

Mate-guarding courtship behaviour: tactics in a changing world



Damian O. Elias^{a,*}, Senthuran Sivalingham^b, Andrew C. Mason^b,
Maydianne C. B. Andrade^b, Michael M. Kasumovic^c

^a Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, U.S.A.

^b Integrative Behaviour and Neuroscience Group, University of Toronto Scarborough, Toronto, ON, Canada

^c 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.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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 (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

vision (Forster, 1982; Land, 1985; Land & Nilsson, 2002), we placed opaque barriers between the cages. All individuals were collected early in the breeding season, when males defend subadult females (Elias, Sivalinghem, et al., 2010; Hoefler, 2007). We weighed all individuals using an Ohaus electronic balance, digitally photographed them (Nikon Digital Camera DXM 1200) using a Zeiss microscope (Stemi 2000C) and measured their cephalothorax width (metric of body size) at its widest point (using Nikon Act-1 software) after collection and again after completion of the experiment.

Signal Recording

We recorded substrate-borne vibrations using a Laser Doppler Vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head) attached to a translation stage (Newport model 421). Small pieces of reflective tape (1 mm²) were placed on the silk nest of a female to serve as measurement points for the LDV. Vibratory courtship on nests occurs whether the female is present or not (*P. johnsoni*: Jackson, 1980; *P. clarus*: Elias & Kasumovic, 2012). While we did not explicitly test for the effect of female presence on male vibratory courtship on nests, preliminary data suggested that female presence influenced the duration, but not the signal properties, of male vibratory courtship (Elias & Kasumovic, 2012). Future work will verify this observation. We measured signal duration, peak frequency and signal rates of courtship signals. It was not possible to record different signal types from the same individuals because of equipment and time constraints. Instead, we compared the male–subadult female interactions recorded in the present study with previous studies of male–male pairings (Elias et al., 2008) and male–mature female pairings (Sivalinghem et al., 2010) recorded from the same population using the same equipment and recording procedures.

Respirometric Analyses

Jumping spiders are rarely still during daylight hours, so we measured oxygen consumption of isolated males during normal daily activity ('routine metabolic rate') and when they were in the presence of a female's empty silk nest ('active metabolic rate'). Males were measured within 5.1 cm³ sealed acrylic containers while alone (routine rate) or in the presence of an empty nest woven by a subadult female the night before the trial (active rate). The first measurement (routine or active rate) was randomized and a minimum of 10 min elapsed between measurements. Males began signalling immediately after contacting the nest. For a subset of males, we used a portable laser vibrometer on males while they were in the respirometry containers (Polytec PDV 100) and verified that males signalled ($N = 8/8$). For each trial, we measured the oxygen consumption for at least 8 min of the behaviour (searching or active courtship) with a maximum of 10 min to ensure that individuals did not begin anaerobic respiration. Throughout the trial, we were able to measure the change in oxygen concentration within the container over time using a Fibox 3 (see below). To estimate a male's maximal (rather than average) oxygen consumption during routine and active trials, we chose a 5 min period demonstrating the greatest change in oxygen concentration (as $\mu\text{mol/litre}$ over time) and used the slope of this change as our measurement of maximal metabolic rate.

We used a Fibox 3 (PreSens; Regensburg, Germany) to measure oxygen consumption. Briefly, the Fibox 3 uses a fibre-optic cable that reads the reflectance of a PSt3 oxygen sensor spot (detection limit 15 ppb, 0–100% oxygen) glued on the inside of the sealed container with silicon (Kwik-sil silicone elastomer, World Precision Instruments Florida, Sarasota, FL, U.S.A.). The Fibox 3 measures and

records oxygen concentration (μmol) within the container every second, allowing a noninvasive means of measuring oxygen consumption in real time. We ran control trials with empty sealed containers to ensure that the change in oxygen concentration was static prior to placing males inside the containers. This system has been used successfully to examine changes in metabolic rate of much smaller spiders (Kasumovic & Seebacher, 2013).

