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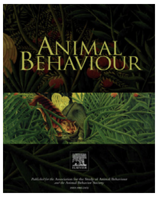

Convenience polyandry and the role of lone and reciprocal calls in a psyllid

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It is widely accepted that receptivity to mating may be asymmetrical between the sexes. While reproductive benefits for males are cumulative, females may not benefit equally from polyandry, especially in species where females can store sperm. Female psyllids (Hemiptera: Psylloidea) are reportedly polyandrous. However, the adaptive significance of this mating strategy has not been thoroughly investigated. Studies involving other insect species indicate that polyandry may be driven by benefits (direct or indirect) or by the need to minimize costs associated with male harassment. Drooping she-oak psyllids, *Aacanthocnema dobsoni* (Triozidae), use substrate-borne vibrations for mate attraction but they are not a prerequisite for mating. We suspected that polyandry in this species could be driven by male harassment because males exhibit indiscriminate mating behaviour (consistent with a scramble competition mating strategy), often mating with unresponsive (mated) females. We investigated relationships between calling, feeding and mating status to test whether females mate to minimize harassment by males and whether they gain any direct benefits from polyandry. We found that lone calls were commonly, but reciprocal calls were rarely followed by mating. As reciprocal calls should reflect female receptivity, copulations without them highlight the existence of sexual conflict over mating. Observations revealed that feeding females were less likely to resist mating than nonfeeding females. We did not find that females obtained any direct benefits from polyandry. Our results suggest that polyandry in this species may be a consequence of male harassment and that mated females, while feeding, may remate for convenience to minimize costs associated with stylet retraction/penetration and location of new feeding sites.

Mating was for a long time regarded as an exclusively mutualistic phenomenon between males and females to achieve successful reproduction (Arnqvist & Rowe, 2005; Chapman, 2006). However, this view has changed in recent years upon realization that although mating partners may share mutual interests in offspring production, they often have divergent interests in many aspects pertaining to the economics (costs versus benefits) of mating and reproduction (Chapman, Arnqvist, Bangham, & Rowe, 2003). Sexual conflict arises from differences in evolutionary interests of males and females derived from anisogamy and can occur over traits related to courtship, mating and fertilization (Chapman, 2006; Chapman et al., 2003; Parker, 1979). Owing to differential optimal mating, conflict over rates of mating between males and females is a taxonomically widespread phenomenon (Parker, 2006). The Darwin–Bateman paradigm stipulates that males gain more reproductive success from polyandry than do females (Dewsbury, 2005). Generally, males can afford to produce relatively larger numbers of gametes compared to females whose gametes are usually larger and costlier to produce (Schärer, Rowe, & Arnqvist, 2012). Consequently, males optimize their reproductive fitness by maximizing the number of mating events, whereas females optimize fitness by selecting and mating with higher quality males (Pashler, Mozer, & Harris, 2001). Nevertheless, females of several taxa, including insect species such as *Drosophila pseudoobscura* (Diptera: Drosophilidae), mate above their optimum despite the associated costs of increased predation risk, energy costs, deleterious male secretions and/or pathogen infection (Brent

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& Hull, 2014; Knell & Webberley, 2004; Price, Lewis, Smith, Hurst, & Wedell, 2010; Sih, Krupa, & Travers, 1990; Watson, Stallmann, & Arnqvist, 1998). This controversy makes polyandry a puzzle that fascinates many behavioural and evolutionary biologists (Arnqvist & Nilsson, 2000; Boulton & Shuker, 2015; Gowaty, 2012).

In insects, polyandry has been reported in almost all taxa (Arnqvist & Nilsson, 2000; Simmons, 2005). Slatyer, Mautz, Backwell and Jennions (2012) suggested three main explanations why this mating strategy is maintained by insects. First, females may benefit directly by obtaining an adequate supply of sperm and gaining access to male resources such as nuptial gifts, nourishment and ovipositional stimulants that increase a female's longevity and/or fecundity (Arnqvist & Nilsson, 2000; Lehmann & Lehmann, 2016). A meta-analysis of 122 experimental studies of 78 insect species found that females gain directly from polyandry in terms of increased lifetime reproductive success (Arnqvist & Nilsson, 2000). Second, polyandry may confer indirect genetic benefits that elevate net offspring fitness. Such benefits may arise from production of more genetically diverse offspring or the opportunity for females to use postcopulatory mate choice to bias paternity towards males that elevate offspring fitness (García-González & Simmons, 2007; McLeod & Marshall, 2009; Tomkins, Penrose, Greeff, & Lebas, 2010). For instance, multiple mating reportedly allows female *Timema cristinae* (Phasmatodea: Timematidae) to bias paternity towards one or a selection of males that increase egg hatching success (Arbuthnott, Crespi, & Schwander, 2015). Third, polyandry may be a harm minimization strategy that females employ to reduce costs incurred due to male harassment (Arnqvist & Rowe, 2005). Females of species such as *Callosobruchus chinensis* (Coleoptera: Chrysomelidae) and *Aquarius paludum* (Hemiptera: Gerridae) reportedly incur fitness costs (longevity and fecundity) that are a direct consequence of male harassment (Harano, 2012; Ronkainen, Kaitala, & Kivelä, 2010; Rönn, Katvala, & Arnqvist, 2006). Males of such species often repeatedly attempt to mate with females until the female either escapes or copulates (Thornhill & Alcock, 1983). Females that refuse to mate often incur time and energy costs by resisting mating attempts by males (Clutton-Brock & Parker, 1995). When these costs are greater than the cost of accepting additional mating, females may choose to remate, a phenomenon referred to as convenience polyandry (Arnqvist & Rowe, 2005). Indeed, Harano (2015) recently showed that females of *C. chinensis* that accepted additional matings mitigated fitness losses associated with male harassment. In Hemiptera, convenience polyandry has been reported in *A. paludum, Gerris buenoi* (Gerridae) and *Cimex lectularius* (Cimicidae) where feeding females reportedly offer relatively less resistance to male mating attempts compared to nonfeeding females (Reinhardt, Naylor, & Siva-Jothy, 2009; Rowe, 1992). Presumably, males exploit situations of low resistance when females are feeding to obtain additional matings (Reinhardt et al., 2009).

