# INFORMATION CONTENT OF
# HOUSE CRICKET *(Acheta domesticus)* SONGS
# AND THE EVOLUTION OF MULTIPLE SIGNALS

By

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# Table of Contents

# Table of Contents, continued

# List of Tables and Figures

# Acknowledgements

# The Information Content of Songs Across Multiple Song Types in Crickets (Orthoptera: Gryllidae)

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**ABSTRACT**

Despite the extensive literature on cricket bioacoustics, little collective understanding has been established that compares the structural and functional significance of the three distinct gryllid song types: calling song, courtship song, and aggressive song. Here, we compile recent work on all three song types that underscores the importance of song in communicating aspects of male phenotype to receivers (females and rival males). In doing so, we uncover similarities and differences between both the information content of each song type and the acoustic structures through which this content is communicated. By placing these comparisons into the context of multiple signaling theory, we can begin to understand how and why male gryllids make use of multiple acoustic signals.

*Key Words*: acoustic communication, aggression, Bioacoustics, courtship, cricket song, Gryllidae, mate choice

**INTRODUCTION**

Acoustical signaling by males is the predominant form of communication in crickets (Orthoptera: Gryllidae). Male crickets generally produce at least three qualitatively distinct types of song, depending on social context: calling song, courtship song, and aggressive song (Alexander, 1961). Acoustically mediated pair formation is widespread in the Gryllidae (crickets, approximately 2000 species) and one of the most studied aspects of cricket mating (Brown & Gwynne, 1997). Wing movements during non-acoustic sexual displays are thought to have been involved in the origins of tegminal stridulation (Alexander, 1962; Alexander & Brown, 1963). The displays became acoustic when the tegmina evolved a file-and-scraper mechanism capable of producing a pulsed calling song. Sexually receptive females were attracted to the male song and approached first by flight, in macropterous taxa, and then on foot. The ancestral grylloid evolved courtship and aggressive songs distinct from calling song (Boake, 1983; Otte, 1992).

Despite a large literature on cricket bioacoustics, we currently know remarkably little about the functional significance of cricket song beyond the importance of calling song in attracting females. What if anything are crickets communicating with song about their health, vigor, quality as a mate, or superiority as a competitor and rival? Moreover, why do they produce structurally different songs in different situations? The evolution of distinct songs types has received very little attention, even though these additional song types exist in most acoustic gryllids, are generally considered to be discrete alternative song types, and are produced in specific social contexts that have strong fitness consequences for the animals. Curiously, multiple songs have not evolved (or have been lost) in the Haglidae and Tettigoniidae, the other large group within the acoustic Ensiferan Orthoptera.

Our goal in this review is to assemble current literature on the functional significance of the structure of cricket songs. Specifically, we assess the extent of information related to individual quality or phenotypic state present in songs.  We also compare the structure and information content of the three song types, to the extent that this information is available. By doing so, we may begin to understand the evolution of multiple song types.

In order for a signal, such as song, to communicate the quality or state of the sender, three conditions must be met. First, the state, or phenotype, of the sender must correlate with signal structure. Second, the information must relate to aspects of phenotype that influence the outcome of social interactions with the receiver. Third, the receiver must act on the information within the signal by altering its behavior in a way that may affect social outcome (e.g., approaching, mating or escalating a fight). Thus, we begin by examining the capacity of the structure of each song type to carry information about aspects of male phenotype relevant to target receivers, be they females or rival males. Next, we review the consequences of these phenotypic components for cricket social interactions, followed by a brief review of the receiver response to variation in song structure. We do not provide a comprehensive review of female phonotaxis preferences as this has been the subject of several previous reviews (e.g., Doherty & Hoy, 1985; Greenfield, 1997; Zuk & Simmons, 1997; Brown, 1999; Gerhardt & Huber, 2002). Lastly, we discuss the implications of multiple signaling theory for understanding the evolution of cricket songs.

**GRYLLID SONGS AND THEIR SOCIAL CONTEXTS**
The acoustic communication system of the Gryllidae consists of three structurally distinct song types produced exclusively by adult males and used in different social contexts. Males produce calling song to attract females, who locate males by phonotaxis. Female choice is often exhibited

at this phase of mate attraction (e.g., Doherty & Hoy, 1985), although it can also be revealed during courtship or post-mating (e.g. Brown & Gwynne, 1997; Brown, 1997; Brown, 1999; Brown & Kuns, 2000; Wagner & Reiser, 2000). Rival males may also respond to calling songs by spacing themselves (e.g., Campbell & Shipp, 1979; Cade, 1981; Simmons, 1988), by approaching the calling male to aggregate (Ulagaraj & Walker, 1973), by challenging territory ownership (Alexander, 1961), or by becoming satellite males that may intercept approaching females (e.g., Cade, 1979; Kiflawi & Gray, 2000).

Once a female has come into physical contact with a male, the male switches from calling song to a distinct courtship song. Though lesser studied than the calling song, courtship song has been shown to be vital to successful copulation, as females mate exclusively with those who produce it (Crankshaw, 1979; Balakrishnan & Pollack, 1996; Nelson & Nolen, 1997; Boake, 1983).

If a rival challenges a male for direct access to a female or for his territory, he produces an aggressive song. The function of aggressive song is poorly understood, though a recent study showed that signaling mitigates the cost of fighting in *Teleogryllus oceanicus* (Logue *et al*. 2010). Brown *et al*. (2006) showed that aggressive song contains information about male body size and outcome of contests. Thus aggressive songs may serve to communicate aspects of resource holding potential before the fight escalates and injures either of the parties involved (Huntingford & Turner, 1987; Brown *et al*., 2006).

Each song type, in itself, has been shown to convey phenotypic information related to male fitness (e.g., Brown *et al*., 1996; Rantala & Kortet, 2004; Brown *et al*., 2006). The outcome of the social interaction for the male signalers (i.e., mating or aggressive contests), then, depends on the presence of song and, potentially, the information about male phenotype within its

structure. The use of information content to determine the outcome of a social interaction is supported by several classic phonotaxis experiments where females orient preferentially towards calling songs with song structure indicative of species identity (e.g., Doherty & Hoy, 1985; Greenfield, 1997; Zuk & Simmons, 1997; Brown, 1999; Gerhardt & Huber, 2002). Intraspecific variation in song structure could be the subject of female preference independent of non-acoustic aspects of male phenotype. Support for females preference for the structure of courtship song is more limited (e.g., Rantala & Kortet, 2003), and it remains to be tested as to whether encounters between rivals males are influenced by variation in aggressive song structure.

**THE INFORMATION CONTENT OF GRYLLID SONGS**

Signals such as cricket songs can come to contain significant information content through three evolutionarily stable conditions. If signal honesty is maintained by physical constraints or a physiological ceiling, an index signal results, in which the form of that signal is unconditionally linked to its information content and conveys intrinsic sender attributes (Maynard Smith & Harper, 1988; Maynard Smith, 1991; Maynard Smith & Harper, 1995; Vehrencamp, 2000). If signal honesty is maintained by costs, including energetic costs, time costs, increased susceptibility to predation, or vulnerability to receiver attack, a handicap signal results, in which a correlation exists between signal intensity and some measure of sender quality, motivation, or intention (Zahavi, 1975; Zahavi,1977; Hasson, 1997; Vehrencamp, 2000). Conventional signals, or signals that are associated with specific contexts by arbitrary convention, can convey motivation or intention and may or may not be correlated to aspects of sender quality (Maynard Smith & Harper, 1988; Guilford & Dawkins, 1995; Vehrencamp, 2000). These signals are only stable if both sender and receiver agree on the optimal receiver response or if the receiver

retaliates against (i.e., punishes) the sender for being deceptive (Vehrencamp, 2000). In this review, we make no distinction between these three signal types, although we specifically examine acoustic components of cricket songs that may be indicators of some aspect of quality or motivation, which may be especially likely within index and handicap signals.

In all the above conditions, signal honesty is required, at least on average, if a stable, meaningful signal is to evolve. Significant information content of acoustic signals, then, requires signal consistency, at least in so much as the phenotypic information being conveyed remains unchanged. Individual consistency in cricket song has been shown in several species (e.g., Brown *et al*., 1996: Brown *et al*., 2006; Drayton *et al*., 2010a; Fedorka & Mousseau, 2007; Ponce-Wainer & Cueva del Castillo, 2008). On the other hand, there must be variation *between* individuals of the same species in song characteristics conveying fitness-related phenotypes (other than species identifiers), as these phenotypes themselves vary between signaling individuals. This variation in song structure and phenotype forms the basis for selection by female choice and male-male competition and has been demonstrated in several cricket species (e.g., Hedrick, 1986; Simmons, 1988; Brown *et al*., 1996; Bertram, 2000). Individual consistency and intraspecific variation, then, are necessary prerequisites for fitness-related phenotypic information to be conveyed through acoustic signals, both of which are satisfied in the Gryllidae.

Phenotypic information content has been shown to be conveyed in song characteristics that span four general categories: frequency, amplitude, amount of calling (e.g., duty cycle, bout duration, and onset of calling), and temporal characteristics (e.g., number of pulses per chirp, pulse duration, and length of interpulse interval). We discuss the information content conveyed by each of these categories and within each of the major song types (calling, courtship and

aggressive songs). We begin by analyzing the information content of cricket songs independent of the ability of receivers to perceive this information. Table I provides a summary of the correlations between song structure and male phenotype as present in all three gryllid songs.

**Frequency**

In gryllids, the carrier frequency of song is a product of coupling between oscillations in the harp (resonator) and oscillations of the tegminal file and scraper (stridulatory mechanism) such that the rate at which the scraper impacts the file teeth is effectively "locked" at the speed that produces the resonating frequency (Koch, 1980). Thus, the frequency produced during male song is directly correlated to the size of the resonating structure, particularly the harp, with males with larger harps producing songs of lower frequencies (Simmons, 1995; Simmons & Ritchie, 1996; Scheuber *et al*., 2003a, 2003b; Jacot *et al*., 2005). A positive linear correlation also exists between male size and harp area (Moradian & Walker, 2008), such that males of larger size produce lower frequency calls (Brown *et al*., 1996; Ponce-Wainer & Cueva del Castillo, 2008; Judge, 2011; Bertram *et al*., 2011). Increasing age has also been correlated to lower frequency calls (Jacot *et al*., 2007; Judge, 2011). Therefore, the frequency of a male's calling song seems to mainly contain information about his size and age, although it has also been linked to flight capability in *Gryllus firmus* (Mitra *et al*., 2011).

