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To compete or not to compete: bushcricket song plasticity reveals male body condition and rival distance

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Males of several animals, including insects, use acoustic signals to attract a sexually receptive conspecific partner. In the orthopteran chorusing genus *Poecilimon* (Tettigoniidae), male signalling as well as female preference can be related to male body condition and to the social environment. Song is thought to be an honest signal of male quality, and song characteristics are therefore often important for sexual and social selection. At the same time, signal expression is plastic and this plasticity depends on the quality of the individual signaller, the acoustic components preferred by females and rivals' body condition and proximity. Using the bushcricket species *Poecilimon ampliatus* as a model, we investigated how both internal (body condition) and external (level of competition) factors affected the expression of temporal song characteristics. We show that both factors significantly affected acoustic signalling activity: when competing against light rivals, heavy males adjusted the characteristics of their songs to different social conditions. However, light males competing against a heavy rival showed less plasticity in their acoustic signals across social conditions. During the most escalated competition, heavier males increased their acoustic signal investment up to the maximum level, signalling with longer verses and higher duty cycles, in comparison to all other treatments. Body condition and the social environment affected male acoustic signal activity, which suggests that these factors mediate the allocation of resources for signalling and different strategies adopted in competition. The adaptive plasticity of acoustic signals in this species raises new questions about the potential role that this process could play in natural choruses, where more than two competitors are signalling simultaneously.

Sexually selected traits are also subject to other natural and social selection pressures present in the environment (Andersson, 1994; West-Eberhard, 1983, 2014). Consequently, individuals that invest in morphologies and behaviours that provide an advantage in fitness (Andersson, 1994; Byers, Hebets, & Podos, 2010) may adjust these traits in response to factors internal to the individual such as age and energetic state, or external such as predation risk and population density (Kasumovic, 2013). Thus, this phenotypic plasticity can have an important impact on the outcome of sexual selection (Snell-Rood, 2013; Zuk, Bastiaans, Langkilde, & Swanger, 2014). For instance, in competition for mates, a male may adjust his mate attraction signals according to his perception of the density and types of surrounding rivals (Bretman, Gage, & Chapman, 2011).

In many species of frogs and insects, the male acoustic communication signals evolved under sexual selection (Gerhardt & Huber, 2002; Greenfield, 2002; Robinson & Hall, 2002). Like other sexually selected traits, the adaptive phenotypic plasticity exhibited in acoustic signals has important consequences for male reproductive success, because males must trade off competing demands to attract mates, repel rivals and avoid predators (Bertram, Harrison, Thomson, & Fitzsimmons, 2013). Energetic costs are a particularly important factor in signalling plasticity: acoustic communication is energetically demanding (Bailey, Withers, Endersby, & Gaull, 1993; Gerhardt & Huber, 2002), increasing an individual's metabolic rate while singing (Prestwich, 1994; Stevens & Josephson, 1977) and even at rest (Reinhold, 1999), and females often prefer more energetically costly signals (Ryan & Keddy-Hector, 1992). Therefore, energetically costly signals can honestly reflect the quality of the sender (Grafen, 1990) with males in poorer condition producing less attractive signals compared to

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males in better condition (Podos & Patek, 2015). At the individual level, the trade-off between being an efficient signaller and coping with the costs of expensive acoustic features (Mowles, Cotton, & Briffa, 2011; Reichert & Gerhardt, 2012; Smith & Harper, 2003) increases with the strength of the competition (Johnstone, 1997; Wilgers & Hebets, 2015). A male's ability to respond to competition may also reflect his quality, because competition requires the production of even more expensive signals (Parker, 1974; Reichert, 2014).

In Orthoptera, acoustic signalling is a fundamental behaviour to attract conspecific females and to compete against rivals (Gerhardt & Huber, 2002; Robinson & Hall, 2002). A high-quality signaller may communicate a superior body condition, a characteristic that is likely to be relevant for both female choice and male–male competition, via its acoustic signalling performance (Schatral & Bailey, 1991; Wilgers & Hebets, 2015). Females may evaluate the qualities of a potential mate using intensity, frequency and/or the temporal structure of male songs (Schatral & Bailey, 1991). They are mostly attracted by signals with high intensity, long duration and high repetition rate (Gerhardt & Huber, 2002; Greenfield, 2002) and usually choose larger or heavier competing males (reviewed in Gwynne, 2001; Lehmann, 2012). Acoustic signals may vary between individuals (Bailey, 1985; Hedrick, 1986; Latimer, 1981a; Samways, 1976; Simmons, 1988). Factors causing this interindividual variation may be internal such as body mass, body size and energetic condition of the signalling male, or external such as the number, quality and proximity of competitors in the environment. Body size affects both the intensity and frequency of the acoustic signal as larger males produce louder songs at a lower fundamental frequency (Bailey & Thiele, 1983; Forrest, 1983; Latimer & Schatral, 1986). The social environment is an important external environmental factor because Orthopterans signal for mates in choruses (Greenfield, 1994) in which males engage in signal competition with their neighbours and males may vary their call characteristics as a consequence of the vocal activity of neighbours (reviewed by Greenfield, 2005). A male signaller might hear the calls of conspecific rivals, gaining acoustic information about size or vigour, fighting ability or ability to attract females (Busnel, 1967; Greenfield & Shaw, 1983; Latimer & Schatral, 1986; Latimer, 1981b; Römer & Bailey, 1986). Notably, male crickets and bushcrickets can modify their chirp interval and chirp duration when rivals are signalling (Brush, Gian, & Greenfield, 1985; Dadour, 1989; Jones, 1974; Samways, 1976; Shaw, 1975). Chorusing behaviour might present a cooperative effect: choruses of many hundreds of individuals even without strict synchronization might increase the calling space (Krobath, Römer, & Hartbauer, 2017) and reduce the individual predation pressure including that of acoustic-orienting parasitoid flies (Lakes-Harlan & Lehmann, 2015; Lehmann & Heller, 1998).

