



## Mate-guarding courtship behaviour: tactics in a changing world



Damian O. Elias<sup>a,\*</sup>, Senthurran Sivalingham<sup>b</sup>, Andrew C. Mason<sup>b</sup>,  
Maydianne C. B. Andrade<sup>b</sup>, Michael M. Kasumovic<sup>c</sup>

<sup>a</sup> Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, U.S.A.

<sup>b</sup> Integrative Behaviour and Neuroscience Group, University of Toronto Scarborough, Toronto, ON, Canada

<sup>c</sup> School of Biological, Earth, and Environmental Sciences, UNSW Australia, Sydney, Australia

### ARTICLE INFO

#### Article history:

Received 17 April 2014

Initial acceptance 2 June 2014

Final acceptance 17 July 2014

Published online

MS. number: A14-00327R

#### Keywords:

jumping spider

mate guarding

mating tactic

multiple signals

*Phidippus clarus*

seismic communication

sexual conflict

signal evolution

sperm competition

vibratory signalling

Mate guarding is one of the most common tactics in sperm competition. Males are expected to guard their mates when costs of guarding (accrued from physical confrontations with rivals and/or reduced foraging) are low relative to the benefits of ensuring mating opportunities and paternity. We investigated mate guarding in the jumping spider *Phidippus clarus*, a species where males defend immature subadult females against rival males and attempt to mate with the females soon after they mature. We assessed a possible social cost of mate-guarding behaviour (male intersexual signalling) using laser vibrometry and respirometry. We found that males produced a unique set of signals when guarding subadult females and that these signals were energetically costly (guarding courtship). Mating success did not differ between males that successfully defended a subadult female and males that located an unmated, mature virgin female. This suggests that guarding courtship does not directly influence mate choice and that males may use different tactics depending on female availability to ensure fitness. To explore further the effect of mate guarding and guarding courtship, we experimentally sealed male's copulatory organs (males could guard normally but were unable to transfer sperm) and compared mating rates of sealed versus intact males. We found that guarding behaviour, and not sperm transfer, significantly influenced female remating behaviour. Placed in the context of *P. clarus* life history, our results highlight the ongoing sexual conflict between males and females and the hidden costs and benefits of mate-guarding behaviour.

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Mate guarding allows males to prevent rivals from copulating with a guarded female and is arguably one of the most reliable defences against direct sperm competition (Birkhead & Møller, 1998; Parker, 1970; Simmons, 2001). Mate guarding can take a variety of forms, and in many systems, males defend a female before she becomes sexually receptive (precopulatory mate guarding) and/or after the male has mated with the female (post-copulatory mate guarding) (Calbacho-Rosa, Cordoba-Aguilar, & Peretti, 2010; Grafen & Ridley, 1983; Jormalainen, 1998; Parker, 1970; Simmons, 2001). The presence and particular type of mate guarding depend largely on (1) sperm use patterns, (2) whether females mature synchronously or asynchronously, (3) the duration of female sexual receptivity, (4) the operational (or adult) sex ratio, (5) the ability of males to assess female mating status and (6) the risk and intensity of sperm competition (Alcock, 1994; Calbacho-Rosa et al., 2010; Elgar, 1992; Hardling, Kokko, & Elwood, 2004; Harts & Kokko, 2013; Jormalainen, 1998; Kokko & Johnstone, 2002;

Neff & Svensson, 2013; Simmons, 2001; Uhl, 2002; Weir, Grant, & Hutchings, 2011). In early game-theory models of male mate guarding, Parker (1974) emphasized the importance of the duration of female receptivity as well as sex ratio in determining the evolutionary stability of mate-guarding strategies. In this and subsequent models of mate guarding, encounter rates between males and females as well as guarding costs for males were identified as key factors affecting male fitness (Elwood & Dick, 1990; Grafen & Ridley, 1983; Jormalainen, 1998; Jormalainen, Tuomi, & Yamamura, 1994; Parker, 1974; Yamamura, 1987).

