY: Cornell University Press.
- Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer.
- Burk, T. (1983). Male aggression and female choice in a field cricket (*Teleogryllus oceanicus*): the importance of courtship song. In D. T. Gwynne, & G. K. Morris (Eds.), *Orthopteran mating systems: Sexual competition in a diverse group of insects* (pp. 97–119). Boulder, CO: Westview Press.
- Cade, W. (1975). Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science*, *190*, 1312–1313.
- Conner, W. E. (1999). 'Un chant d'appel amoureux': acoustic communication in moths. *Journal of Experimental Biology*, *202*, 1711–1723.
- Conner, W. E. (2014). Adaptive sounds and silences: acoustic anti-predator strategies in insects. In B. Hedwig (Ed.), *Insect hearing and acoustic communication* (Vol. 1, pp. 65–79). Heidelberg, Germany: Springer-Verlag.
- Conner, W. E., & Corcoran, A. J. (2012). Sound strategies: the 65-million-year-old battle between bats and insects. *Annual Reviews in Entomology*, *57*, 21–39.
- Dabelsteen, T. (2005). Public, private or anonymous? Facilitating and countering eavesdropping. In P. K. MacGregor (Ed.), *Animal communication networks* (pp. 38–62). Cambridge, U.K.: Cambridge University Press.
- Dabelsteen, T., McGregor, P. K., Lampe, H. M., Langmore, N. E., & Holland, J. (1998). Quiet song in song birds: an overlooked phenomenon. *Bioacoustics*, *9*, 89–105.
- Ewing, A. M. (1989). *Arthropod bioacoustics: Neurobiology and behaviour*. Ithaca, NY: Cornell University Press.
- Fitch, W. T., & Hauser, M. D. (2003). Unpacking 'honesty': vertebrate vocal production and the evolution of acoustic signals. In A. Simmons, R. R. Fay, & A. N. Popper (Eds.), *Acoustic communication* (pp. 65–137). New York, NY: Springer.
- Fitzpatrick, M. J., & Gray, D. A. (2001). Divergence between the courtship songs of the field crickets *Gryllus texensis* and *Gryllus rubens* (Orthoptera, Gryllidae). *Ethology*, *107*, 1075–1085.
- Fullard, J. H., Fenton, M. B., & Simmons, J. A. (1979). Jamming bat echolocation: the clicks of arctiid moths. *Canadian Journal of Zoology*, *57*, 647–649.
- Gerhardt, H. C. (1991). Female mate choice in tree frogs: static and dynamic acoustic criteria. *Animal Behaviour*, *42*, 615–635.
- Ghose, K., & Moss, C. F. (2003). The sonar beam pattern of a flying bat as its tracks tethered insects. *Journal of the Acoustical Society of America*, *114*, 1120–1131.
- Gray, D. A., Banuelos, C., Walker, S. E., Cade, W. H., & Zuk, M. (2007). Behavioural specialization among populations of the acoustically orienting parasitoid fly *Ormia ochracea* utilizing different cricket species as hosts. *Animal Behaviour*, *73*, 99–104.

- Gray, D. A., & Eckhardt, G. (2001). Is cricket courtship song condition dependent? *Animal Behaviour*, 62, 871–877.
- Greenfield, M. D. (2014). Acoustic communication in the nocturnal Lepidoptera. In B. Hedwig (Ed.), *Insect hearing and acoustic communication* (Vol. 1, pp. 81–100). Heidelberg: Germany Springer-Verlag.
- Griffin, D. R. (1946). Supersonic cries of bats. *Nature*, 158, 46–48.
- Griffin, D. R. (1950). Measurements of ultrasonic cries of bats. *Journal of the Acoustical Society of America*, 22, 247–257.
- Hack, M. A. (1998). The energetics of male mating strategies in field crickets (Orthoptera: Gryllinae: Gryllidae). *Journal of Insect Behavior*, 11, 853–867.
- Harrison, S. J., Thomson, I. R., Grant, C. M., & Bertram, S. M. (2013). Calling, courtship, and condition in the fall field cricket, *Gryllus pennsylvanicus*. *PLoS One*, 8, e60356.
- Higgins, L. A., & Waugaman, R. D. (2004). Sexual selection and variation: a multivariate approach to species-specific calls and preferences. *Animal Behaviour*, 68, 1139–1153.
- Mhatre, N., & Balakrishnan, R. (2006). Male spacing behaviour and acoustic interactions in a field cricket: implications for female choice. *Animal Behaviour*, 72, 1045–1058.
- Mowles, S. L. (2014). The physiological cost of courtship: field cricket song results in anaerobic metabolism. *Animal Behaviour*, 89, 39–43.
- Nakano, R., Ishikawa, Y., Tatsuki, S., Skals, N., Surlykke, A., & Takanashi, T. (2009a). Private ultrasonic whispering in moths. *Communicative & Integrative Biology*, 2, 123–126.
