1 Title: Stridulated soft song by singing insects

2

3

4 Author: Susan L. Balenger

5

6 *Department of Ecology, Evolution and Behavior, University of Minnesota – Twin Cities, MN,*

7 *U.S.A.*

8 *E-mail address:* sbalenge@umn.edu (S. L. Balenger).

9 Word count: 4738

10

The study of low amplitude or “soft” songs and calls has largely been limited to organisms that produce multiple call types which 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.

Keywords:

tympanate moths;

field crickets;

acoustic communication;

courtship song;

eavesdropping avoidance

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 human range of hearing and sounds that are produced often enough to be noticed (Bradbury & Vehrencamp 2011). Over the last century, the study of acoustic communication and signaling 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 (Noyes & Pierce 1938, Griffin 1950, Ghose & Moss 2003). 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 signaling 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 feet 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 et al. 2014).

Low-amplitude signaling, 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 et al. 1998). Although much of the research

with respect to quiet acoustic signals has dealt with song birds, 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 signaling is a prevalent phenomenon among birds and 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 (Ballentine et al. 2008, Akçay et al. 2011) and courtship (Dabelsteen et al. 1998, Reichard et al. 2011), and 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 (Dabelsteen 1998, Searcy and Nowicki 2006, Conner 2014). Avian soft song is generally characterized as falling into one of two categories: a low amplitude version of species typical long range songs or low amplitude song that vary considerably in temporal characteristics from the typical long range song (Anderson et al. 2008, Reichard et al. 2011).

In singing insects, however, the best examples of low amplitude signaling 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 signaling 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 song birds. 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 NON-VOCALIZING 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 non-vocal means (Fitch & Hauser 2003). Non-vocal 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 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” (p. 16). Acoustic signaling 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 behavioral 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 non-vocal 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 song birds as “low volume singing with a probably social function during the breeding season” (p.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 et al. 2011, 2013). 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 are distinct spectrally and temporally from the species-typical long range song (short-range song; Titus 1998, Reichard et al. 2011, 2013). 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 dialog 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 and Pollack 1998, Mhatre & Balakrishnan 2006, Vedenina & Pollack 2012, Nandi & Balakrishnan 2013). 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 & Welkin 2015). Recently, Reichard and Welkin (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” (p. 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 defense mechanism allowing avoidance of predation by bats (Conner and Corcoran 2012). Subsequently, inter- and

intraspecific ultrasonic communication evolved repeatedly in this lineage via sensory bias, utilizing a variety of sound producing mechanisms (Conner and 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. 2003). Therefore, moths represent a fascinating group in which to study acoustic signaling from a comparative perspective. In the majority of families, though, it is not only unknown what structures produce the sounds and what their function is, but it is also unknown if sounds are produced at all (Nakano et al. 2013).

At first glance, acoustic signaling 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 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 10cm). 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 under-appreciated mode of sexual signaling, that has evolved repeatedly in moths.

169 A series of studies over the last decade from researchers in Japan and Denmark have greatly
170 added to our understanding of the evolution and function of acoustic communication in moths.
171 These studies suggest that sexual sound communication may be more common in moths than
172 generally believed because many species may be using low amplitude high frequency channels
173 (Nakano et al. 2003, 2014). Beginning with studies of the Asian corn borer moth (*Ostrinia*
174 *furnacalis*), the researchers identified extremely quiet ultrasonic sounds produced by the
175 stridulation of specialized wing and thorax scales only found on males (Nakano et al. 2006,
176 2008). These “whispered courtship songs” are produced when females are in extremely close
177 proximity, and are not detected by females more than 3 cm away (Nakano et al. 2008). In *O.*
178 *furnacalis*, these whispered songs by males cause females in the immediate vicinity to behave as
179 though they have just heard a bat in the distance; females freeze in place to avoid bat detection
180 and predation and males exploit this behavioral response to mate with the frozen females
181 (Nakano et al. 2013). This led the researchers to hypothesize that whispering might be a
182 widespread form of courtship song among moths attempting to simultaneously avoid bat
183 detection and obtain copulations (Nakano et al. 2008, 2009a). To test this idea, Nakano et al.
184 (2009b) looked for low-amplitude, whispered courtship songs in 13 tympanate moth species
185 across four families. Of the species that did produce ultrasonic signals when near females, all
186 nine were at a relatively low amplitude (43-76 dB SPL at 1 cm), suggesting that quiet courtship
187 may in fact be a relatively common phenomenon among singing moths (Nakano et al. 2009b).