Since guarding males attempt to diminish the level of female polyandry, mate guarding is often thought of in terms of intersexual conflict (Birkhead & Møller, 1998; Jormalainen, 1998; Parker, 1979; Rodríguez-Muñoz, Bretman, & Tregenza, 2011; Zeiss, Martens, & Rolff, 1999). Several studies demonstrate that costs imposed on guarded females lead to optimal guarding times that differ for males and females (Benvenuto & Weeks, 2011, 2012; Cothran, 2008; Jormalainen, 1998; Jormalainen et al., 1994; Parker, 1979; Yamamura & Jormalainen, 1996). Recent research, however, suggests that male mate guarding may also be beneficial to females. For example, because successful guarders are also competitively

\* Correspondence: D. O. Elias, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, U.S.A.

E-mail address: [doelias@berkeley.edu](mailto:doelias@berkeley.edu) (D. O. Elias).

superior males, females gain indirect benefits by mating with them (Benton, 1992; Prenter, Elwood, & Montgomery, 2003). Females can also gain direct benefits through the reduction of predation (Cothran, Chapman, Stiff, & Relyea, 2012; Rodríguez-Muñoz et al., 2011) and male harassment (Davis, 2002). Finally, females cohabiting with males during precopulatory mate guarding have a prolonged period for assessing their potential mate prior to sexual maturity, and this experience may allow females to refine choices made later (Hebets, 2003; Johnson, 2005; Kasumovic, 2013; Rutledge, Miller, & Uetz, 2010). Females may thus facilitate guarding by particular males under certain circumstances, thereby reducing sexual conflict.

Here we focus on the dynamics of precopulatory mate guarding, which is interesting for several reasons. First, males that guard females while awaiting a chance to copulate are engaging in a particularly risky tactic by investing before mating has occurred. This is in contrast to postcopulatory guarding where males invest in guarding only after successfully inseminating the female. Gambling on precopulatory guarding should be more likely when this form of guarding (1) increases mating success relative to courting a female that is not guarded and/or (2) decreases the likelihood that females will mate with additional males relative to the remating likelihood of unguarded females. Precopulatory mate guarding can directly increase mating success by restricting female access to alternative mates, and this has been well studied (Jormalainen, 1998; Neff & Svensson, 2013; Parker & Vahed, 2010). Less well studied is whether and how precopulatory guarding affects female remating (Pruitt, Burghardt, & Riechert, 2012; Pruitt & Riechert, 2011). Since the opportunity for female remating arises after the previous male has left, any effects will depend on whether guarding decreases the female's subsequent receptivity. Interactions between mating pairs during precopulatory guarding may have such an effect. Precopulatory guarding behaviours may also be necessary to minimize female resistance to guarding and to increase the probability of mating upon maturity. However, precopulatory interactions could also increase the cost of guarding for males. Information on the costs and consequences of social interactions during precopulatory guarding, however, are largely lacking in the literature (but see Pruitt & Riechert, 2011).

Here we examined the potential costs and benefits of precopulatory mate guarding in the jumping spider, *Phidippus clarus*. *Phidippus clarus* is found in early successional fields throughout eastern North America (Edwards, 2004) and, as in many other invertebrates, adult males guard immature females until they are able to mate (Bennett, Smith, & Betts, 2012; Benton, 1992; Dodson & Beck, 1993; Fahey & Elgar, 1997; Hoefler, 2007; Jackson, 1986; Jormalainen, 1998; Miller & Miller, 1986; Parker & Vahed, 2010; Rowe, 1994; Schroder, 2003). Like other jumping spider species, males spin a silk retreat next to subadult females and live with them in a process termed 'cohabitation' (Fahey & Elgar, 1997; Fernandez-Montraveta & Cuadrado, 2003; Jackson, 1986; Miller & Miller, 1986; Robinson, 1982; Suter & Walberer, 1989). Extensive work on the mating behaviour of *P. clarus* suggests that their short breeding season is partitioned into two major selective bouts driven by near-synchronous female maturation (Elias, Andrade, & Kasumovic, 2011; Elias, Kasumovic, Punzalan, Andrade, & Mason, 2008; Elias, Sivalingham, Mason, Andrade, & Kasumovic, 2010; Hoefler, 2007, 2008; Kasumovic, Elias, Punzalan, Mason, & Andrade, 2009; Kasumovic, Elias, Sivalingham, Mason, & Andrade, 2010; Kasumovic, Mason, Andrade, & Elias, 2011; Sivalingham, Kasumovic, Mason, Andrade, & Elias, 2010).

