



The role of sexual conflict in the evolution of facultative parthenogenesis: a study on the spiny leaf stick insect



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Parthenogenesis is an asexual mode of reproduction that is rare in nature compared to sex. Parthenogenetic animals are derived from sexual progenitors, but little is known about how transitions to parthenogenesis evolve and persist. One hypothesis is that selection promotes transitions to parthenogenesis when males are rare or when mating is impossible (the mate scarcity hypothesis). However, we hypothesized that selection might also favour sex-to-parthenogenesis transitions when sexual interactions are costly (the sexual conflict hypothesis). These hypotheses lead to contrasting predictions about the nature of male–female interactions and their effects on female fitness. To test these hypotheses, we conducted a series of life history and behavioural experiments on the facultatively parthenogenetic spiny leaf stick insect, *Extatosoma tiaratum*. As predicted by sexual conflict theory, we found that females appeared to neutralize the costs of sex by utilizing counterevolved resistance traits: male-paired females resisted matings by curling their abdomens and kicking their legs during copulation attempts, prereproductive virgin females produced an antiaphrodisiac that repelled males, and parthenogenetic females made themselves inconspicuous to males by altering their pheromonal signals. Although measures of offspring viability point to possible advantages of sexual reproduction, females that were experimentally switched from a parthenogenetic to a sexual reproductive mode suffered elevated mortality and egg production costs that were not observed in exclusively parthenogenetic or exclusively sexual females. Our results suggest that females can benefit by avoiding mating in at least some circumstances, therefore supporting the hypothesis that sexual conflict mediated by female resistance could contribute to the evolution of facultative parthenogenesis.

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Parthenogenesis occurs when embryos develop from unfertilized ova. Although rarer than sex (De Meeûs, Prugnolle, & Agnew, 2007), parthenogenetic reproduction has evolved multiple times in angiosperms (Richards, 2003) and in all major animal groups except mammals (Avisé, Quattro, & Vrijenhoek, 1992). Phylogenetic evidence suggests that the vast majority of parthenogenetic species evolved recently from sexual ancestors (Butlin, 2002). But the selective forces that may favour or impede evolutionary transitions from sex to parthenogenesis remain poorly understood (Archetti, 2010; Corley, Blankenship, & Moore, 2001; D'Souza & Michiels,

2010; Engelstaedter, 2008; Hadany & Beker, 2007; Moore & Moore, 2003; Yamauchi & Kamite, 2003).

Facultative parthenogenesis is the capacity to reproduce either sexually or asexually (Normark, 2003) and is considered an important evolutionary stepping stone in transitions from obligate sex to obligate parthenogenesis (Schwander, Vuilleumier, Dubman, & Crespi, 2010). Although it is unclear how facultative parthenogenesis evolves, selection is thought to promote occasional parthenogenetic reproduction if mating is impossible or opportunities to mate are rare (Kramer & Templeton, 2001; Schwander et al., 2010; Stalker, 1956). This hypothesis (hereafter referred to as the mate scarcity hypothesis) assumes that sex is the selectively favoured or 'preferred' mode of reproduction, and that females that engage in parthenogenetic reproduction merely make the best of a bad (i.e. mateless) situation. Although the mate scarcity hypothesis has some empirical support (e.g. Kramer & Templeton, 2001; Schwander et al., 2010), its assumption that

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sex invariably confers higher fitness than parthenogenesis in facultative species is problematic in light of theoretical and empirical evidence of the ‘two-fold cost’ of sex (e.g. D’Souza & Michiels, 2010; Jokela, Lively, Dybdahl, & Fox, 1997; Maynard Smith, 1978; Yamauchi & Kamite, 2003), and theoretical studies suggesting that rare sex can confer the same benefits as frequent sex (Green & Noakes, 1995; D’Souza & Michiels, 2010). The mate scarcity hypothesis also fails to account for the additional costs of sexual conflict (see Lehtonen, Jennions, & Kokko, 2012) and the important role that sexual conflict plays in life history evolution (see Connallon, Cox, & Calsbeek, 2009).

Sexual conflict may offer an additional or alternative set of conditions under which selection can favour facultative parthenogenesis. Kawatsu (2013) showed mathematically that the coexistence of sexual and asexual reproduction in facultative systems can be maintained by antagonistic coevolution between male coercion and female resistance. Following Kawatsu (2013), we propose that the benefits of parthenogenesis relative to sex in facultative species might be amplified when the costs to females that do not resist mating are large (hereafter referred to as the sexual conflict hypothesis). If parthenogenetically reproducing females incur large costs as a consequence of switching to sex, for example, then female resistance to mating could evolve and thereby maintain parthenogenetic reproduction, as long as the costs of resistance are not so great as to negate any benefits gained (see Rowe, Arnqvist, Sih, & Krupa, 1994).