188 Nakano et al. (2014) refer to the quiet ultra-sonic communication used by some male moths
189 as both “whispers” and “soft song.” In a recent review of acoustic communication in nocturnal
190 Lepidoptera, Greenfield (2014) uses the term “soft song” to discuss this phenomenon. It,

therefore, appears that some researchers studying quiet ultra-sonic 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 produced 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 employ to announce their location to females (Alexander 1961, 1962). Aggressive songs are loud, sharp signals used in mediating male-male interactions or territory or dominance (Alexander 1961, 1962). Courtship songs are produced when a pair is in physical contact with one another, allowing for quiet acoustic communication as well as simultaneous chemical signaling via cuticular hydrocarbon profiles (Alexander 1961, 1962, Thomas & Simmons 2009, Simmons et al. 2013). 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, that suggest 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 et al. 2013), sperm quality (*Teleogryllus oceanicus*, Simmons et al. 2010), immune function (*Gryllus bimaculatus*, Rantala & Kortet 2003; *T. oceanicus*, Tregenza et al. 2006, Simmons et al. 2010), 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, all a male needs to induce him to begin calling is darkness and a reasonable temperature; 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 be important to also 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” that are short and sharp and have a relatively high fundamental frequency (generally ~14-17 kHz), and “chirps” that are less intense and have a fundamental frequency similar to that of *Gryllus* calling songs (~3.5-5 kHz) (Fig. 1; Alexander 1961, Walker 1974, Fitzpatrick & Gray 2001). Vedenina & 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 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 *G. rubens*, Fitzpatrick and Gray (2001) found that amplitude is the same on average (79.8 dB at 19cm) 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 19cm). The within species CV for the amplitudes of

both ticks and chirps are 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 is 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 and Waugaman 2004).

The courtship song of *Teleogryllus 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 7-9 pulses, which increase in intensity with each pulse (see Fig. 1). The trill, on the other hand, contains a long series of pulses at a constant intensity (see 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 find clear evidence that amplitude modulation of the chirp portion (1st chirp: ~88dB SPL, last chirp: ~100dB SPL at 46 cm) is unnecessary for female acceptance and mounting. In all song manipulations, however, the trill component (a.k.a., the soft pulses) were held constant at 90dB 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” 90dB 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 on average several hours each night producing this song but only a few brief seconds to minutes on 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 loudly calling 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 and Pollack 1996). While such loud elements in courtship song are often brief, suggesting that courtship song may be on average less likely to be heard, one would expect selection against these loud elements entirely when if doing so reduced 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 the North American continent. Gray et al. (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 by 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 neighboring males, a caller

might limit the likelihood of courtship interference from competitors if they are not capable of detecting the quiet song. As described earlier, however, some crickets also have high amplitude elements in their courtship songs (Fig. 1), which could notify neighboring males of the presence of a female (unintended receivers) or provide a warning to those males to stay away (intended receivers). Studies which 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 have been shown to behave as satellite males, in which they themselves forego 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 (Zuk et al. 2008, Rebar et al. 2009). Furthermore, the relatively common satellite behaviour by males makes courtship song a reliable signal for females who 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 100dB 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 signaling modality that is not as easily detected by predators/parasitoids (e.g., substrate vibrations, chemosensory cues, visual displays). Both moths and field crickets use olfactory cues, moths using pheromones and crickets using cuticular hydrocarbons, but acoustic signals are still common in courtship. If acoustic signaling is under strong sexual selection, then another way to avoid eavesdropping is to get up close and whisper your message. Many moths appear to be doing 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 signaling and to provide examples of research on acoustic communication in insects that falls 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 reviewers 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, MD. (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.

372 Alexander, R.D. (1962). Evolutionary change in cricket acoustical communication. *Evolution*,
 373 16, 443-467.

374 Anderson, R.C., Nowicki, S., & Searcy, W.A. (2007). Soft song in song sparrows: response of
 375 males and females to an enigmatic signal. *Behavioral Ecology and Sociobiology*, 61,
 376 1267-1274.