In the courtship song, frequency again decreased with increasing size in *Teleogryllus commodus*, but was also shown to be affected by inbreeding, with inbred males calling at higher frequencies that outbred controls (Drayton *et al*., 2010a). Frequency characteristics have not yet been connected to aspects of phenotype conveyed through aggressive song.

**Amplitude**

Although information conveyed through the amplitude or intensity of calling song is very likely subject to the problems of attenuation and the influence of the environment (Simmons, 1988), some phenotypic attributes have nevertheless been correlated to this aspect of male song. These include size, with larger males producing more intense calls (Simmons, 1988; Gray, 1997; Ryder & Siva-Jothy, 2000; Bertram *et al*., 2011), and age, with amplitude decreasing with time (Jacot *et al*., 2007; Verburgt *et al*., 2011).

The information content conveyed by amplitude has not yet been examined in either courtship or aggressive song. In these signals, amplitude could potentially convey more reliable information, because with a decreased need for propagation, attenuation may not be a limiting factor. In contrast, at close range, greater amplitude may be beyond a range that is perceivable by the receiver.

**Amount of calling**

Males vary in the total amount and the proportion of time that they spend calling. Several studies have linked various measures of call output to phenotypic attributes, suggesting that the amount a male calls contains some information content. An increase in call output has been linked to large size (Forrest, 1991; Bertram, 2000; Bertram *et al*., 2011)*,* high competitive ability (Simmons, 1986a), flight capability (Bertram, 2007, but see Mitra *et al*., 2011); superior nutritional condition (Holzer *et al*., 2003; Judge *et al*., 2008; Wagner & Hoback, 1999), age (Maklakov, 2009), availability of dietary phosphorus (Bertram *et al*., 2009), and increased pyruvate kinase activity (Bertram *et al*., 2011). Additionally, males of large size call more on average throughout their entire lives and tend to begin calling earlier in the evening (Verburgt *et*

*al*., 2011; Bertram, 2000). Decreases in call output have been linked to inbreeding (Drayton *et al*. 2007, 2010b), poor nutritional condition (Hedrick, 2005), extreme old age (Judge *et al*., 2008), slower development time (Drayton *et al*., 2010b), and the presence of an immune response (Jacot, *et al*., 2004; Scheuber *et al*., 2003b) or parasite (Cade, 1984; Orozco & Bertram, 2004).

Duty cycle, a ratio of time spent actively calling to the amount of available time, has been correlated to male age, with younger males having higher duty cycles than their elders (Verburgt *et al*., 2011). Due to the nature of courtship and aggressive song, which are only produced in limited quantities in specific situations, many measures of call output, such as amount of nightly calling, do not apply. However, the use of a measure of duty cycle could potentially indicate if males communicate aspects of their phenotype or motivation through call output in these song types.

**Temporal characteristics**

Here, we use the term "temporal characteristics" to refer to the structural patterning of song, i.e., the duration of the pulses and chirps (or trills), the duration of the intervals between pulses and chirps, and the number of pulses per chirp. In previous work, the duration of the pulse and the inter-pulse interval have sometimes been grouped into one measurement, termed "pulse period." We prefer the separate treatment of pulse duration and interval; a change in pulse period is ambiguous given that it could be due to a change in either the duration of the pulse or the inter-pulse interval or both. A related concept, pulse (or chirp) rate, the number of pulses (or chirps) divided by total duration, suffers from the same problem. Nevertheless, we will report results of studies that measured these characteristics, bearing in mind the inherent ambiguities.

Several phenotypes have been correlated to temporal characteristics of male song. Age, which has been more frequently tested in calling song, exhibits a negative relationship with pulse duration (Brown *et al*., 1996; Verburgt *et al*., 2011; Judge, 2011) and chirp duration (Jacot *et al*., 2007), while its relationship with the inter-chirp and inter-pulse intervals remains equivocal (Verburgt *et al*., 2011; Drayton *et al*., 2010a, b). The number of pulses per chirp increased with age in *Gryllus pennsylvanicus* (Judge, 2011) but decrease with age in *Gryllus campestris* (Jacot *et al*., 2007). In *Gryllus pennsylvanicus*, age is negatively correlated to pulse period (Judge, 2011), likely because of decreased pulse duration. Some studies found that older males demonstrated more variability in the temporal aspects of their calls (Simmons & Zuk, 1992; Judge, 2011). A single study demonstrated that the courtship song can also contain information about age, with older *Teleogryllus commodus* males having shorter intervals between the chirp and trill portions of their songs (Drayton *et al*., 2010a).

Size has been shown to be conveyed in all three gryllid songs, although most data comes from the calling song. In *Acheta domesticus* calling song, size shows a positive relationship with pulses per chirp (Gray, 1997), although the opposite relationship was observed in *Teleogryllus commodus* when only mass was taken into account (Drayton *et al*., 2010b). Inter-pulse interval increased with size in one study of *Acheta domesticus* (Bertram *et al*., 2011). The relationship between size and pulse duration remains equivocal, with positive correlations reported by Simmons & Zuk, 1992, and Bertram *et al*., 2011, and negative correlations reported by Brown *et al*., 1996, Champagnon & Cueva del Castillo, 2008, and Judge, 2011. One study found a negative relationship between size and chirp duration (Ponce-Wainer & Cueva del Castillo, 2008). Simmons & Zuk (1992) found an increase in pulse duration with size and a decrease in

pulse rate, which is negatively correlated with pulse duration.  However, in a separate study,

Simmons (1988) reported an increase in pulse rate with size for this species.

In courtship song, heavier males had longer first trills in a song characterized by a single

chirp followed by a variable number of trills (Drayton *et al*., 2010a). Heavier males also had

greater courtship call rates (Ketola *et al*., 2009).

In aggressive song, males of large size have a greater number of pulses per chirp and

shorter inter-pulse intervals (Brown *et al*., 2006).

Information about immunocompetence, or the male's ability to produce an immune

response after exposure to an antigen, is present in both calling and courtship song, although the

trends appear to differ for chirping and trilling species, perhaps due to the different energetic

investments required.  In the courtship song of *Gryllus bimaculatus*, composed of chirps that

feature both high- and low-frequency pulses, males with a high encapsulation rate, one measure

of immunocompetence, had longer high-frequency pulse durations and an increased pulse rate

(Rantala & Kortet, 2003).  In the courtship song of *Teleogryllus oceanicus*, a trilling species,

immunocompetence was negatively correlated to the number of pulses per trill, suggesting a

trade-off between energetically costly courtship song production and the ability to resist infection

(Simmons *et al*., 2010).  In calling song, immunocompetence was positively correlated to the

number of pulses per chirp in *Acheta domesticus* (Ryder & Siva-Jothy, 2000) but negatively

correlated to pulse duration in *Teleogryllus commodus* (Simmons *et al*., 2005).

The presence of a parasite has been shown to decrease the trill duration of a signaling

male (Orozco & Bertram, 2004). However, even in the absence of a parasite or pathogen, the

activation of an immune response can change the temporal patterning of song, as demonstrated

by Fedorka & Mousseau (2007).  After the injection of bacterial lipopolysaccharides, which

elicit an immune response without introducing the pathogen, males increased their inter-pulse interval and decreased their pulse duration. This suggests that eliciting an immune response, in itself, can have a lasting effect on the signals of male crickets.

A negative relationship has been demonstrated in the calling song of *Gryllus pennsylvanicus* between degree of symmetry, a potential measure of genetic quality (Van Valen, 1962), and number of pulses per chirp, with more symmetric males producing fewer pulses per chirp (Judge, 2011). In the same study, degree of symmetry was positively correlated with pulse duration and pulse period and negatively correlated to pulse period variability. Inbreeding, which also influences genetic quality, has been shown to increase the inter-pulse interval and number of pulses per chirp present in calling song (Drayton *et al*., 2007) as well as the inter-pulse interval of the courtship song (Drayton *et al*., 2010a). In the latter study, as well as a companion study on calling song (Drayton *et al*., 2010b), males that took longer to develop had more pulses per chirp in their songs, even though no effect of inbreeding could be demonstrated.

Superior nutritional condition resulted in an increase in chirp rate (Scheuber *et al*., 2003b; Wagner & Hoback, 1999) and a decrease in the inter-chirp interval of the calling song (Scheuber *et al*., 2003b), while the ability to catabolize carbohydrates (as measured by activity of the enzyme pyruvate kinase) appears to positively affect the inter-pulse interval (Bertram *et al*., 2011). Wagner (2005) demonstrated that males may face a trade-off between two nutritionally-linked traits, as males with slower chirp rates produced spermatophores more quickly than those with higher chirp rates. Similar trade-offs may be experienced between calling song characteristics and flight capability, as flight-capable *Gryllus firmus* males had shorter pulse durations, fewer pulses per chirp, and a decreased chirp rate compared to their flight-capable rivals (Mitra *et al*., 2011).

**THE SOCIAL OUTCOMES OF MALE PHENOTYPES ASSOCIATED WITH SONGS**

The phenotype-related information content being conveyed through male gryllid song can affect social interactions in two major ways: (1) by acting as a substrate for female mate choice and (2) by influencing the intensity and/or outcome of male competition for mates. There is potential for certain phenotypes, especially male body size, to be beneficial in both of these social situations. For example, large males of several gryllid species are more attractive to females (Simmons, 1986a; Simmons, 1986b; Zuk, 1988; Forrest, 1991; Bateman *et al*., 2001; Savage *et al*., 2005) and win more fights with conspecific males (Simmons, 1986a; Hack, 1997; Savage *et al*., 2005; Brown *et al*., 2006). In species with nuptial gift allocation, large male size can provide direct benefits to female mates (Brown *et al*., 1996). A heritability study on measures of male size in *Gryllus bimaculatus* showed that indirect benefits could also favor female choice for large size (Simmons, 1987a).

Yet size is not the sole determinant of male fitness. After finding that females allowed to choose their mates had improved fitness over females allocated large males, Simmons (1987b) concluded that females must make their decisions based on a mixture of characters, male size being only one. Some of these additional characters could be decreased parasite load (Zuk, 1988), older age (Zuk, 1987, 1988), dominance (Crankshaw, 1979) or immunocompetence (Tregenza *et al*., 2006). Immunocompetence has, in turn, been linked to a male's competitive ability and dominance status (Rantala & Kortet, 2004). However, females did not distinguish between inbred and outbred males in a field-based attractiveness experiment (Drayton *et al*., 2010b).