- Nakano, R., Ishikawa, Y., Tatsuki, S., Surlykke, A., Skals, N., & Takanashi, T. (2006). Ultrasonic courtship song in the Asian corn borer moth, *Ostrinia furnacalis*. *Naturwissenschaften*, 93, 292–296.
- Nakano, R., Skals, N., Takanashi, T., Surlykke, A., Koike, T., Yoshida, K., et al. (2008). Moths produce extremely quiet ultrasonic courtship songs by rubbing specialized scales. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 11812–11817.
- Nakano, R., Takanashi, T., Fujii, T., Skals, N., Surlykke, A., & Ishikawa, Y. (2009b). Moths are not silent, but whisper ultrasonic courtship songs. *Journal of Experimental Biology*, 212, 4072–4078.
- Nakano, R., Takanashi, T., Skals, N., Surlykke, A., & Ishikawa, Y. (2010). To females of a noctuid moth, male courtship songs are nothing more than bat echolocation calls. *Biology Letters*, 6, 582–584.
- Nakano, R., Takanashi, T., & Surlykke, A. (2014). Moth hearing and sound communication. *Journal of Comparative Physiology A*, 201, 111–121. <http://dx.doi.org/10.1007/s00359-014-0945-8>.
- Nakano, R., Takanashi, T., Surlykke, A., Skals, N., & Ishikawa, Y. (2013). Evolution of deceptive and true courtship songs in moths. *Scientific Reports*, 3, 2003. <http://dx.doi.org/10.1038/srep02003>.
- Nandi, D., & Balakrishnan, R. (2013). Call intensity is a repeatable and dominant acoustic feature determining male call attractiveness in a field cricket. *Animal Behaviour*, 86, 1003–1012.
- Noyes, A., & Pierce, G. W. (1938). Apparatus for acoustic research in the supersonic frequency range. *Journal of the Acoustical Society of America*, 9, 205–211.
- Poole, A., & Gill, F. (Eds.). (2005). *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/>.
- Rantala, M. J., & Kortet, R. (2003). Courtship song and immune function in the field cricket *Gryllus bimaculatus*. *Biological Journal of the Linnean Society*, 79, 503–510.
- Rebar, D., Bailey, N. W., & Zuk, M. (2009). Courtship song's role during female mate choice in the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology*, 20, 1307–1314.
- Reichard, D. G., Rice, R. J., Schultz, E. M., & Schrock, S. E. (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.
- Reichard, D. G., Rice, R. J., Vanderbilt, C. C., & Ketterson, E. D. (2011). Deciphering information encoded in birdsong: male songbirds with fertile mates respond most strongly to complex, low-amplitude songs used in courtship. *American Naturalist*, 178, 478–487.
- Reichard, D. G., & Welklin, J. F. (2015). On the existence and potential functions of low-amplitude vocalizations in North American birds. *Auk*, 132, 156–166.
- Searcy, W. A., & Nowicki, S. (2006). Signal interception and the use of soft song in aggressive interactions. *Ethology*, 112, 865–872.
- Simmons, L. W., Thomas, M. L., Simmons, F. W., & Zuk, M. (2013). Female preferences for acoustic and olfactory signals during courtship: male crickets send multiple messages. *Behavioral Ecology*, 24, 1099–1107.
- Simmons, L. W., Tinghitella, R. M., & Zuk, M. (2010). Quantitative genetic variation in courtship song and its covariation with immune function and sperm quality in the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology*, 21, 1330–1336. <http://dx.doi.org/10.1093/beheco/arq154>.
- Thomas, M. L., & Simmons, L. W. (2009). Sexual selection on cuticular hydrocarbons in the Australian field cricket, *Teleogryllus oceanicus*. *Journal of Evolutionary Biology*, 23, 707–714.
- Thorpe, W. H., & Griffin, D. R. (1962). Ultrasonic frequencies in bird song. *Nature*, 193, 595. <http://dx.doi.org/10.1038/193595a0>.
- Titus, R. C. (1998). Short-range and long-range songs: use of two acoustically distinct song classes by dark-eyed juncos. *Auk*, 115, 386–393.
- Tregenza, T., Simmons, L. W., Wedell, N., & Zuk, M. (2006). Female preference for male courtship song and its role as a signal of immune function and condition. *Animal Behaviour*, 72, 809–818.
- Vedenina, V. Y., & Pollack, G. S. (2012). Recognition of variable courtship song in the field cricket *Gryllus assimilis*. *Journal of Experimental Biology*, 215, 2210–2219.
- Wagner, W. E., Jr., & Reiser, M. G. (2000). The importance of calling song and courtship song in female mate choice in the variable field cricket. *Animal Behaviour*, 59, 1219–1226.
- Zuk, M., & Kolluru, G. (1998). Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology*, 73, 415–438.
- Zuk, M., Rebar, D., & Scott, S. P. (2008). Courtship song is more variable than calling song in the field cricket *Teleogryllus oceanicus*. *Animal Behaviour*, 76, 1065–1071.