377 Anderson, R.C., Searcy, W.A., Peters, S., & Nowicki, S. (2008). Soft song in song sparrows:
 378 acoustic structure and implications for signal function. *Ethology*, 114, 662-676.

379 Balakrishnan, R., & Pollack, G.S. (1996). Recognition of courtship song in the field cricket,
 380 *Teleogryllus oceanicus*. *Animal Behaviour*, 51, 353-366.

381 Ballentine, B., Searcy, W.A., & Nowicki, S. (2008). Reliable aggressive signaling in swamp
 382 sparrows. *Animal Behaviour*, 75, 693-703.

383 Bennet-Clark, H.C. (1970). The mechanism and efficiency of sound production in mole crickets.
 384 *Journal of Experimental Biology*, 52, 619-652.

385 Bennet-Clark, H.C. (1989). Songs and the physics of sound production. In F. Huber, T.E. Moore,
 386 & W. Loher (Eds.), *Cricket behavior and neurobiology*. (pp. 227-261). Ithaca, NY:
 387 Cornell University Press.

388 Bradbury, J.W., & Vehrencamp, S.L. (2011). *Principles of animal communication*, 2nd edition.
 389 Sunderland, MA: Sinauer Associates.

390 Burk, T. (1983). Male aggression and female choice in a field cricket (*Teleogryllus oceanicus*):
 391 the importance of courtship song. In D.T. Gwynne & G.K. Morris (Eds.), *Orthopteran*
 392 *mating systems: sexual competition in a diverse group of insects*. (pp. 97-119). Boulder,
 393 CO: Westview Press.

394 Cade, W. (1975). Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science*, 190,
395 1312-1313.

396 Conner, W.E. (1999). ‘Un chant d’appel amoureux’: acoustic communication in moths. *Journal*
397 *of Experimental Biology*, 202, 1711-1723.

398 Conner, W.E., & Corcoran, A.J. (2012). Sound strategies: the 65-million-year-old battle between
399 bats and insects. *Annual Reviews in Entomology*, 57, 21-39.

400 Conner, W.E. (2014). Adaptive sounds and silences: acoustic anti-predator strategies in insects .
401 In B. Hedwig (Ed.), *Insect hearing and acoustic communication* (Vol. 1, pp. 65-79).
402 Heidelberg, Germany: Springer-Verlag.

403 Dabelsteen, T. (2005). Public, private or anonymous? Facilitating and countering eavesdropping.
404 In P.K. MacGregor (Ed.), *Animal communication networks* (pp.38-62). Cambridge, UK:
405 Cambridge University Press.

406 Dabelsteen, T., McGregor, P.K., Lampe, H.M., Langmore, N.E., & Holland, J. (1998). Quiet
407 song in song birds: an overlooked phenomenon. *Bioacoustics*, 9, 89-105.

408 Ewing, A.M. (1989). *Arthropod bioacoustics; neurobiology and behaviour*. Ithaca, NY: Cornell
409 University Press.

410 Fitch, W.T., & Hauser M.D. (2003). Unpacking “honesty”: vertebrate vocal production and the
411 evolution of acoustic signals. In A. Simmons, R.R. Fay, & A.N. Popper (Eds.), *Acoustic*
412 *Communication* (pp. 65-137). New York, USA: Springer.

413 Gerhardt, H.C. (1991). Female mate choice in tree frogs: static and dynamic acoustic criteria.
414 *Animal Behaviour*, 42, 615-635.

415 Ghose, K., & Moss, C.F. (2003). The sonar beam pattern of a flying bat as its tracks tethered
416 insects. *The Journal of the Acoustical Society of America*, 114, 1120-1131.

417 Gray, D.A., Banuelos, C., Walker, S.E., Cade, W.H., & Zuk, M. (2007). Behavioural
 418 specialization among populations of the acoustically orienting parasitoid fly *Ormia*
 419 *ochracea* utilizing different cricket species as hosts. *Animal Behaviour*, 73, 99-104.

420 Gray, D.A., & Eckhardt, G. (2001). Is cricket courtship song condition dependent? *Animal*
 421 *Behaviour*, 62, 871-877.