In species with nuptial gift allocation, such as *Allonemobius socius*, gift size is positively correlated to lysozyme activity, a measure of immunocompetence (Fedorka *et al*., 2005). Females have been shown to allow more sperm transfer when offered a large gift (Fedorka *et al*., 2005). Thus, immunocompetent males may experience increased fitness due to their ability to provide these large gifts. Additionally, experimentally-induced immune activation can decrease the size of the gift (Fedorka & Mousseau, 2007), which could limit reproductive potential.

Nutritional condition similarly affects paternal investment in *Gryllus lineaticeps,* with males on a high-quality diet able to produce spermatophores quicker than those on a low-quality diet (Wagner, 2005). Better nutritional condition and the lack of an induced immune response also contributed to increased longevity of *Gryllus campestris* males (Jacot *et al*., 2004), which may contribute to a greater number of lifetime mating opportunities.

In aggressive encounters, condition (the residuals of correlation between size and body mass) is also a predictor of fight outcome, with males in better condition (or heavier for a given body size) winning more fights (Brown *et al*., 2006), thus gaining greater access to females. Such dominant males may also induce females to lay more eggs (Bretman *et al*., 2006). Table II summarizes these social outcomes of male phenotypes.

**THE SOCIAL OUTCOMES OF SELECTED SONG STRUCTURES**

Theoretically, males and females could react to a conspecific's song structure not because of an associated phenotype but as a result of Fisherian dynamics, a correlation with another aspect of song structure (that does convey phenotype), or improved transmission/reception (sensory bias). The sections above demonstrate that significant information content can be conveyed through the structures of all three gryllid songs, and that male phenotypes can affect social outcomes. We

now briefly discuss the implications of phenotypically-linked song structure for the fitness of the signaler. Again, we do not comprehensively review female phonotaxis experiments, but rather we highlight general trends and focus our discussion on studies of social outcomes of the song structures listed in Table I. It is important to note that not all of these studies were explicitly interested in the relationship between song structure and phenotype.

### Frequency

When *Oecanthus nigricornis* females were presented with simultaneous playbacks of calling songs of different frequencies and allowed to freely choose between them, they preferentially oriented towards the lower frequency call (Brown *et al*., 1996).  In similar setups, two independent studies found that *Gryllus campestris* females exhibited the same preference (Simmons & Ritchie, 1996; Scheuber *et al*., 2004). Drayton *et al*. (2010b) similarly reported strong linear selection favoring decreased frequency in *Teleogryllus commodus* calling song. However, there has also been support for near-mean (Shaw & Herlihy, 2000) and higher (Mitra *et al*., 2011) frequency preferences.

### Amplitude

Stout and McGhee (1988) demonstrated that differences of 5 dB were sufficient in simultaneous playbacks of model *Acheta domesticus* calling songs to elicit female preference for the more intense call. Similar female preferences were demonstrated for both relative and absolute intensity in *Eunemobius carolinus* (Farris *et al*., 1997). In addition, more intense calls can be transmitted farther from the signaler (Simmons, 1988), perhaps reaching, and thus attracting, more females. While more intense calls have been linked to both size and age (Gray, 1997; Jacot

*et al*., 2007; Ryder & Siva-Jothy, 2000; Simmons, 1988; Verburgt *et al*., 2011), this result could also reflect a female preference for a closer potential mate, which would reduce her search time, energy expenditure, and risk of predation.

**Amount of calling**

In the trilling species *Gryllus integer*, females in both single and simultaneous playback experiments preferred the calling songs of males with longer bout durations and those with uninterrupted calling bouts (Hedrick, 1986; Leonard & Hedrick, 2009). Interestingly, rival males will display a similar phonotactic preference for longer bout durations when offered a simultaneous choice, especially when they themselves produce attractive songs or are likely to win fights (Leonard & Hedrick, 2009). Similarly, females favor shorter silent intervals between male calls (Drayton *et al*., 2010b) and greater proportions of longer chirps (Simmons *et al*., 2001).

In courtship songs, females have been shown to prefer males that produce songs with higher duty cycles, or more sound per unit time (Rebar *et al*., 2009). In addition, mating success in *Gryllodes sigillatus* has been linked to higher courtship call rates (Ketola *et al*., 2007). Although these preferences could potentially be explained by a male phenotype that allows for greater song output, it is also possible that males are taking advantage of a female sensory bias. In addition, males in the field have a greater chance of attracting potential mates if they call for a greater proportion of available time.

**Temporal characteristics**

Among temporal characteristics found to have social outcomes for male signalers, longer pulse durations appear to be beneficial in all three song types (but see Champagnon & Cueva del Castillo, 2008). Using an attractiveness assay based on virgin female willingness to mate, Fedorka and Mousseau (2007) found that the more attractive males produced calling songs with longer pulses. In addition, Shaw & Herlihy (2000) demonstrated female preference for longer pulse durations in the Hawaiian cricket *Laupala cerasina*. In the courtship song of *Teleogryllus oceanicus*, females preferred the trill section to contain longer pulses (Rebar *et al.*, 2009) and *Gryllus bimaculatus* females preferred courtship songs with longer high-frequency pulses (Rantala & Kortet, 2003). In the aggressive songs of *Acehta domesticus*, males with longer pulse durations won more fights, even though this song component was not correlated with resource-holding potential (Brown *et al.*, 2006). Beneficial social outcomes of longer chirp durations, on the other hand, have only been shown in the calling song of *Allonemobius socius* (Olvido & Wagner, 2004).

The length of the silent intervals between pulses and chirps also appears to be important in all three song types. Shorter inter-pulse intervals were preferred by females in both the calling (Wagner *et al.*, 1995) and courtship songs (Rebar *et al.*, 2009), although stabilizing selection may maintain the length of intervals in *Teleogryllus commodus* (Drayton *et al.*, 2010b). In aggressive song, a decrease in both the inter-pulse and inter-chirp interval was correlated with male fighting success (Brown *et al.*, 2006). In this study, the length of the inter-pulse interval was significantly related to a male phenotype, size, but the length of the inter-chirp interval was not. This is a potential example of how the social outcome of one non-phenotypically linked song structure could be due to a relationship with another, information-carrying parameter, as measures of the length of pulse and chirp intervals are highly correlated.

Female preferences for a greater number of pulses per chirp (Wagner *et al*., 1995; Gray 1997; Drayton *et al*., 2010b; but see Gray & Cade, 1999) and chirps per second (chirp rate; Wagner & Reiser, 2000; Rantala & Kortet, 2003; Scheuber *et al*., 2004; Wagner & Basolo, 2007) have been demonstrated (although see Shaw & Herlihy, 2000, for a demonstration of unimodal pulse rate preference functions). In an interesting playback experiment that determined both female and male preference for calling song characteristics, Kiflawi and Gray (2000) demonstrated another social outcome of the number of pulses per chirp for calling males. They found that both females and small males preferred songs with a greater number of pulses per chirp. The finding that small (but not large) males show the same phonotactic response as females suggests that they may try to increase their own reproductive success (likely reducing the calling male's fitness) by acting as satellites around a male producing a female-preferred song.

Interestingly, it seems that female preference for temporal characteristics is consistently in the direction of greater acoustical energy (more sound per unit time), as also demonstrated by female preference for increased duty cycle. Thus, in addition to any information content that could be displayed by such song structures, male gryllids could potentially be taking advantage of an existing female sensory bias. Thus female preferences could be explained either based on phenotypic information or sensory biases (passive attraction). Experiments to distinguish these alternatives would be an interesting avenue for future research endeavors.

**THE APPLICATION OF THE MULTIPLE SIGNALING HYPOTHESES TO GRYLLID ACOUSTIC COMMUNICATION**

Multiple cues may be used by receivers during mate choice because: (1) it increases the receiver's fitness by reducing mate choice errors or costs, (2) the signaler is manipulating pre-existing sensory biases of the receiver, reducing mating resistance, and/or (3) one or more cues are a remnant of past selection or have arisen in another context (Candolin, 2003). Often, the hypotheses surrounding the evolution of multiple signals are applied to multimodal signals, or those signals that contain cues in more than one modality (e.g. Table 2 in Candolin, 2003) or to the evolution multiple elaborate ornaments (e.g. Moller & Pomiankowski, 1993). Here, we aim to apply multiple signaling hypotheses to three acoustic signals – calling, courtship, and aggressive songs – produced sequentially during cricket social interactions. This differs from previous approaches with crickets which considered different temporal characteristics of single songs as multiple signals.

There are several hypotheses, reviewed extensively by Candolin (2003), that set out to explain the use of multiple cues during mate choice, including: (1) the multiple messages hypothesis, which purports that different signals provide information about different aspects of mate quality (Moller & Pomiankowski, 1993; Johnstone, 1996); (2) the back-up signal hypothesis, where each cue reflects the same quality with some error, thus allowing a more accurate picture of the signaler (Moller & Pomiankowski, 1993; Johnstone, 1996); (3) the species recognition hypothesis, where one signal serves solely as a species identifier and subsequent signals communicate mate quality (Ryan & Rand, 1993a); (4) unreliable and Fisherian cues that do not indicate mate quality but rather arise through runaway (Fisher, 1930), exploit sensory biases (Ryan & Rand, 1993b), or are remnants of past selection (Holland & Rice, 1998); (5) the multiple sensory environments hypothesis, where receivers pay attention to different cues under different conditions, such as distance (e.g. López & Martín, 2001); and (6)

the multiple receivers hypothesis, where different signals arise to communicate to different receivers, such as potential mates and rivals (Andersson *et al.*, 2002); among others.

In the gryllid system, single song types, often the calling song, have been viewed as multicomponent signals, with each song parameter (i.e., number of pulses per chirp, amplitude, frequency, etc.) potentially acting as its own signal. Scheuber and colleagues (2003a, 2003b, 2004) demonstrated that the components of *Gryllus campestris* calling song convey multiple messages about an individual's nutritional history. In the aggressive songs of *Acheta domesticus*, both the number of pulses per chirp and the length of the inter-pulse interval were significantly correlated to male size (Brown *et al.*, 2006), which could suggest redundancy (i.e., back-up signals). In tree crickets, females have been shown to exhibit stabilizing preferences for pulse rate (in trilling species) and chirp rate (in chirping species), which suggests that these characteristics could be used for species identification (reviewed in Brown, 1999). Unreliable signals were alluded to in the section on social outcomes of song structures, as a beneficial outcome of a song parameter that did not have to do with male phenotype could be due to sensory exploitation, Fisherian dynamics, and/or correlations with other "reliable" aspects of song structure.