During the early part of the breeding season, the operational sex ratio is strongly male biased; males seek and cohabit with subadult females and defend them against rivals, and after the females moult, they presumably mate with them (Elias et al., 2008; Hoefler,

2007; Kasumovic et al., 2011). Fighting is costly, with selection for increased size, weight and signalling rate in intersexual aggressive signals (Elias et al., 2008; Hoefler, 2007). Most importantly however, is development time, as males that arrive first to a subadult female are much more likely to win contests even against larger, heavier males (Kasumovic et al., 2011), and this is further reinforced by a winner effect (Kasumovic et al., 2009, 2010). To date, fitness in *P. clarus* has been inferred through contest success, which is based on the assumption that winners are more likely to be successful guarders, resulting in increased mating success with guarded females. This, however, may not necessarily be the case since females are larger than males and subadult females are aggressive towards intruders (Elias, Botero, Andrade, Mason, & Kasumovic, 2010), which may result in females driving away potential suitors. In addition, evidence suggests that male *P. clarus* court subadult females during cohabitation (Hoefler, 2008), as in a congener *Phidippus johnsoni* (Jackson, 1977, 1978a, 1978b, 1980), suggesting that costs associated with mate guarding may be higher than initially assumed.

While male precopulatory mate guarding typically occurs early in the season when adult sex ratios are heavily male biased, almost all females mature within a 3-day window, during which the operational sex ratio rapidly shifts towards equality (Hoefler, 2007, 2008). This leads to a second selective period in *P. clarus* where female choice is thought to be the primary form of selection. This latter part of the breeding season is typified by intense male courtship directed at adult females outside of nests (Elias, Sivalingham, et al., 2010; Sivalingham et al., 2010). Selection on male traits differs at this point, with mature virgin females preferentially mating with males with longer legs that court at higher rates (visual and vibratory signals) (Elias, Sivalingham, et al., 2010; Sivalingham et al., 2010). Previous studies using virgin females that did not have a cohabiting partner also demonstrated that these females mate multiply (Sivalingham et al., 2010), which may suggest little paternity assurance for guarding males, and therefore, that the risk and intensity of sperm competition may be quite high. However, it is not yet clear whether remating rates of females are altered by cohabitation.

The goals of this study were thus (1) to analyse mate-guarding courtship behaviour (male courtship targeted to subadult and newly moulted females in nests) and quantify its energetic costs and (2) to determine whether successful cohabitation affects subsequent remating rates of females outside of their nests. Since female receptivity frequently decreases after copulation, even in species that do not cohabit, we also examined the effects of copulation separately from cohabitation and associated behaviours. We did this by comparing female remating behaviour after three treatments: (1) no cohabitation prior to copulation; (2) normal cohabitation coupled with copulation; and (3) cohabitation when copulation was not possible (males were manipulated to prevent sperm transfer). If males invest in costly guarding courtship, we predicted that cohabitation alone, independent of copulation, would decrease remating rates. By understanding these three aspects of this system, we will better understand the costs and benefits of mate guarding in this species, and in general.

## METHODS

We collected adult male and juvenile female *P. clarus* from the Koffler Scientific Reserve at Joker's Hill, King, Ontario, Canada (44°03'N, 79°29'W). We housed the males in individual clear plastic cages (3 × 3 × 5 cm) and housed the females in larger plastic containers (10 × 10 × 3 cm). Both were kept on a 12:12 h light:dark cycle and fed size-appropriate *Acheta domestica* and *Drosophila hydei* twice weekly. Since jumping spiders have well-developed

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