422 Greenfield, M.D. (2014). Acoustic communication in the nocturnal Lepidoptera. In B. Hedwig
 423 (Ed.), *Insect hearing and acoustic communication* (Vol. 1, pp. 81-100). Heidelberg,
 424 Germany Springer-Verlag.

425 Griffin, D.R. (1946). Supersonic cries of bats. *Nature*, 158, 46-48.

426 Griffin, D.R. (1950). Measurements of ultrasonic cries of bats. *The Journal of the Acoustical*
 427 *Society of America*, 22, 247-257.

428 Hack, M.A. (1998). The energetics of male mating strategies in field crickets (Orthoptera:
 429 Gryllinae: Gryllidae). *The Journal of Insect Behavior*, 11, 853-867.

430 Harrison, S.J., Thomson, I.R., Grant, C.M., & Bertram, S.M. (2013). Calling, courtship, and
 431 condition in the Fall Field Cricket, *Gryllus Pennsylvanicus*. *PLoS One*, 8, e60356.

432 Higgins, L.A., & Waugaman, R.D. (2004). Sexual selection and variation: a multivariate
 433 approach to species-specific calls and preferences. *Animal Behaviour*, 68, 1139-1153.

434 Mhatre, N., & Balakrishnan, R. (2006). Male spacing behaviour and acoustic interactions in a
 435 field cricket: implications for female choice. *Animal Behaviour*, 72, 1045-1058.

436 Mowles, S.L. (2014). The physiological cost of courtship: field cricket song results in anaerobic
 437 metabolism. *Animal Behaviour*, 89, 39-43.

438 Nakano, R., Ishikawa, Y., Tatsuki, S., Surlykke, A., Skals, N., Takanashi, T. (2006). Ultrasonic
 439 courtship song in the Asian corn borer moth, *Ostrinia furnacalis*. *Naturwissenschaften*,
 440 93, 292-296.

441 Nakano, R., Takanashi, T., & Syrlykke, A. (2014). Moth hearing and sound communication.
 442 *Journal of Comparative Physiology A*, doi: 10.1007/s00359-014-0945-8.

443 Nakano, R., Takanashi, T., Surlykke, A., Skals, N., & Ishikawa, Y. (2013). Evolution of
 444 deceptive and true courtship songs in moths. *Scientific Reports*, 3, doi:
 445 10.1038/srep02003.

446 Nakano, R., Skals, N., Takanashi, T., Surlykke, A., Koike, T., Yoshida, K., Maruyama, H.,
 447 Tatsuki, S., & Ishikawa, Y. (2008). Moths produce extremely quiet ultrasonic courtship
 448 songs by rubbing specialized scales. *Proceedings of the National Academy of Sciences of*
 449 *the United States of America*, 105, 11812-11817.

450 Nakano, R., Ishikawa, Y., Tatsuki, S., Skals, N., Surlykke, A., & Takanashi, T. (2009). Private
 451 ultrasonic whispering in moths. *Communicative & Integrative Biology*, 2, 123-126.

452 Nakano, R., Takanashi, T., Fujii, T., Skals, N., Surlykke, A., & Ishikawa, Y. (2009). Moths are
 453 not silent, but whisper ultrasonic courtship songs. *The Journal of Experimental Biology*,
 454 212, 4072-4078.

455 Nakano, R., Takanashi, T., Skals, N., Surlykke, A., & Ishikawa, Y. (2010). To females of a
 456 noctuid moth, male courtship songs are nothing more than bat echolocation calls. *Biology*
 457 *Letters*, 6, 582-584.

458 Nandi, D., & Balakrishnan, R. (2013). Call intensity is a repeatable and dominant acoustic feature
 459 determining male call attractiveness in a field cricket. *Animal Behaviour*, 86, 1003-1012.

460 Noyes, A. & Pierce, G.W. (1938). Apparatus for acoustic research in the supersonic frequency
 461 range. *The Journal of the Acoustical Society of America*, 9, 205-211.

462 Poole, A., & Gill, F. (Editors) (2005). The Birds of North America Online. Cornell Lab of
 463 Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/>

464 Rantala, M.J., & Kortet, R. (2003). Courtship song and immune function in the field cricket
 465 *Gryllus bimaculatus*. *Biological Journal of the Linnean Society*, 79, 503-510.