The differing acoustical environments and potential receivers of each song type have likely also contributed to some of the divergence in structure between the calling, courtship, and aggressive songs. For example, calling song is produced for far more distant receivers than either of the courtship and aggressive songs. One obvious result is the increase in intensity by males singing calling song. However, distant receivers may also necessitate use of lower frequencies and more simplistic temporal patterning, as calls using higher frequencies and more complex patterning are more subject to sound attenuation. In addition, the potential presence of

eavesdroppers (conspecifics and/or predators and parasites) during calling song may affect both the type of information present in song as well as the song structures utilized.

　　We suggest taking an additional approach that has, to date, not yet been considered:  why do most gryllids exhibit *three* distinct song types?  Even taking into account that there are different receivers (i.e., females and males) for certain gryllid songs, why are there two signals directed at females (the calling song and courtship song) and two signals directed at males (the calling song and aggressive song)?  Most likely, as suggested by Wagner and Reiser's (2000) work with calling and courtship song in *Gryllus lineaticeps*, each song type conveys some different aspect of mate quality (i.e. multiple messages), although there may be some overlap between what is communicated to males and females (as suggested by Nelson & Nolen, 1997) and males may repeat certain critical information in more than one social situation. Crucially, however the amount and identity of distinct vs. shared information content in the three cricket song types has yet to be delineated, and we suggest that future research focus on this substantial "hole" in the knowledge base of gryllid acoustic communication.

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**TABLES AND FIGURES**

Table 1-1: *Studies demonstrating a song structure-phenotype relationship in gryllids.*

| Component of song structure | Direction of association | Non-acoustic Phenotype | Species | Reference(s) |
|---|---|---|---|---|
| <u>Frequency</u> | Decrease | Larger harp area | *Gryllus campestris* | Jacot *et al.* (2005); Scheuber *et al.* (2003*a*, 2003*b*); Simmons (1995); Simmons & Ritchie (1996) |
| | | Larger size | *Acheta domesticus* | Bertram *et al.* (2011) |
| | | | *Gryllus pennsylvanicus* | Judge (2011) |
| | | | *Oecanthus nigricornis* | Brown *et al.* (1996) |
| | | | *Oecanthus niveus* | Ponce-Wainer & del Castillo (2008) |
| | | Greater age | *Gryllus campestris* | Jacot *et al.* (2007) |
| | | | *Gryllus pennsylvanicus* | Judge (2011) |
| | | Flight incapable | *Gryllus firmus* | Mitra *et al.* (2011) |
| | Decrease[a] | Larger mass | *Teleogryllus commodus* | Drayton *et al.* (2010*a*) |
| | Increase[a] | Greater inbreeding | *Teleogryllus commodus* | Drayton *et al.* (2010*a*) |
| | | | | |
| <u>Amplitude</u> | Decrease | Older | *Gryllus campestris* | Jacot *et al.* (2007) |
| | Increase | Larger size | *Acheta domesticus* | Gray (1997); Ryder & Siva-Jothy (2000); Bertram *et al.* (2011) |
| | | | *Gryllus bimaculatus* | Simmons (1988) |
| | | Younger | *Gryllus bimaculatus* | Verburgt *et al.* (2011) |
| | | | | |
| <u>Amount of Calling</u> | Non-specific decrease | Extreme old age | *Gryllus pennsylvanicus* | Judge *et al.* (2008) |
| | | Induced immune response | *Gryllus campestris* | Jacot *et al.* (2004); Scheuber *et al.* (2004) |
| | | Inbred | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |

| Component of song structure | Direction of association | Non-acoustic Phenotype | Species | Reference(s) |
|---|---|---|---|---|
| <u>Amount of Calling</u>, cont'd. | Non-specific decrease, cont'd. | Slower development time | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | | Parasitized | *Gryllus texensis* | Orozco & Bertram (2004) |
| | | | *Gryllus integer* | Cade (1984) |
| | | Poor nutritional condition | *Gryllus integer* | Hedrick (2005) |
| | Decrease due to greater intervals of silence | Inbred | *Teleogryllus commodus* | Drayton *et al.* (2007) |
| | | Slower development time | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | | Younger | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | Decrease duty cycle | Older | *Gryllus bimaculatus* | Verburgt *et al.* (2011) |
| | Earlier start | Larger size | *Gryllus integer* | Bertram (2000) |
| | Non-specific increase | Flight-capable | *Gryllus texensis* | Bertram (2007) |
| | | Flight-incapable | *Gryllus firmus* | Mitra *et al.* (2011) |
| | | Good nutritional condition | *Gryllus campestris* | Holzer *et al.* (2003) |
| | | | *Gryllus lineaticeps* | Wagner & Hoback (1999) |
| | | | *Gryllus pennsylvanicus* | Judge *et al.* (2008) |
| | | High competitive ability | *Gryllus bimaculatus* | Simmons (1986*a*) |
| | | Increased dietary phosphorus | *Acheta domesticus* | Bertram *et al.* (2009) |
| | | Increased pyruvate kinase activity | *Acheta domesticus* | Bertram *et al.* (2011) |
| | | Larger size | *Acheta domesticus* | Bertram *et al.* (2011) |
| | | | *Gryllus integer* | Bertram (2000) |
| | | | *Neonemobius sp.* | Forrest (1991) |
| | | Older | *Teleogryllus commodus* | Maklakov *et al.* (2009) |
| | Increase call rate[a] | High endurance | *Gryllodes sigillatus* | Ketola *et al.* (2009) |
| | | Larger mass | *Gryllodes sigillatus* | Ketola *et al.* (2009) |
| | Increase lifetime | Good nutritional condition | *Gryllus pennsylvanicus* | Judge *et al.* (2008) |

32

| Component of song structure | Direction of association | Non-acoustic Phenotype | Species | Reference(s) |
|---|---|---|---|---|
| <u>Amount of Calling, cont'd.</u> | Increase lifetime, cont'd. | Larger size | *Gryllus bimaculatus* | Verburgt *et al.* (2011) |
| | | | | |
| <u>Temporal characteristics</u> | | | | |
| Chirp/Trill duration | Decrease | Older | *Gryllus campestris* | Jacot *et al.* (2007) |
| | | Parasitized | *Gryllus texensis* | Orozco & Bertram (2004) |
| | Increase | Flight-incapable | *Gryllus firmus* | Mitra *et al.* (2011) |
| | Increase first trill[a] | Larger mass | *Teleogryllus commodus* | Drayton *et al.* (2010*a*) |
| Chirp rate | Decrease | Dominant | *Acheta domesticus* | Crankshaw (1979) |
| | | Less time to produce spermatophore | *Gryllus lineaticeps* | Wagner (2005) |
| | Increase | Good nutritional condition | *Gryllus campestris* | Scheuber *et al.* (2003*b*) |
| | | | *Gryllus lineaticeps* | Wagner & Hoback (1999) |
| | | Histolysed flight muscles | *Gryllus firmus* | Mitra *et al.* (2011) |
| Inter-chirp interval | Decrease | Good nutritional condition | *Gryllus campestris* | Scheuber *et al.* (2003*b*) |
| | | Younger | *Gryllus bimaculatus* | Verburgt *et al.* (2011) |
| | Decrease chirp-trill interval[a] | Older | *Teleogryllus commodus* | Drayton *et al.* (2010*a*) |
| Inter-pulse interval | Decrease | Decreased pyruvate kinase activity | *Acheta domesticus* | Bertram *et al.* (2011) |
| | | Older | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | | Younger | *Gryllus bimaculatus* | Verburgt *et al.* (2011) |
| | Decrease[b] | Larger size | *Acheta domesticus* | Brown *et al.* (2006) |
| | Increase | Immunocompromised | *Allonemobius socius* | Fedorka & Mousseau (2007) |
| | | Inbred | *Teleogryllus commodus* | Drayton *et al.* (2007) |
| | | Larger size | *Acheta domesticus* | Bertram *et al.* (2011) |
| | Increase[a] | Inbred | *Teleogryllus commodus* | Drayton *et al.* (2010*a*) |
| Pulse duration | Decrease | High immunocompetence | *Teleogryllus commodus* | Simmons *et al.* (2005) |

| Component of song structure | Direction of association | Non-acoustic Phenotype | Species | Reference(s) |
|---|---|---|---|---|
| Pulse duration, cont'd. | Decrease, cont'd. | Induced immune response | *Allonemobius socius* | Fedorka & Mousseasu (2007) |
| | | Larger size | *Oecanthus nigricornis* | Brown *et al.* (1996) |
| | | | *Gryllodes sigillatus* | Champagnon & Cueva del Castillo (2008) |
| | | Less symmetrical | *Gryllus pennsylvanicus* | Judge (2011) |
| | | Older | *Gryllus pennsylvanicus* | Judge (2011) |
| | | | *Oecanthus nigricornis* | Brown *et al.* (1996) |
| | | Small size | *Gryllus pennsylvanicus* | Judge (2011) |
| | Increase | Larger size | *Acheta domesticus* | Bertram *et al.* (2011) |
| | | | *Gryllus bimaculatus* | Simmons & Zuk (1992) |
| | | | *Gryllus pennsylvanicus* | Judge (2011) |
| | | Younger | *Gryllus bimaculatus* | Verburgt *et al.* (2011) |
| | Increase high-freq[a] | High immunocompetence | *Gryllus bimaculatus* | Rantala & Kortet (2003) |
| Pulses per chirp | Decrease | Older | *Gryllus campestris* | Jacot *et al.* (2007) |
| | | Larger mass | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | Decrease[a] | High immunocompetence | *Teleogryllus oceanicus* | Simmons *et al.* (2010) |
| | Increase | Flight-incapable | *Gryllus firmus* | Mitra *et al.* (2011) |
| | | High immunocompetence | *Acheta domesticus* | Ryder & Siva-Jothy (2000) |
| | | Inbred | *Teleogryllus commodus* | Drayton *et al.* (2007) |
| | | Larger size | *Acheta domesticus* | Gray (1997) |
| | | | *Oecanthus niveus* | Ponce-Wainer & del Castillo (2008) |
| | | Less symmetrical | *Grllyus pennsylvanicus* | Judge (2011) |
| | | Older | *Grllyus pennsylvanicus* | Judge (2011) |
| | | Slower development time | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | Increase[a] | High immunocompetence | *Gryllus bimaculatus* | Rantala & Kortet (2003) |

