



Substrate-borne vibrations of male psyllids vary with body size and age but females are indifferent



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During sexual selection members of the opposite sex utilize a variety of signal modalities to acquire information about potential mates. As a prerequisite, signal modalities must exhibit intraspecific variation and correlate with desirable traits that reflect the fitness of the signaller. Anecdotal accounts suggest that female psyllids (Hemiptera: Sternorrhyncha) utilize substrate-borne vibrations (SBVs) to choose between males. However, comprehensive studies investigating the role of SBVs in Psylloidea are lacking. We used laser vibrometry and playback experiments to study the mating and calling behaviours of a psyllid, *Aacanthocnema dobsoni* (Triozidae). Specifically, we quantified call parameters and asked whether they vary intraspecifically and correlate with male body size and age. We also tested whether female responsiveness is influenced by the body size and age of calling males. Calls were sex-specific: male calls were more complex and comprised long and short syllables while female calls comprised only short syllables. Temporal and spectral parameters of male calls differed significantly from those of female calls. Calls of both sexes exhibited a high level of intraspecific variation. Larger males produced calls with a lower dominant frequency and older males produced calls of higher intensity and pulse rate. We used playback to test female responsiveness to calls recorded from males of contrasting sizes and ages. Surprisingly, female responsiveness was not influenced by body size or the age of calling males. Interestingly, females are polyandrous but only virgins called or responded to male calls. Conversely, males called frequently and attempted (and often succeeded) to mate with unresponsive females. These results demonstrate that *A. dobsoni* utilizes SBVs for mate attraction but not for precopulatory mate selection. We suggest that polyandry in *A. dobsoni* potentially evolved in response to male harassment and, as a consequence of polyandry, sexual selection is probably achieved via postcopulatory sexual selection mechanisms.

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According to the ‘ardent male, coy female hypothesis’ females are expected to be highly choosy and sexually ‘coy’ and to be courted by sexually indiscriminate males (Dewsbury, 2005). Males compete for access to territories or resources utilized by females while females choose mates on the basis of traits such as relative body size and weaponry that provide a competitive advantage to an individual male over his rivals (Andersson & Simmons, 2006; Emlen, 2008). Multiple studies involving diverse vertebrate and invertebrate taxa have demonstrated that exaggerated traits reflect relative male fitness and are therefore relevant to female choice (Andersson, 1986; Kodric-Brown, Sibly, & Brown, 2006; Lavine, Gotthard, Brent, Dworkin, & Emlen, 2015) and male–male

competition (Callander, Kahn, Maricic, Jennions, & Backwell, 2013). While this is typical for female and resource defence male mating strategies, there is evidence that this stratagem may not apply in polyandrous mating systems in which copulation by itself does not guarantee male reproductive success (Eberhard, 2009; Kvarnemo & Simmons, 2013). When a female successfully copulates with more than one male, this often sets a stage for sperm competition (Simmons, 2001). In some cases, female bias may increase the likelihood that one male rather than another with which she has mated will sire her offspring (Eberhard, 1996). This phenomenon has been referred to as cryptic female choice because female selection is invisible with respect to Darwinian criteria for reproductive success, i.e. all copulations are equally effective in producing offspring (Eberhard, 2009). Traditionally, female reproductive success has been viewed as independent of the number of matings (Bateman, 1948). Nevertheless, there are several reasons why females of various insect species mate multiple times. For

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instance, in *Gerris buenoi* (Hemiptera: Gerridae) and *Coelopa frigida* (Diptera: Coelopidae) sexual conflict over mating is prevalent and females accept additional matings to mitigate costs associated with male harassment (Rowe, 1992; Shuker & Day, 2001). In several Orthoptera, females obtain direct benefits such as increased access to food in the form of nuptial gifts from each additional mating (Fedorka & Mousseau, 2002; Gwynne, 2008). In *Tribolium castaneum* (Coleoptera: Tenebrionidae), single matings do not result in transfer of sufficient sperm; therefore, females obtain indirect benefits and ensure full fertility by mating multiple times (Pai, Bennett, & Yan, 2005).

Psyllids or psyllids (Hemiptera: Sternorrhyncha) are exclusively phytophagous and comprise over 3850 described species distributed worldwide in all major zoogeographical regions (Burckhardt, Ouvrard, Queiroz, & Percy, 2014). Currently, mechanisms of sexual selection, mating and calling behaviours of psyllids are poorly understood. Some studies have suggested that female psyllids mate once in their lifetime (Percy, Taylor, & Kennedy, 2006; Taylor, 1985); however, none of these studies presented data regarding mating frequency. Conversely, other studies have shown that some species, such as *Diaphorina citri* (Hemiptera: Psyllidae), *Trioza erytrae* (Hemiptera: Triozidae) and *Cacopsylla pyricola* (Hemiptera: Psyllidae), are polyandrous (van den Berg, Deacon, & Thomas, 1991; Burt & Fischer, 1967; Eberhard, 2009; Wenninger & Hall, 2008). Female polyandry makes the Psylloidea an interesting taxon to study aspects of sexual selection that are often overlooked in the bulk of sexual selection studies that mainly focus on male mating success.