466 Reichard, D.G., Rice, R.J., Vanderbilt, C.C., & Ketterson, E.D. (2011). Deciphering information
 467 encoded in birdsong: male songbirds with fertile mates respond most strongly to
 468 complex, low-amplitude songs used in courtship. *The American Naturalist*, 178, 478-487.

469 Reichard, G.G., Rice, R.J., Schultz, E.M., & Schrock, S.E. (2013). Low amplitude songs
 470 produced by male dark-eyed juncos (*Junco hyemalis*) differ when sung during intra- and
 471 inter-sexual interactions. *Behaviour*, 150, 1183-1202.

472 Reichard, D.G., & Welklin, J.F. (2015). On the existence and potential functions of low-
 473 amplitude vocalizations in North American birds. *The Auk*, 132, 156-166.

474 Searcy, W.A., & Nowicki, W. (2006). Signal interception and the use of soft song in aggressive
 475 interactions. *Ethology*, 112, 865-872.

476 Simmons, L.W., Thomas, M.L., Simmons, F.W., & Zuk, M. (2013). Female preferences for
 477 acoustic and olfactory signals during courtship: male crickets send multiple messages.
 478 *Behavioral Ecology*, 24, 1099-1107.

479 Simmons, L.W., Tinghitella, R.M., & Zuk, M. (2010). Quantitative genetic variation in courtship
 480 song and its covariation with immune function and sperm quality in the field cricket
 481 *Teleogryllus oceanicus*. *Behavioral Ecology*, doi: 10.1093/beheco/arq154.

482 Thomas, M.L., & Simmons, L.W. (2009). Sexual selection on cuticular hydrocarbons in the
 483 Australian field cricket, *Teleogryllus oceanicus*. *Journal of Evolutionary Biology*, 23,
 484 707-714.
 485 Thorpe, W.H., & Griffin, D.R. (1962). Ultrasonic frequencies in bird song. *Nature*, 595.
 486 Titus, R.C. (1998). Short-range and long-range songs: use of two acoustically distinct song
 487 classes by dark-eyed juncos. *Auk*, 115, 386-393.
 488 Tregenza, T., Simmons, L.W., Wedell, N., & Zuk, M. (2006). Female preference for male
 489 courtship song and its role as a signal of immune function and condition. *Animal*
 490 *Behaviour*, 72, 809-818.
 491 Vedenina, V.Y., & Pollack, G.S. (2012). Recognition of variable courtship song in the field
 492 cricket *Gryllus assimilis*. *The Journal of Experimental Biology*, 215, 2210-2219.
 493 Wagner, Jr., W.E., & Reiser, M.G. (2000). The importance of calling song and courtship song in
 494 female mate choice in the variable field cricket. *Animal Behaviour*, 59, 1219-1226.
 495 Zuk, M., & Kolluru, G. (1998). Exploitation of sexual signals by predators and parasitoids. *The*
 496 *Quarterly Review of Biology*, 73, 415-438.
 497 Zuk, M, Rebar, D., & Scott, S.P. (2008). Courtship song is more variable than calling song in the
 498 field cricket *Teleogryllus oceanicus*. *Animal Behaviour*, 76, 1065-1071.
 499

500 Figure 1. Examples of field cricket courtship songs. Oscillograms of (*top*) *Gryllus texensis* and
501 (*middle*) *G. ovisopis* demonstrating the stereotypical loud, high frequency “ticks” alongside
502 softer lower frequency “chirps”. Oscillogram of (*bottom*) *Teleogryllus oceanicus* courtship song
503 showing the stereotypical “chirps” that increase in intensity followed by the long series of
504 constant, lower amplitude pulses that make up the “trill.” (*Top*) Entire recording available at
505 <http://macaulaylibrary.org/audio/130070>. Recording made by T.J. Walker, Arkansas, August
506 1973. (*Middle*) Entire recording available at <http://macaulaylibrary.org/audio/129871>. Recording
507 made by T.J. Walker, Florida, September 1972. (*Bottom*) Entire recording available upon
508 request. Recording made by S.L. Balenger, Minnesota, March 2013.

Figure 1

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 reviewers 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).