| Component of song structure | Direction of association | Non-acoustic Phenotype | Species | Reference(s) |
|---|---|---|---|---|
| Pulses per chirp, cont'd. | Increase[a], cont'd. | Slower development time | *Teleogryllus commodus* | Drayton *et al.* (2010a) |
| | Increase[b] | Larger size | *Acheta domesticus* | Brown *et al.* (2006) |
| Pulse period | Decrease | Older | *Grllyus pennsylvanicus* | Judge (2011) |
| | Increase | More symmetrical | *Gryllus pennsylvanicus* | Judge (2011) |
| | More variable | Less symmetrical | *Gryllus pennsylvanicus* | Judge (2011) |
| | | Older | *Grllyus pennsylvanicus* | Judge (2011) |
| Pulse rate | Decrease | Larger size | *Gryllus bimaculatus* | Simmons & Zuk (1992) |
| | Increase | Larger size | *Gryllus bimaculatus* | Simmons (1988) |
| | Increase[a] | High immunocompetence | *Gryllus bimaculatus* | Rantala & Kortet (2003) |
| [a]Courtship song, [b]Aggressive song; All others calling song. | | | | |

| Non-acoustic phenotype | Social outcome | Species | Reference(s) |
|---|---|---|---|
| **Table 1-2:** *Studies examining the social outcomes of male phenotypes associated with songs.* | | | |
| **Non-acoustic phenotype** | **Social outcome** | **Species** | **Reference(s)** |
| Better condition | Win more fights | *Acheta domesticus* | Brown *et al.* (2006) |
| Dominance | Female preference | *Acheta domesticus* | Crankshaw (1979) |
| | Increased female egg production | *Gryllus bimaculatus* | Bretman *et al.* (2006) |
| Good nutritional condition | Increased longevity | *Gryllus campestris* | Jacot *et al.* (2004) |
| | | *Gryllus pennsylvanicus* | Judge *et al.* (2008) |
| | Less time to produce spermatophore | *Gryllus lineaticeps* | Wagner (2005) |
| High competitive ability | Greater mating success | *Gryllus bimaculatus* | Simmons (1986*a*) |
| High degree of symmetry | More attractive | *Gryllus veletis* | Zuk (1987) |
| High immunocompetence | Larger nuptial gift | *Allonemobius socius* | Fedorka *et al.* (2005) |
| | More attractive | *Teleogryllus oceanicus* | Tregenza *et al.* (2006) |
| Induced immune response (w/o pathogen) | Decreased longevity | *Gryllus campestris* | Jacot *et al.* (2004) |
| | Smaller nuptial gift | *Allonemobius socius* | Fedorka & Mousseau (2007) |
| Larger size | Increased female egg production | *Oecanthus nigricornis* | Brown *et al.* (1996) |
| | More attractive | *Acheta domesticus* | Savage *et al.* (2005) |
| | | *Gryllus bimaculatus* | Bateman *et al.* (2001); Simmons (1986*a*, 1986*b*); Simmons & Zuk (1992) |
| | | *Gryllus pennsylvanicus* | Zuk (1988) |
| | | *Gryllus veletis* | Zuk (1987) |
| | | *Neonemobius* sp. | Forrest (1991) |
| | Win more fights | *Acheta domesticus* | Brown *et al.* (2006); Hack (1997); Savage *et al.* (2005) |
| | | *Gryllus bimaculatus* | Simmons (1986*a)* |
| Less parasitized | More attractive | *Gryllus pennsylvanicus* | Zuk (1987) |

Table 1-3: *Studies examining the social outcomes of selected song structures.*

| Component of song structure | Direction of association | Social outcome | Species | Reference(s) |
|---|---|---|---|---|
| <u>Frequency</u> | Higher | Female preference | *Gryllus firmus* | Mitra *et al.* (2011) |
| | Near Mean | Female preference | *Laupala cerasina* | Shaw & Herlihy (2000) |
| | Lower | Female preference | *Gryllus campestris* | Simmons & Ritchie (1996); Scheuber *et al.* (2004) |
| | | | *Oecanthus nigricornis* | Brown *et al.* (1996) |
| | | | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | | | | |
| <u>Amplitude</u> | Louder | More attractive | *Acheta domesticus* | Stout & McGhee (1988) |
| | | | *Eunemobius carolinus* | Farris *et al.* (1997) |
| | | | | |
| <u>Amount of Calling</u> | Greater proportion of long chirp | Female preference | *Teleogryllus oceanicus* | Simmons *et al.* (2001) |
| | Higher call rate[a] | Greater mating success | *Gryllodes sigillatus* | Ketola *et al.* (2007) |
| | Higher duty cycle[a] | Female preference | *Teleogryllus oceanicus* | Rebar *et al.* (2009) |
| | Longer bout duration | Female preference | *Gryllus integer* | Hedrick (1986); Leonard & Hedrick (2009) |
| | | Rival male preference | *Gryllus integer* | Leonard & Hedrick (2009) |
| | Shorter interval between calls | Female preference | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | | | | |
| <u>Temporal characteristics</u> | | | | |
| | | | | |
| Chirp duration | Longer | Female preference | *Allonemobius socius* | Olvido & Wagner (2004) |
| Inter-chirp interval | Shorter[b] | Win more fights | *Acheta domesticus* | Brown *et al.* (2006) |
| Chirp rate | Higher | Female preference | *Gryllus bimaculatus* | Rantala & Kortet (2003) |
| | | | *Gryllus campestris* | Scheuber *et al.* (2004) |
| | | | *Gryllus firmus* | Mitra *et al.* (2011) |

| Component of song structure | Direction of association | Social outcome | Species | Reference(s) |
|---|---|---|---|---|
| Chirp rate, cont'd. | Higher, cont'd. | Female preference, cont'd. | *Gryllus lineaticeps* | Wagner & Reiser (2000); Wagner & Basolo (2007) |
| Inter-pulse interval | Near mean | Female preference | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | Shorter | Female preference | *Gryllus integer* | Wagner *et al.* (1995) |
| | Shorter[a] | Female preference | *Teleogryllus oceanicus* | Rebar *et al.* (2009) |
| | Shorter[b] | Win more fights | *Acheta domesticus* | Brown *et al.* (2006) |
| Pulse duration | Longer | Female preference | *Laupala cerasina* | Shaw & Herlihy (2000) |
| | | More attractive | *Allonemobius socius* | Fedorka & Mousseau (2007) |
| | Longer[a] | Female preference | *Teleogryllus oceanicus* | Rebar *et al.* (2009) |
| | Longer high-freq[a] | Female preference | *Gryllus bimaculatus* | Rantala & Kortet (2003) |
| | Longer[b] | Win more fights | *Acheta domesticus* | Brown *et al.* (2006) |
| | Shorter | Female preference | *Gryllodes sigillatus* | Champagnon & Cueva del Castillo (2008) |
| Pulses per chirp/trill | More | Female preference | *Acheta domesticus* | Gray (1997); Kiflawi & Gray (2000) |
| | | | *Gryllus integer* | Wagner *et al.* (1995) |
| | | | *Teleogryllus commodus* | Drayton *et al.* (2010*b*) |
| | | Small rival male preference | *Acheta domesticus* | Kiflawi & Gray (2000) |
| | Near mean | Female preference | *Gryllus integer* | Gray & Cade (1999) |
| | | Preference of parasitoid fly | *Gryllus integer* | Gray & Cade (1999) |
| Pulse rate | Near mean | Female preference | *Laupala cerasina* | Shaw & Herlihy (2000) |

[a] Courtship song; [b] Aggressive song; All others calling song

38

# An Examination of Multiple Signaling in the Acoustic Communication System of House Crickets *(Acheta domesticus)*

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**ABSTRACT**

Despite the extensive literature on cricket bioacoustics, little collective understanding has been established that compares the structural and functional significance of the three distinct gryllid song types: calling song, courtship song, and aggressive song. Here, we measured all three song types from a cohort of male house crickets (*Acheta domesticus*) throughout their natural lifespan in order to make direct comparisons of song structure and phenotypic information content between the calling, courtship, and aggressive songs. Through statistical analysis of eight acoustic parameters of song, we established that there are significant structural differences between the three song types. By looking for correlations between phenotype and song structure, we also determined the phenotypic information content present in all three house cricket songs and that the distribution of information content may differ depending on song type. This suggests that the evolutionary persistence of three song types in the gryllid family may be due to the presence of multiple messages.


*Key Words:* aggression, bioacoustics, communication, courtship, crickets, *Gryllidae,* signaling

**INTRODUCTION**

Acoustical signaling by males is the predominant form of communication in crickets (Orthoptera: Gryllidae). Male crickets generally produce at least three qualitatively distinct types of song, depending on social context: calling song, courtship song, and aggressive song (Alexander, 1961). Males produce calling song to attract females, who locate males by phonotaxis. Female choice is often exhibited at this phase of mate attraction (e.g., Doherty & Hoy, 1985), although it can also be revealed during courtship or post-mating (e.g. Brown & Gwynne, 1997; Brown, 1997; Brown, 1999; Wagner & Reiser, 2000). Rival males may also respond to calling songs by spacing themselves (e.g., Campbell & Shipp, 1979; Cade, 1981; Simmons, 1988), by approaching the calling male to aggregate (Ulagaraj & Walker, 1973), challenging him for his territory ownership (Alexander, 1961), or by becoming satellite males that may intercept approaching females (e.g., Cade, 1979; Kiflawi & Gray, 2000).

Once a female has come into physical contact with a male, the male switches from calling song to a distinct courtship song. Though lesser studied than the calling song, courtship song has been shown to be vital to successful copulation, as females mate exclusively with those who produce it (Crankshaw, 1979; Balakrishnan & Pollack, 1996; Nelson & Nolen, 1997; Boake, 1983).

If a rival challenges a male for direct access to a female or for his territory, he produces an aggressive song. The function of aggressive song is poorly understood, though a recent study showed that signaling mitigates the cost of fighting in *Teleogryllus oceanicus* (Logue *et al.,* 2010). Brown *et al.* (2006) showed that aggressive songs contain information about male body size and outcome of contests. Thus aggressive songs may serve to communicate aspects of

resource holding potential before the fight escalates and injures either of the parties involved (Huntingford & Turner, 1987; Brown *et al.,* 2006).