Remarkably little work has been done in orthopterans to test how different internal and external sources of variation may cause the plasticity of the acoustic features produced during song competition. Here, we studied contests between males of different body mass in combination with manipulation of the social environment (the intermale rival distance) to investigate how both may affect the acoustic signal behaviour of males of the bushcricket species *Poecilimon ampliatus* (Orthoptera: Tettigoniidae: Phaneropterinae) during acoustic contests. As male body mass is an important factor for female choice (Lehmann & Lehmann, 2008) and reflects a male's condition (Lehmann & Lehmann, 2009), we examined the role of this factor during song contests between males of different body mass. Moreover, since close-range acoustic competition occurs naturally in this species which aggregates in high-density populations (Lehmann, & Lehmann n.d.), we evaluated the signal production activity under varying competition, with different intermale rival distances. First, we compared the acoustic signalling behaviour of heavy and light males, both in isolation and under four competition treatments: we predicted a significant signalling discrepancy between the two body mass classes both in competition and in isolation. Heavy males might always signal better than the light rivals. Second, we tested whether male signalling activity is plastic with respect to the distance to a rival by comparing song characteristics across different rival distances. If intensity of competition increases when the rival comes closer, we predicted that both heavy and light males would show a plastic response to the variation in the social context, by increasing signal production in terms of sound duration, rate and total amount of time spent signalling, when hearing rivals close by.

METHODS

Study Species

Poecilimon ampliatus is a flightless species in a genus distributed predominantly in southeastern Europe. Despite an ancestral bidirectional communication system with males signalling and females responding, *P. ampliatus* belongs to those species that secondarily reverted to a unidirectional system; only males produce acoustic signals and females locate them by phonotaxis (Heller & von Helversen, 1993). Males usually start signalling 4 days after moulting to adulthood and their song consists of subunits, called verses, which are separated by silent pauses (Heller, 1988; Heller & Lehmann, 2004; Fig. 1).

Male nymphs were collected near the village of Gabrče (45°42′40″N, 14°01′05″E) in Slovenia. They were individually caged in 200 ml marked boxes (*Drosophila* rearing boxes; Greiner Bio-one GmbH, Kremsmünster, Austria) and transferred to the laboratory, at the Institute of Biology at the Humboldt University Berlin, where

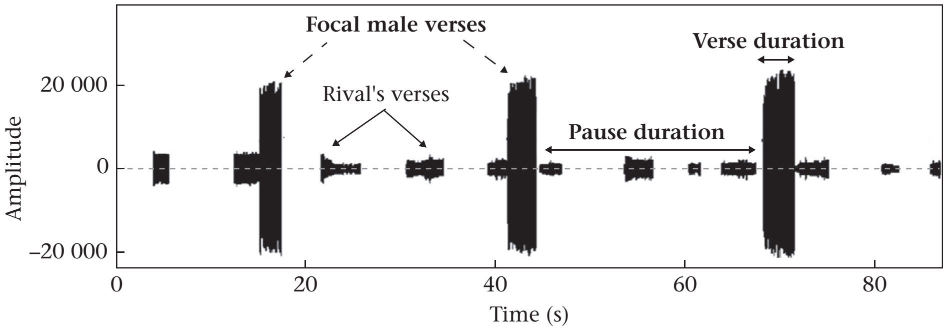

Figure 1. Oscillogram representing the temporal acoustic features of *P. ampliatus*. During a sampling period of 90 s, the focal male produced three verses separated by two pauses. A total of 12 verses of the rival male were detected as background noise. Verse and pause duration of the focal male are indicated. Sample rate 96 kHz, amplitude threshold = 30 dB, minimum verse duration = 0.5 s.