The sexual conflict and mate scarcity hypotheses yield sharply contrasting predictions. According to the mate scarcity hypothesis, virgin and parthenogenetically reproducing females should generally benefit from mating, especially if they have been unable to find a mate for a long time. Virgin and parthenogenetically reproducing females should strongly attract mates if sex is beneficial, and should therefore show few signs of resistance when mating opportunities arise. Virgin females might also be expected to delay onset of parthenogenetic reproduction in anticipation of the arrival of mates. In contrast, the sexual conflict hypothesis predicts that females should exhibit a high degree of mating reluctance by either avoiding sex entirely, or avoiding switching to sex once parthenogenetic reproduction has commenced. Additionally, females that make themselves unattractive to potential mates or that stop signalling their reproductive status might be favoured by selection if mating is costly. If parthenogenesis is favoured over sex, females might also be expected to hasten the onset of parthenogenetic reproduction. Finally, in at least some contexts, females should achieve higher fitness through parthenogenetic reproduction than through sexual reproduction. The fitness benefits of mating avoidance may be direct (e.g. enhanced longevity or fecundity) and/or indirect (e.g. enhanced offspring quality).

The Australian spiny leaf stick insect, *Extatosoma tiaratum*, is a facultatively parthenogenetic species whose life history and ecology have been interpreted as being broadly consistent with the mate scarcity hypothesis (Schneider & Elgar, 2010). However, no one has yet tested for sexual conflict in this species. Very little is known about the sex ratio of wild populations, but it is assumed that parthenogenetic production of all-female offspring and the relatively short life span of males result in a female-biased operational sex ratio (Schneider & Elgar, 2010). Unlike males, which are fully capable of flight, *E. tiaratum* females possess vestigial wings and are flightless (Brock, 2001). Males possess clasping organs (modified cerci) that facilitate copulation (personal observation). The characteristic posture of females (curling the abdomen over the back) is thought to be an antipredator defence, although it also

occurs during courtship and could therefore play a role in female resistance to mating. Both sexes produce a nontoxic repugnatorial secretion that is limited in its effectiveness as a predator repellent (Carlberg, 1985, 1987), but could play a role in sexual signalling (Strong, 1975).

We carried out an experimental investigation of sexual behaviour and reproductive performance in *E. tiaratum* to test the contrasting predictions of the sexual conflict and mate scarcity hypotheses. First, we compared fitness components (including egg output, hatching success and offspring juvenile viability) of unmated females that reproduced parthenogenetically and mated females exposed to males either prior to or following the start of parthenogenetic oviposition. Second, we tested for antagonistic pheromone signalling. Third, we looked for evidence of female behaviours and chemical defences that function to deter or repel male mating attempts.

METHODS

Animal Maintenance

Focal female and male individuals were obtained as hatchlings and young instar nymphs from a professional insect breeder (Insectpets, Gisborne, Victoria, Australia). A small number of supplementary individuals were also obtained from amateur breeders in the Greater Sydney Region, Australia. All individuals were the North Queensland race of *E. tiaratum tiaratum* (Brock, 2001). Nymphs were initially fed *Agonis flexuosa* leaves and housed in a single 12-litre plastic terrarium, but were later segregated by sex into groups of no more than 10 same-sex individuals. At maturity, males were housed in 40-litre plastic tubs each containing no more than 20 individuals at a time. Mature, focal females were housed individually in plastic cylinders with fibreglass fly screen lids (diameter: 20 cm; height: 40 cm; see mmc2 Supplementary Fig. S1). Stock females were housed communally in a large glass tank (76 × 47 cm and 50 cm high) covered with fly screen. Leaves of *A. flexuosa* and various species of *Eucalyptus* were fed to adult stick insects and replaced weekly. All leaves were sprayed once a day with tepid water. Female body length at time of death was determined by measuring abdomen tip to antennae base using a ruler.

Experiment Design

All experimental assays were conducted in the laboratory at room temperature (20–25 °C) from March to August 2013, and were based on three treatment groups, established as follows. Fifteen focal females of roughly equal size and age were haphazardly allocated 1 week after their final moult to each of three treatment groups: ‘sexual’, ‘parthenogenetic’ and ‘interrupted’. Depending on the treatment, focal females were paired with either same- or opposite-sex individuals for 3 consecutive days per week: Sexual females were paired with males, parthenogenetic females were paired with stock females to control for density effects, and interrupted females were initially paired with stock females, but, following an initial 5 weeks of parthenogenetic reproduction, were paired with males. The switch to sex was initiated at 5 weeks to ensure that interrupted females had fully invested in the parthenogenetic pathway before males were introduced. At the end of the 3-day pairing period each week, males and stock females were removed from all focal-female enclosures. A subset of nine focal females from each of the three treatments was used for all assays except for those for pheromone

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