In addition to the situational specificity of cricket song, the calling, courtship, and aggressive songs have generally been considered distinct due to structural differences (Figure 1). However, the evolution of these distinct song types has received little attention. While the importance of calling song in attracting females is well documented (reviewed in Doherty & Hoy, 1985; Greenfield, 1997; Zuk & Simmons, 1997; Brown, 1999; Gerhardt & Huber, 2002), the functional significance of courtship and aggressive songs has received much less attention. Furthermore, the question "Why *three*?" has yet to even be asked. Multiple songs have not evolved (or have been lost) in the Haglidae and Tettigoniidae, the other large group within the acoustic Ensiferan Orthoptera, so why do they persist within the Gryllidae? In a recent review (Covey & Brown, in preparation), we suggest that multiple signaling hypothesis may be able to help us understand the significance of multiple song types in crickets.

There are several hypotheses, reviewed extensively by Candolin (2003), that set out to explain the use of multiple signals during mate choice, including: (1) the multiple messages hypothesis, which purports that different signals provide information about different aspects of mate quality (Moller & Pomiankowski, 1993; Johnstone, 1996); (2) the redundant (or back-up) signal hypothesis, where each cue reflects the same quality with some error, thus allowing a more accurate picture of the signaler (Moller & Pomiankowski, 1993; Johnstone, 1996); (3) the species recognition hypothesis, where one signal serves solely as a species identifier and subsequent signals communicate mate quality (Ryan & Rand, 1993a); (4) unreliable and Fisherian cues that do not indicate mate quality but rather arise through runaway (Fisher, 1930), exploit sensory biases (Ryan & Rand, 1993*b*), or are remnants of past selection (Holland & Rice,

1998); (5) the multiple sensory environments hypothesis, where receivers pay attention to different cues under different conditions, such as distance (e.g. López & Martín, 2001); and (6) the multiple receivers hypothesis, where different signals arise to communicate to different receivers, such as potential mates and rivals (Andersson *et al.*, 2002); among others.

In the gryllid system, single song types, often the calling song, have been viewed as multicomponent signals, with each song parameter (i.e., number of pulses per chirp, amplitude, frequency, etc.) potentially acting as its own signal. Scheuber and colleagues (2003*a*, 2003*b*, 2004) demonstrated that the components of *Gryllus campestris* calling song convey multiple messages about an individual's nutritional history. In the aggressive songs of *Acheta domesticus*, both the number of pulses per chirp and the length of the inter-pulse interval were significantly correlated to male size (Brown *et al.*, 2006), which could suggest redundancy (i.e., back-up signals). In tree crickets, females have been shown to exhibit stabilizing preferences for pulse rate (in trilling species) and chirp rate (in chirping species), which suggests that these characteristics could be used for species identification (reviewed in Brown, 1999).

In this study, however, we take a different approach, one that has not yet been applied to any gryllid species. Here, we view each song type as one complete signal. Each signal contains multiple components (including amplitude, frequency, and temporal aspects of the song), but, for our purposes, is considered only one signal. We take this approach in order begin to determine why three song types persist within the cricket communication system.

First, we test for significant structural differences between the song types of male house crickets, *Acheta domesticus*, in order to confirm that they are indeed three distinct signals. We examine the variability of each song type and song parameter as a measure of the ability to carry unique phenotypic information. Then, we determine what phenotypic information is present in

these songs and compare it across song type. In doing so, we hope to differentiate between the two information-based multiple signaling hypotheses: multiple messages and redundant signals. Because each signal is composed of multiple components, each song could potentially contain both multiple messages and redundant signals. However, the distribution of new information to repeated information, as well as the identity of that information, can begin to shed some light on the persistence of these three song types. We predict that calling song will be the least variable song type and will contain the most fundamental information (i.e., basic information that is applicable in all cricket social interactions). Courtship and aggressive songs will be more variable and more likely to contain information not present in calling song (i.e., a multiple message). However, because cricket songs are made up of multiple components, the presence of new information does not preclude the presence of a redundant signal, so it is expected that some of the fundamental information present in calling song will still be present in the other two song types.

We found strong evidence that the calling, courtship, and aggressive songs are structurally distinct signals. Courtship and aggressive song are both more variable than the calling song, suggesting the potential to hold additional information content (multiple messages). Male body condition, age, and symmetry were found to be communicated through aspects of song. Body condition and age were not communicated differently based on song type, so they may be redundant in all three songs. Although nonsignificant after correcting for multiple tests, there was a trend for symmetry, our proxy measure of genetic quality, to be communicated only in courtship song, suggesting that the presence of multiple messages may necessitate the persistence of additional acoustic signals in crickets.

**METHODS**

**Cricket Culturing**

Crickets were purchased as early-instar juveniles from reptilefood.com (Dayton, Ohio, USA) and reared to adulthood in the laboratory. Upon receipt, up to 250 individuals were housed in a 55-liter plastic container, which contained cardboard egg cartons for substrate and shelter. Focal males were physically (but not acoustically) isolated from the colony pre-eclosion, so that adult ages could be unambiguously assigned, and were reared in individual 15 x 9 x 12 cm plastic containers with a piece of egg carton for shelter. All crickets were fed an ad libitum diet of Tetra Min tropical fish flakes (Tetra Werke, Melle, Germany) and Purina Puppy Chow (Nestlé Purina PetCare Company, Vevey, Switzerland) and were occasionally supplemented with slices of organic apples. Water was provided in shallow trays filled with sand and was changed as needed. Crickets were held in a temperature-controlled chamber at 21° C on a 12:12 h light:dark cycle. Focal crickets were maintained in the laboratory until their natural death, at which point they were numbered and frozen for later phenotypic analysis.

**Song Recording**

Attempts were made to record all three song types from each focal male at two ages, 10 and 20 d post-adult eclosion (+/- 1 d). Male house crickets are generally sexually mature and begin calling for mates by 5 d post-eclosion (A. Covey, personal observation) and begin to senesce around 40 d post-eclosion (Nowosielski & Patton, 1965). Thus, we selected ages for recording to represent relatively younger (10 d) and relatively older (20 d) males.

Within one day (+/-) of the target age, the focal male's body mass was measured to 0.01 mg using an A&D HR-202 balance (A&D Engineering, Inc., Milpitas, California, U.S.A.). The

focal male was then transferred, along with its calling burrow (egg carton shelter), into a clean 15 x 9 x 12 cm plastic container. It was placed in a sound-insulated room to acclimate. During this acclimation period, the focal male was allowed acoustical interaction with the nearby colony of adult crickets via an open door. Once the focal male had been calling for at least 30 s, the door was closed and calling song was recorded for 180 s.

A rival male was then added to the plastic container to stimulate aggressive song in the focal male. This stimulus male was size-matched by mass to be within 0.05 g of the focal male. We temporarily muted this male before placing it into the chamber by reversing its forewings so that the plectrum of the right wing could not engage the file of the left wing. The stimulus male was identified with a drop of white liquid adhesive on its back. After at least 30 s of singing by the focal male, 180 s of aggressive song was recorded.

Lastly, the stimulus male was removed from the chamber and an adult female was added from the colony. This stimulated courtship song in the focal male. After at least 30 s of continuous singing, 180 s of courtship song was recorded. The focal male was then returned to its rearing container and the stimulus male and female were returned to the adult colony.

Attempts were made to record all three song types at both target ages for each focal male. If a focal male did not produce calling song within 1 day (+/-) of the first target age (10 d), it was returned to the rearing chamber and attempts were made to record his songs at the next target age (20 d). If no songs were produced at either target age, the focal male was not maintained for phenotypic analysis. Successful recordings (all three song types from at least one target age) were collected from 24 males.

All songs were recorded using an Olympus WS-600S digital voice recorder (Olympus Imaging Corporation, Tokyo, Japan) in a sound-insulated room during the focal male's night

cycle. A single SONY ECM 717 microphone (Sony Corporation, Tokyo, Japan) was placed 13 cm directly above the male's calling burrow. The room was illuminated by red light for data collection. Temperature within the recording chamber was measured with a Springfield PreciseTemp temperature probe (Springfield Precision Instruments, Wood Ridge, New Jersey, U.S.A.) and included as a covariate in all statistical models. Plastic recording containers were washed with soap and water followed by a 70% ethanol solution before being used for another focal male.

**Acoustical measurements**

Digital song files were analyzed using Raven 1.2 for Macintosh (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA). Three random sections of each song file were chosen for analysis using a random number generator (of numbers between 0-180). The first full chirp nearest the random number generated was used for analysis. At each selection, the following song parameters were measured: the amplitude of the loudest pulse in the chirp (kU), the peak frequency of the chirp (Hz), the range of frequencies used in the chirp ($\Delta$ frequency; Hz), and five measures of temporal structure, including the number of pulses per chirp, pulse duration (s), chirp duration (s), and the inter-pulse and inter-chirp intervals (s). Figure 2 shows an amplitude waveform depicting a typical pattern of pulses and chirps in house cricket calling song.

**Phenotypic measurements**

Within 24 h of a focal male's natural death, longevity was recorded and the male was numbered and frozen for phenotypic analysis. An Olympus SX2 bifocal microscope (Olympus Imaging

Corporation, Tokyo, Japan) and Hitachi HVC20 camera (Hitachi Denshi, Ltd., Japan) captured color images that were then digitized using iMovie 'll (version 9.0.4) for Macintosh (Apple Inc., Cupertino, CA, USA). Still images were generated of both femurs and both wings for each male, unless the body part was lost or severely damaged during natural life. Using Image J 1.45S for Macintosh (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2012.), three digital measurements of both the left and right femur length and the left and right harp area were made and converted to metric dimensions using a slide micrometer (1 ImageJ length unit = 57.6 mm; 1 ImageJ area unit = 3404.5 mm$^2$). Femur length spanned the distance from the trochanter-femur joint to the femur-tibia joint (see Laksanacharoen *et al*., 2000) and was measured using the line tool in Image J. Harp area was bounded by the file, Cu1 and Cu2 veins and was measured using the polygon tool in Image J (following Judge, 2011). These three measurements were then averaged for each femur and each harp, resulting in an average left femur length, an average right femur length, an average left harp area, and an average right harp area.

Femur asymmetry was calculated as the difference between the average left femur length and the average right femur length. Harp asymmetry was calculated as the difference between the average left harp area and the average right harp area. Asymmetry in femur length may reflect an individual's inability to maintain developmental homeostasis (Van Valen, 1962), while asymmetry in harp area may more directly impact cricket song production (Simmons & Ritchie, 1996).

The means were taken of the two average femur length measurements and the two average harp area measurements to generate an average femur length and an average harp area

for each focal male. A condition index was generated using male masses taken within one day of song recording at each target age.