Several anecdotal accounts have suggested female psyllids to be choosy (Lubanga, Guédot, Percy, & Steinbauer, 2014); however, no studies have directly investigated sexual selection in this superfamily. Most of what is known regarding sexual selection in psyllids comes from studies whose main focus was either systematics or basic intersexual communication (Percy et al., 2006; Wenninger, Hall, & Mankin, 2009). Although semiochemicals mediate mate attraction in some species (Guédot, Horton, & Landolt, 2010; Guédot, Millar, Horton, & Landolt, 2009; Wenninger, Stelinski, & Hall, 2008), the use of substrate-borne vibrations (SBVs) is more widely spread. Lubanga et al. (2014) reported that of the species studied, four and 26 use semiochemicals versus SBVs, respectively. Psyllids produce vibrations by means of stridulatory structures that involve movement of the fore- and hindwings to allow teeth-like structures on the anal vein to rub against similar structures on protruding ridges of the meso- and metathorax (Heslop-Harrison, 1960; Taylor, 1985; Wood, Peters, Taylor, & Steinbauer, 2016). Psyllid SBVs are species- and sex-specific and are purportedly utilized for both species and mate recognition (Percy et al., 2006; Tishechkin, 2007). Male calls are structurally more complex with longer syllable durations and higher frequencies than female calls (Eben, Mühlethaler, Gross, & Hoch, 2014; Percy et al., 2006; Tishechkin, 2007; Wood et al., 2016). Longer and more complex calls enable male insects, e.g. *Poecilimon sanctipauli* (Orthoptera: Phaneropteridae), to encode more qualitative information in their calls which is required for effective female choice of mates (Bailey, 2003).

The potential use of SBVs by psyllids for mate recognition and assessment has not been explicitly studied. For instance, not all reciprocal calls between the sexes results in mating (Percy et al., 2006; Wenninger et al., 2009). This suggests that females could be using SBVs to assess and choose between males. Although Percy et al. (2006) showed that females of *Schedotrioza multitudinea* (Hemiptera: Triozidae) could discriminate between intraspecific male calls, their study only tested a single female. Recently, Wood et al. (2016) showed that females of *Anoeconeossa bundoorensis* (Hemiptera: Aphalaridae) could choose between males based on

the rate of energy production associated with the male calls. If SBVs are indeed utilized for mate selection, then some call parameters (spectral, temporal or both) should vary between individuals and should correlate with desirable morphological traits that reflect individual fitness. Although no such traits have been identified in psyllids, traits such as body size and age are indicators of male fitness that have been investigated in other insect taxa including Hemiptera (De Luca, 2015; Judge, 2011; Lehmann & Lehmann, 2008). Larger males of *Margus obscurator* (Hemiptera: Coreidae) reportedly performed better than smaller males during male–male competition for access to females (McLain, Burnette, & Deeds, 1993). Also, older males of *Umbonia crassicornis* (Hemiptera: Membracidae) reportedly have a significant mating advantage compared to younger males (De Luca and Coccoft, 2008). Females of some insect species may choose to mate with older males because old age may code for proof of longevity and greater fitness (Brooks & Kemp, 2001). Body size and age correlate with physiological traits such as immunocompetence and condition and females possessing and exercising preferences for such traits may benefit by having more desirable male offspring (Prokop, Michalczyk, Drobnik, Herdegen, & Radwan, 2012). Interestingly, Wenninger et al. (2009) reported a significant negative correlation between fundamental frequency and male body mass in *D. citri*. This implies that females could infer the size and possibly condition of males from their calls. Furthermore, van den Berg et al. (1991) showed that the reproductive fitness of *T. erytrae* males varies with age. *Trioza erytrae* males mate multiple times during their life. However, their ability to successfully fertilize females decreases with age. In this species, mating with younger rather than older males may represent a trade-off between reproductive fitness (younger males) and good genes (older males). *Trioza erytrae* provides a good example where variation of call parameters with age would enable females to infer age-related information and possibly choose between males.

In this study, we investigated the mating, calling behaviour and female choice of *Acanthocnema dobsoni* (Hemiptera: Triozidae). We studied *A. dobsoni* because it communicates via SBVs and lives on a unique host, the branchlets of which are suggested to favour call transmission over long distances (Lubanga, Drijfhout, Kevin, & Steinbauer, 2016; Percy et al., 2006). Specifically, we quantified SBVs utilized by *A. dobsoni* and asked whether call parameters vary intraspecifically and correlate with body size and vary with age. Finally, we tested whether female responsiveness is influenced by body size and age of the calling male.

METHODS

Study Species

Acanthocnema dobsoni is a monophagous species that lives on the drooping she-oak, *Allocasuarina verticillata* (Casuarinaceae) (Taylor, Jennings, Purcell, & Austin, 2011). Adults often form large aggregations at the base of branchlets, which has been suggested to be a behaviour that may reduce the risk of dislodgement by wind at the exposed ends of branchlets and lead to enhanced mate-finding opportunities (Steinbauer, Lubanga, & Taylor, 2016). Both sexes reach sexual maturity within 24 h after eclosion and a sex ratio of 1:1 is maintained throughout the year. Females live for about 30 days and oviposit about 182 ± 23 (mean \pm SE) eggs (Lubanga, Taylor, & Steinbauer, n.d.). *Allocasuarina verticillata* is a 4–10 m tall, wind-pollinated, dioecious, evergreen tree with drooping foliage which is endemic to southeastern Australia (Wilson & Johnson, 1989). Its photosynthetic branchlets superficially resemble pine needles, can grow to over 80 cm long (Steinbauer et al., 2016) and attain a diameter of 0.7–1.5 mm (Wilson &

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