Psyllids are a highly diverse taxon (approximately 3850 species) composed exclusively of phytophagous insects distributed worldwide in all major zoogeographical regions (Burckhardt, Ouvrard, Queiroz, & Percy, 2014). Hollis (2004) suggested that female psyllids only mate once in their lifetime but provided no supporting data. It is now commonly accepted that most species are polyandrous (Lubanga, Peters & Steinbauer, 2016; Mehrnejad & Copland, 2006; Wenninger & Hall, 2008). Species such as *Diaphorina citri* (Psyllidae), *Trioza erytreae* (Triozidae), *Agonoscena pistaciae* (Psyllidae) and *Cacopsylla pyricola* (Psyllidae) are known to accrue direct benefits (increased female fecundity and egg viability) from polyandry (van den Berg, Deacon, & Thomas, 1991; Burts & Fischer, 1967; Mehrnejad & Copland, 2006; Wenninger & Hall, 2008). Conversely, females of *Tyora* (*Mesohomotoma*) *tessmanni* (Carsidaridae) do not accrue such benefits (Igboekwe & Adenuga, 1983). Interestingly, although polyandry is required to achieve high fecundity in *D. citri* and *T. erytreae,* oviposition is reduced by the continued presence of males (van den Berg et al., 1991; Wenninger & Hall, 2008). In these two species, females presumably mate at a rate above their optima as a consequence of male harassment which is linked to a male-biased operational sex ratio (OSR; Guédot, Horton, Landolt, & Munyaneza, 2013; Lubanga, Guédot, Percy, & Steinbauer, 2014).

Some species of psyllid are largely sedentary, often remaining on the same few plant modules throughout life, because they have limited capacity to survive for long away from their host (van Klinken, 2000). When feeding, the piercing-sucking feeding habit fixes hemipteran insects to a location where their stylets are inserted (Brożek, Mróz, Wylężek, Depa, & Węgierek, 2015; Garzo, Bonani, Lopes, & Fereres, 2012). The fine, hair-like stylets probe intra- and intercellularly to tap into plant tissues, often at distances longer than their body length (Bonani et al., 2010; Brożek et al., 2015; Civolani et al., 2011; Hollis, 2004). Stylet penetration is accompanied by secretion of a solidifying saliva that forms a sheath around the stylets (Hollis, 2004; Resh & Cardé, 2003). When the stylets reach the plant tissues from which the psyllid feeds and the insect begins imbibing nutrients, the stylets are often fully extended and retracting them can be a time-consuming process (Pollard, 1970). Owing to oogenesis, females have higher nutritional requirements than males (Blanckenhorn, 2005) and consequently are usually more sedentary. To improve our understanding of the adaptive significance of polyandry, we investigated whether females may remate for convenience to minimize costs associated with male harassment such as withdrawing their stylets from the host which would interrupt feeding and adversely affect their survival.

Our study species, *Aacanthocnema dobsoni*, is endemic to southeastern Australia where it is monophagous on drooping sheoaks, *Allocasuarina verticillata* (Casuarinaceae; Taylor, Jennings, Purcell, & Austin, 2011; Steinbauer, Lubanga, & Taylor, 2016). Nymphs can occur in large aggregations at the base of branchlets (Steinbauer et al., 2016). The species is multivoltine, the functional sex ratio is usually 1:1 and females attain reproductive maturity within 24 h posteclosion (Lubanga, Drijfhout, Kevin & Steinbauer, 2016). Individuals communicate via substrate-borne vibrations (SBVs; Lubanga, Drijfhout, Kevin & Steinbauer, 2016; Lubanga, Peters & Steinbauer, 2016; Percy, Taylor, & Kennedy, 2006). Presumably, the long cylindrical branchlets of the host plant provide a unique, two-dimensional active space that favours communication via SBVs over other modalities such as semiochemicals utilized by other psyllids such as *C. pyricola* (Guédot, Millar, Horton, & Landolt, 2009; Lubanga, Drijfhout, Kevin & Steinbauer, 2016). Lubanga, Peters, and Steinbauer (2016) showed that females are polyandrous but call and respond to male calls only if unmated. Males, on the other hand, utilize a scramble competition mating strategy (where all competing males have equal access to sexually receptive females; Lubanga, Peters & Steinbauer, 2016). They call, search and frequently attempt to mate (and often succeed) with unresponsive females. The use of SBV for mate location has also been reported in other psyllid species, e.g. *Anoeconeossa bundoorensis* (Aphalaridae; Wood, Peters, Taylor, & Steinbauer, 2016). In *A. dobsoni*, the refractory period of females is longer than that of males leading to a male-biased OSR that sets the stage for male harassment (Lubanga, Peters & Steinbauer, 2016). Although SBVs are not a prerequisite for mating, and female responsiveness is not influenced by male call characteristics (Lubanga, Peters & Steinbauer, 2016), in some instances males and females participate in reciprocal calling prior to mating (Lubanga, Guédot, Percy, & Steinbauer, 2015; Percy et al., 2006). However, we do not know whether *A. dobsoni* males and females alter call parameters of lone and reciprocal calls as has been reported in some other hemipteran insects (Čokl, Virant-Doberlet,