**Analyses**

All statistical models were run using SPSS for Macintosh (IBM North America, New York, NY, USA). Principle components analysis (PCA) was used to reduce the number of phenotypic variables to be included in our statistical model. Our PCA included: mass, average femur length, average harp area, femur asymmetry, harp asymmetry, age, and longevity. This resulted in two principles components, the first of which represented body size and the second of which represented symmetry (see Results).

Condition was measured as the residual of the exponential regression of size on body mass. Thus, males in better condition were relatively heavy for their femur length and males in poorer condition were relatively light (Brown *et al*., 2006; Jakob *et al*., 1996).

We then created a linear mixed model where the dependent variable was the mean acoustic song parameter, the factors were song type and age (young vs. old), and the covariates were the two principles components (PC1 and PC2), longevity, condition, and temperature. This model compared all main effects and all interaction effects for song type and age. We used backwards removal until all nonsignifcant interaction effects were removed.

To compare variability between song type and song parameters, we first calculated the coefficient of variation (CV) for each of 8 song parameters. We then use a univariate ANOVA to test for significant differences in CV between song type. The dependent variable was the CV for each song parameter (e.g., amplitude) and the fixed factors were song type and age.

Lastly, because some of our analyses contained multiple tests, we used the false discovery rate correction to control for type I errors (Verhoeven *et al.*, 2005). We report our P values both before and after correcting for false discovery rate (listed as $P_{adj}$).

## RESULTS

### Structural differences between song types

All measured song parameters except $\Delta$ frequency and the inter-pulse interval were significantly different between song types, and these results were robust to corrections for false discovery rate (Linear mixed model; Amplitude: $F = 15.844$, df = 2, 100, $P = 0.0000011$, $P_{adj} < 0.05$; Frequency: $F = 6.498$, df = 2, 99, $P = 0.002$, $P_{adj} < 0.05$; $\Delta$ Frequency: $F = 1.492$, df = 2, 98, $P = 0.230$; PPC: $F = 10.94$, df = 2, 98, $P = 0.000052$, $P_{adj} < 0.05$; Pulse duration: $F = 3.9$, df = 2, 100, $P = 0.023$, $P_{adj} < 0.05$; Chirp duration: $F = 9.155$, df = 2, 98, $P = 0.00023$, $P_{adj} < 0.05$; IPI: $F = 2.979$, df = 2, 99, $P = 0.055$; ICI: $F = 5.858$, df = 2, 100, $P = 0.004$, $P_{adj} < 0.05$). Table 2-1 gives the mean values for each significantly different song parameter by song type.

### Differences in variability of song parameters by song type

All measured song parameters except pulse duration and the inter-pulse interval had significantly different coefficients of variation between song type (Univariate ANOVA; Amplitude: $F = 14.293$, df = 2, $P = 0.000003$; Frequency: $F = 7.478$, df = 2, $P = 0.001$; $\Delta$ Frequency: $F = 10.046$, df = 2, $P = 0.000009$; PPC: $F = 16.513$, df = 2, $P = 0.0000005$; Pulse duration: $F = 2.135$, df = 2, $P = 0.123$; Chirp duration: $F = 13.733$, df = 2, $P = 0.000004$; IPI: $F = 2.665$, df = 2, $P = 0.074$; ICI: $F = 4.294$; df = 2, $P = 0.016$). Table 2-2 provides the mean values of the coefficient of variation for all measured song parameters by song type.

Overall, the courtship song was the most variable (mean CV = 0.3931), followed by the aggressive song (mean CV = 0.3409) and the calling song (mean CV = 0.2117). Of the measured song parameters, the inter-chirp interval was most variable (mean CV = 0.5859), followed by amplitude (mean CV = 0.4206) and chirp duration (mean CV = 0.4076). Delta frequency was the least variable song parameter measured (mean CV = 0.0658), followed by peak frequency (mean CV = 0.1541).

### Phenotypic information present in song

Using PCA, we identified two principle components that together explained 72% of the total variation (Table 2-3). Average femur length, mass, and average harp area loaded most heavily on PC1, which we take as a measure of overall body size. Harp asymmetry and femur asymmetry loaded most heavily on PC2, which we take as an overall measure of asymmetry.

Of the phenotypic measurements taken on the focal males, condition, age, PC1 (body size), and PC2 (asymmetry) were significantly communicated through parameters of song. However, not all of these results were robust to false discovery rate corrections. Condition was correlated with both amplitude (Linear mixed model; F = 4.932, df = 1, 100, P = 0.029, $P_{adj}$ > 0.05) and the inter-chirp interval (F = 9.169, df = 1, 100, P = 0.003, $P_{adj}$ < 0.05), though the effect only remained significant for the latter.

Frequency differed significantly with focal male age, with young males producing lower mean frequencies across song type than older males (F = 5.898, df = 1, 100, P = 0.017, $P_{adj}$ > 0.05), though this result was not significant after correcting for false discovery rate. The variability of a male's frequency and the number of pulses per chirp produced also differed significantly with age (Univariate ANOVA; Frequency: F = 4.659, df = 1, P = 0.033; PPC: F =

5.189, df = 1, P = 0.025), with older males producing more variable peak frequencies and having a more variable number of pulses per chirp than younger males.

PC1, a measure of male body size, varied with the chirp duration, such that larger males produced longer chirps, though the result was not robust to false discovery rate corrections (Linear mixed model; F = 6.502, df = 1, 98, P = 0.012, $P_{adj} > 0.05$). PC2, a measure of symmetry, was significantly related to both the number of pulses per chirp and the chirp duration after correcting for false discovery rate (PPC: F = 8.321, df = 1, 98, P = 0.005, $P_{adj} < 0.05$; Chirp duration: F = 14.003, df = 1, 98, P = 0.00031, $P_{adj} < 0.05$).

**Differences in communication of information content between song types**

Significant interaction effects between song type and phenotype in our model indicate that the relationship between the song parameter and the information content differ depending on song type. Three such interaction effects were found, although they were nonsignificant after correcting for false discovery rate. Longevity is positively associated with Δ Frequency in calling song but negatively associated with it in both the aggressive and courtship songs (Linear mixed model; F = 3.576, df = 2, 98, P = 0.032, $P_{adj} > 0.05$). PC2 (a measure of symmetry) was positively associated with the chirp duration and the number of pulses per chirp in courtship song (Chirp duration: F = 4.031, df = 2, 98, P = 0.021, $P_{adj} > 0.05$; PPC: F = 4.574. df = 2, 98, P = 0.013, $P_{adj} > 0.05$) but showed no correlation with these song parameters in either of the other two song types.

**DISCUSSION**

**Song types are distinct from each other**

To our knowledge, ours is the first study to statistically determine the differences in the three song types of a gryllid species based on acoustic parameters. These relationships between song types were generally in the expected direction; for example, calling song was the loudest and courtship song was the quietest.

Courtship song had the greatest amount of acoustically-filled temporal space, with the longest chirps, shortest inter-chirp intervals, and most pulses per chirp. This result is concurrent with the finding that *A. domesticus* males invest over twice as much energy in courtship song than in calling song (Hack, 1998) and may indicate that courtship song is a more reliable indicator of mate quality that calling song. Courtship song also exhibited the most variation out of the three song types. This suggests that courtship song may have the greatest ability for carrying unique phenotypic information. Thus, courtship song may be used in addition to calling song to more reliably communicate certain (redundant) information while, at the same time, communicating unique phenotypic messages.

The only song parameters that were not significantly different between song types were Δ frequency and the inter-pulse interval. The first may be constrained by physiology, as frequencies produced outside of the resonating frequency of the male's harp would suffer from a reduction in amplitude and, resultantly, ability to be transmitted. Thus, only a certain range of frequencies would be available to each male and may be used during all three songs.

**Males use songs to communicate phenotypic information**

Males in our population communicated aspects of body size and condition, age, and symmetry through song. Our finding that male house crickets use song to communicate phenotypic information is not novel (e.g., Bertram *et al*. 2009, 2011; Brown *et al*., 2006; Cranshaw, 1979;

53

Gray, 1997; Ryder & Siva-Jothy, 2000). However, we did find that asymmetry was communicated strongly through acoustic parameters of song, which had only been reported in one other study of gryllid species (*Gryllus pennsylvanicus*, Judge, 2011; see also Simmons & Ritchie, 1996).

## Communication of male phenotype through song may differ based on song type

Although none of the interaction effects in our statistical model remained significant after correcting for false discovery rate, it is possible that a larger sample size would yield results more robust to such corrections. Based on the nonsignificant trends seen in this study, it appears as if male house crickets may be able to partition certain information content to single song types, suggesting that three song types may be evolutionarily maintained in order to communicate new messages to the intended receivers. Particularly interesting is the finding that symmetry information may be communicated most strongly through courtship song. Since symmetry is our proxy measurement of genetic quality, it would make sense for that information to be present in the situation where mating is most likely to occur. Trying to convey this information through the chirp duration and number of pulses per chirp may become too energetically costly over an entire evening of calling. If a male's ability to maintain developmental homeostasis (as measured by symmetry) does not correlate well with his competitive ability, this information would be impractical to include in the aggressive song. Thus, courtship song becomes necessary to communicate this information to potential mates.

Both femur asymmetry and harp asymmetry loaded heavily on PC2, and thus we consider PC2 to be a measure of symmetry. Curiously, however, the two measures of asymmetry loaded in opposite directions, suggesting a negative correlation between them. Such negative

relationships may be caused by tradeoffs during development. Both pulses per chirp and chirp duration increased with PC2, indicating that these temporal components of song increased with greater femur asymmetry and lower harp asymmetry.

We found no significant difference in the communication of male body size, condition, or age between song types. It is possible that this represents redundancy in information content across song type and these phenotypes are included in the courtship and aggressive songs as a "back-up" of the information present in calling song. We predicted that some redundant information would present across song type, especially information that is relevant to all cricket social interactions, such as body size. Male house crickets of large size and better condition tend to win more fights (Brown *et al.*, 2006; Hack, 1997; Savage *et al.*, 2005) and are more attractive to females (Savage *et al.*, 2005). Thus, it would be worth the energetic investment to communicate this information in all three song types.

The differing acoustical environments and potential receivers of each song type have likely also contributed to some of the divergence in structure between the calling, courtship, and aggressive songs. For example, calling song is produced for far more distant receivers than either of the courtship and aggressive songs. One obvious result is the increase in intensity by males singing calling song. However, distant receivers may also necessitate use of lower frequencies and more simplistic temporal patterning, as calls using higher frequencies and more complex patterning are more subject to sound attenuation. In addition, the potential presence of eavesdroppers (conspecifics and/or predators and parasites) during calling song may affect both the type of information present in song as well as the song structures utilized.

