



Effects of juvenile and adult condition on long-distance call components in the Jamaican field cricket, *Gryllus assimilis*

Emily M. Whattam*, Susan M. Bertram

Department of Biology, Carleton University

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Complex signals may arise through either content- or efficacy-based selection. Content-based signals are thought to evolve because of the information content they provide to the receiver. Such signals may function as multiple messages, each relaying different information or types of information. For example, some signals or signal components may indicate different aspects of condition, or condition at different life stages (quality signals), while others relay information on signaller location, or function in species recognition. Or they may act as redundant signals of overall condition, or as backup signals of the same aspect of condition. Efficacy-based signals are proposed to evolve because of the way in which they influence the production, transmission, reception or processing of the signal. We manipulated juvenile and adult condition in male Jamaican field crickets, *Gryllus assimilis*, to test whether changes in components of the male's long-distance acoustic mate attraction signal were consistent with content- or efficacy-based selection. Several call components exhibited condition-dependence, and may be under content-based selection. Interpulse duration, pulse rate and chirp duration appeared to honestly signal juvenile condition, while dominant frequency appeared to signal adult condition. Thus, these signal components appeared to be acting as multiple messages of quality. Pulse number, interchirp duration and chirp rate were highly stereotyped and probably function in species recognition. Call number increased with decreasing condition and was likely under efficacy-based selection. No call components appeared to have the potential to act as redundant signals.

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Many species possess multiple sexual signals (Møller & Petrie 2002). Despite the prevalence of such signals in nature, the reason for their occurrence remains unclear (reviewed in Candolin 2003). There are several hypotheses regarding the evolution of complex signalling (reviewed in: Candolin 2003; Hebets & Papaj 2005). Some invoke content-based selection, in which signals are proposed to have evolved because of the information content that they provide to the receiver. Others are efficacy-based in that they propose that complex signals have evolved because of the way in which they influence the production, transmission, reception or processing of the signal (Hebets & Papaj 2005).

Two widely investigated, content-based hypotheses for the evolution of complex signals are the multiple messages and redundant signals hypotheses (reviewed in: Candolin 2003; Hebets & Papaj 2005). In a recent review, Hebets & Papaj (2005) expanded

the multiple message hypothesis to include three alternative hypotheses: quality, quality plus and species recognition. The quality model proposes that each signal relays information about a different aspect of signaller condition, or of condition at a different life stage (Møller & Pomiankowski 1993; Johnstone 1996; Hebets & Papaj 2005). For example, in male bowerbirds, feather ultraviolet-violet brightness and bower quality are correlated with endoparasite load and ectoparasite load, respectively (Doucet & Montgomerie 2003). Thus, females can determine the amount of each parasite type a male is carrying by assessing these two traits. The quality plus hypothesis is that one signal, or signal component, gives information on signaller quality, while another signal conveys other information, such as signaller location or territory quality (Hebets & Papaj 2005). Finally, the species recognition hypothesis proposes that one signal conveys information on signaller quality, while another signal functions in species recognition.

The redundant signals hypothesis has been described in two main ways throughout the literature. Møller & Pomiankowski (1993) proposed that redundant signals each provide independent estimates of overall condition and that each signal differs in

* Correspondence and present address: E. M. Whattam, Simon Fraser University, Department of Biological Sciences, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada.

E-mail address: emily_whattam@sfu.ca (E.M. Whattam).

the magnitude and direction of the error associated with signalling overall condition. Thus, a female should assess all signals in order to obtain the most accurate estimate of overall male condition. Alternatively, Johnstone (1996) proposed a 'backup' hypothesis in which multiple signals convey information about the same aspect of condition, rather than overall condition. For example, in male curassow, knob weight, wattle height and wattle width are all indicators of male age, a character used by females during mate selection (Buchholz 1991).

Finally, hypotheses invoking efficacy-based selection propose that complex signals have evolved because of their function in signal production, transmission, reception and/or processing (reviewed in Hebets & Papaj 2005). Traits under efficacy-based selection are thought to have evolved in response to environmental variability, or sensory constraints in the receiver (reviewed in Hebets & Papaj 2005). For example, Maynard Smith & Harper (2003) describe a nightingale system in which males spend the majority of the night calling in order to attract females flying overhead to mate with them. However, males can never be sure of the presence of females and must, therefore, signal as much as possible to maximize their likelihood of being heard by a passing female. In doing so, males can lose up to 5–10% of their body mass. Thus, rather than signalling effort being an index of condition, constant signalling is a cost of efficacy. Ryan & Cummings (2005) predict that this is the case for most examples of long-distance signalling. Thus, signals selected for efficacy should also exhibit condition-dependence but function differently in female choice. Alternatively, males in poor current condition may choose to invest even more into signalling because their reduced condition means that they are less likely to survive and reproduce long term. As such, investment in efficacy-based signals may actually increase with decreasing condition, as males attempt to compensate for decreasing future reproduction.