In summary, we have experimentally demonstrated significant structural differences between the three song types of male house crickets. Across all males in the laboratory

population, calling song was the least variable of all three song types, which could potentially limit the ability to communicate unique phenotypic information. Coupled with the environmental constraints on sound transmission and the presence of two distinct receivers, calling song is likely to only communicate the male phenotypes most fundamental to cricket social interactions. Aggressive and courtship songs were more variable than the calling song, and a unique phenotype, male symmetry, was found to be communicated solely through courtship song, though the result was not significant after correcting for multiple tests. Thus there is a possibility that, in addition to the information present redundantly across all three song types – condition, age, and body size (nonsignificant after correcting for FDR) – courtship and aggressive songs have been evolutionarily maintained in order to communicate unique phenotypes, potentially providing support to the multiple messages hypothesis. Since limited sample sizes likely affected our power once we corrected for false discovery rate, we cannot conclusively support or reject this hypothesis. However, this study has begun to shed light on why multiple signals exist within the Gryllidae, a question that has yet to be explored despite substantial interest in cricket bioacoustics. We suggest that additional work be done in order to expound upon the relationship between information content in all three song types, and urge that these three signals not always be studied in isolation of each other.

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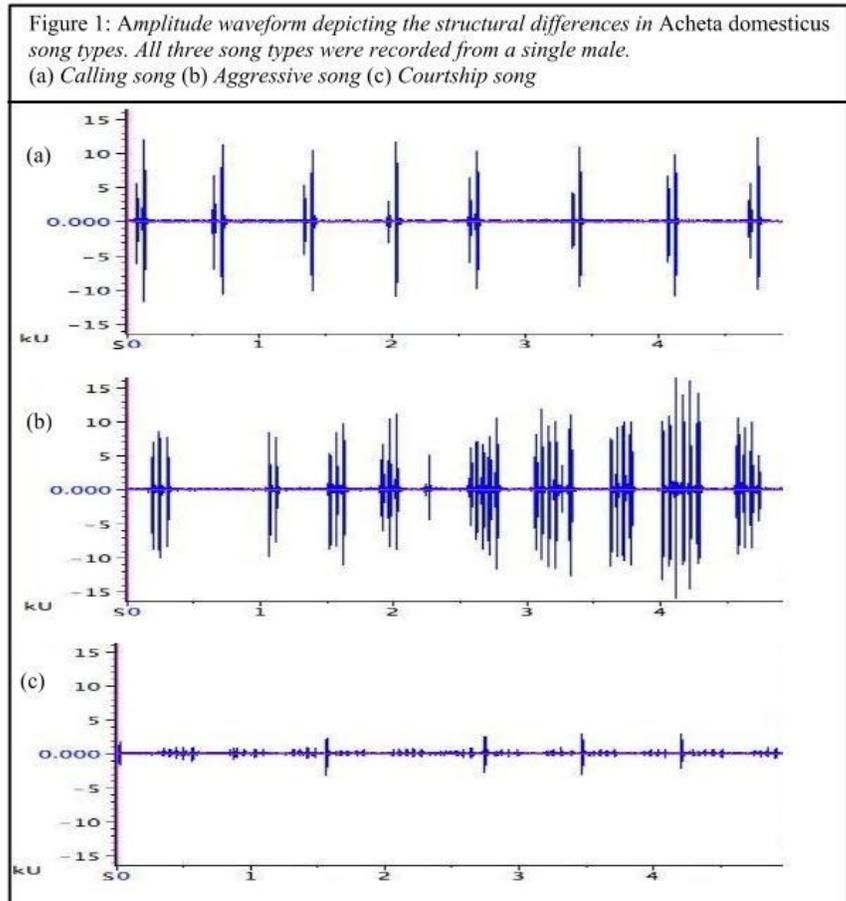
**TABLES AND FIGURES**



Figure 1: *Amplitude waveform depicting the structural differences in* Acheta domesticus *song types. All three song types were recorded from a single male.*
*(a) Calling song (b) Aggressive song (c) Courtship song*

Figure 2: *The temporal aspects of* Acheta domesticus *song structure. A pulse is a produced by one wing swipe, and a chirp is a grouping of these pulses. The silent portions between pulses and chirps are termed the inter-pulse and inter-chirp interval.*
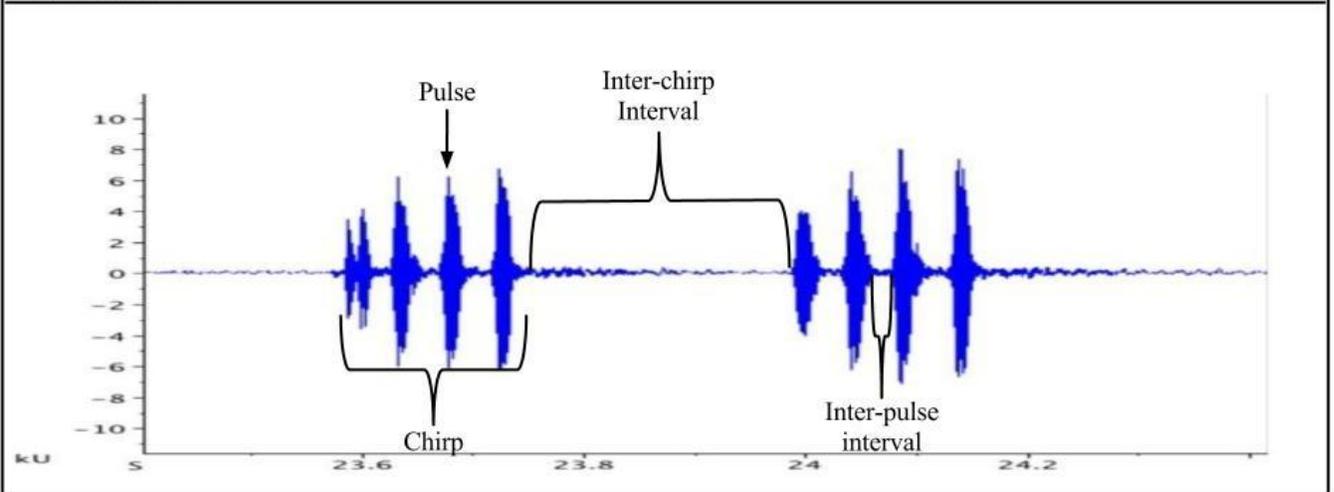
Table 2-1: *Means and 95% confidence intervals for each song parameter that was significantly different between song type. Post-hoc pairwise comparisons are included.*

| Song Parameter | Mean Values (95% CI's) | | | Pairwise Comparisons |
|---|---|---|---|---|
| | Calling song | Aggressive song | Courtship song | |
| Amplitude (kU) | 8292 | 6905 | 3128 | Calling vs. Aggressive: P = 0.313 |
| | | | | Calling vs. Courtship: P = 0.0000005* |
| | (6353 - 10492) | (5290 - 8737) | (2396 - 3958) | Aggressive vs. Courtship: P = 0.00003* |
| Frequency (Hz) | 5167 | 4851 | 5855 | Calling vs. Aggressive: P = 0.230 |
| | | | | Calling vs. Courtship: P = 0.020* |
| | (4799 - 5184) | (4506 - 4868) | (5427 - 5872) | Aggressive vs. Courtship: P = 0.001* |
| Pulses per chirp | 2.37 | 3.06 | 3.57 | Calling vs. Aggressive: P = 0.003* |
| | | | | Calling vs. Courtship: P = 0.000006* |
| | (2.10 - 2.65) | (2.72 - 3.43) | (3.15 - 4.01) | Aggressive vs. Courtship: P = 0.077 |
| Pulse duration (s) | 0.025 | 0.025 | 0.021 | Calling vs. Aggressive: P = 0.929 |
| | | | | Calling vs. Courtship: P = 0.015* |
| | (0.023 - 0.027) | (0.022 - 0.027) | (0.019 - 0.023) | Aggressive vs. Courtship: P = 0.019* |
| Chirp duration (s) | 0.096 | 0.139 | 0.156 | Calling vs. Aggressive: P = 0.002* |
| | | | | Calling vs. Courtship: P = 0.00007* |
| | (0.081 - 0.112) | (0.117 - 0.162) | (0.131 - 0.182) | Aggressive vs. Courtship: P = 0.321 |
| Inter-chirp interval (s) | 0.967 | 0.549 | 0.458 | Calling vs. Aggressive: P = 0.014* |
| | | | | Calling vs. Courtship: P = 0.002* |
| | (0.688 - 1.29) | (0.391 - 0.735) | (0.323 - 0.619) | Aggressive vs. Courtship: P = 0.432 |

Table 2-2: *Mean coefficient of variation for each song parameter by song type and age.*

| | Calling song | | Aggressive Song | | Courtship Song | |
|---|---|---|---|---|---|---|
| | Young | Old | Young | Old | Young | Old |
| Amplitude | 0.2089 | 0.2767 | 0.4749 | 0.4467 | 0.5346 | 0.5815 |
| Frequency | 0.0593 | 0.1322 | 0.0616 | 0.1345 | 0.2071 | 0.3300 |
| Δ Frequency | 0.0427 | 0.0308 | 0.0824 | 0.0614 | 0.0994 | 0.0779 |
| PPC | 0.1290 | 0.1743 | 0.2944 | 0.3313 | 0.3204 | 0.4846 |
| Pulse Duration | 0.2131 | 0.2392 | 0.2864 | 0.3000 | 0.2360 | 0.3593 |
| Chirp Duration | 0.2152 | 0.2595 | 0.4240 | 0.4160 | 0.4705 | 0.6602 |
| IPI | 0.2361 | 0.2906 | 0.4302 | 0.3488 | 0.2314 | 0.4224 |
| ICI | 0.4253 | 0.4538 | 0.7263 | 0.6360 | 0.6699 | 0.6041 |

Table 2-3: *Loadings and percentage variance explained by two principle components of six phenotypes.*

| Phenotype | PC1 | PC2 |
|---|---|---|
| Avg. Femur Length | 0.934 | 0.114 |
| Mass | 0.881 | 0.091 |
| Avg. Harp Area | 0.752 | -0.030 |
| Longevity | 0.661 | -0.220 |
| Harp Asymmetry | -0.622 | -0.596 |
| Femur Asymmetry | -0.496 | 0.785 |
| *% Variance* | *54.722* | *17.360* |