Here we distinguish between the various content- and efficacy-based hypotheses by manipulating male cricket condition at the juvenile and adult stages of life and observing the effects on components of the male's sexual signal. Male field crickets signal acoustically to attract females by raising their forewings and rubbing them together, producing a pulse of sound with each

closing stroke. These pulses are concatenated into chirps (Fig. 1). Females are known to approach (e.g. Wagner et al. 1995; Gray & Cade 1999) and select mates (e.g. Cade & Cade 1992) based on the acoustic properties of the male's long-distance call. Once a female makes physical contact with a male, he switches to a short-distance courtship call (E. M. Whattam, personal observation). Long-distance and courtship calls are multicomponent signals, consisting of several call parameters. Some of these call parameters are at least partly uncorrelated and, thus, have the potential to act as separate signals (Scheuber et al. 2003a). For example, Scheuber et al. (2003a, b) found that in the field cricket *Gryllus campestris*, chirp rate decreases when adult condition is decreased, and carrier frequency increases (due to decreased wing size) when juvenile condition is decreased. In cricket species in general, calling behaviour tends to decrease when different aspects of condition are decreased. This is not surprising, given that calling behaviour is energetically expensive (Hoback & Wagner 1997). For example, Hedrick (2005) found that when adult male field crickets (*G. integer*) are fasted for 2 days, their mass decreases (indicating a decrease in condition), as does their long-distance calling bout duration (average time for which males call continuously). Moreover, Hedrick (2005) found that the decrease in mass is proportional to the reduction in bout duration. This suggests that bout duration is an accurate signal of current condition in this species.

Female crickets exhibit distinct preferences for many components of the male long-distance mate attraction call, most of which involve an increase in calling (Wagner & Hoback 1999). For example, female Texas field crickets, *G. texensis*, prefer males that spend the most time calling throughout the night (Cade & Cade 1992), that produce the largest number of pulses per trill (Gray & Cade 1999) and that produce short intercall intervals (Wagner et al. 1995). Similarly, female variable field crickets, *G. lineaticeps*, prefer males with high chirp rates and long chirp durations (Wagner & Hoback 1999).

Females also receive fitness benefits by mating with males that advertise condition through these call parameters; for example, female variable crickets that are mated to males that produce high chirp rates experience increased lifetime fertility, while females

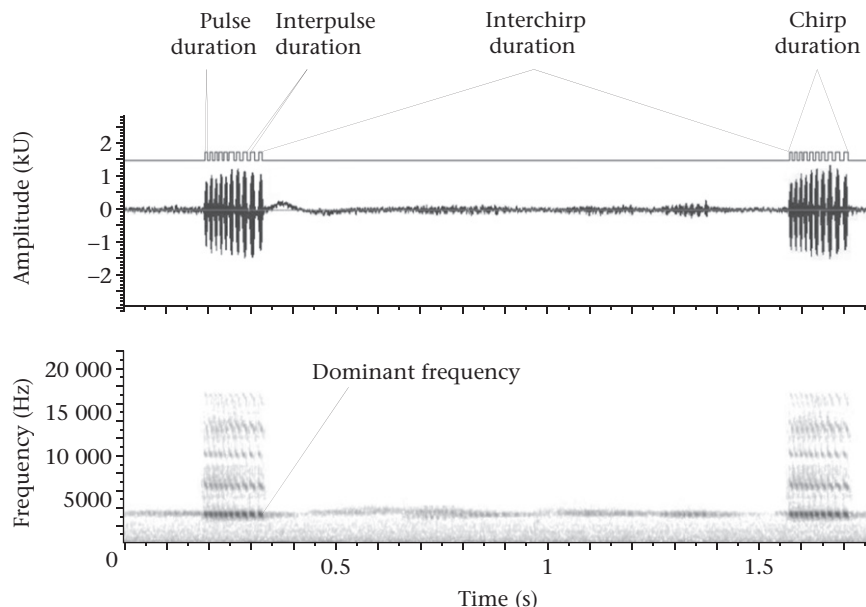


Figure 1. Several parameters of the long-distance mate attraction call of *G. assimilis*.

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