Mating Trials

We provided each subadult female with a translucent rubber tube (1.5 cm in diameter, 4 cm long) secured with pressure-sensitive adhesive as a substrate to establish nests (Hoefler & Jakob, 2006; Kasumovic et al., 2011). All four walls of a female's cage were covered with petroleum jelly to prevent individuals from climbing the walls. We then randomly assigned females to one of three rearing groups for subsequent trials: (1) cohabiting with an intact male (intact-cohabiting, $N = 26$); (2) cohabiting with a male whose intromittent organs were experimentally sealed and was thus incapable of sperm transfer (guarding-only cohabiting, $N = 19$; see below); or (3) females held in isolation until maturity (isolated-control, $N = 15$).

For guarding-only cohabiting treatments, males were anaesthetized with CO₂ and had a small drop of wax placed on the pedipalps, effectively preventing the possibility of sperm transfer. We observed males during feeding, and we confirmed that complex locomotor activities such as predation were not affected by this procedure. The guarding-only cohabiting treatment allowed us to investigate the effects of guarding behaviour independent of sperm transfer, as proteins transferred in the seminal fluid during mating often have strong effects on female remating rates in some species (Aisenberg & Costa, 2005; Avila, Sirot, LaFlamme, Rubinstein, & Wolfner, 2010). For both cohabitation treatments, we allowed females to spin a nest, after which we randomly placed an intact or guarding-only male within each container. We allowed a single day for males to build their own nests next to the subadult female's nest (=cohabitation). We only included data from pairs where the male built a nest directly in contact with the female's nest and where the female matured to adulthood while cohabiting. Males that did not cohabit were replaced with another randomly chosen male after 1 day. New males were given 1 day to cohabit. We continuously monitored subadults for maturity and removed males as soon as we observed that females had matured to adults. Each male was used only once. For all mating trials we measured copulation and courtship duration for all mating trials.

Effect of cohabitation on female mating rates

To investigate whether mating rates of females that mature with a male (successful cohabitation) and that do not mature with a male (unsuccessful cohabitation, or females not located by males prior to maturity) differ, we compared mating rates of females that cohabited with intact males until mature (intact-cohabiting) and that were held in isolation until mature (isolated-control). We observed mating rates for three male suitors presented in sequence. For males in the intact-cohabiting treatment, we continuously recorded female cages using a 24 h digital video system with low-light-sensitive cameras (Panasonic WV BP330) equipped with macro-zoom lenses (Navitar 7000) from the time of pairing until female maturation. Arenas were kept in a room on a 12:12 h light cycle and were illuminated with low-lux red light during the scotophase. Because we had a limited number of cameras and because females mature nearly synchronously, we could monitor only a subset of intact-cohabiting (7/26) males. A single intact-cohabiting pair was monitored with each camera. For subsequent pairings, we placed a randomly chosen male in the arena when the female was

outside of her nest (simulating how males would find wandering females in the latter half of the breeding season). Females were paired with these males 2 days after their previous mating encounter.

For the isolated-control treatments, approximately 2 days after females became sexually mature (moulted) and exited their nests, we placed one randomly chosen intact male in the arena. These trials lasted 15 min, and only males that interacted with females during this time were included in the analysis. In the field, nests with subadult females and no males are routinely observed (Elias & Kasumovic, 2012). Females were sequentially presented with two additional males, 2 days after their previous pairing. Thus, cohabited females experienced a single male during cohabitation and two males afterward (for a total of three males), while isolated females encountered all three males after maturation.

Effect of sperm transfer and cohabitation on female mating rates

To assess the role of sperm transfer on female mating rates, we compared mating rates of the first two intact males that each female experienced. For intact-cohabiting and isolated-control females, we compared mating rates of the first two males that each female was paired with. For the third treatment (guarding-only cohabiting), we compared mating rates of the second and third male since the first male that each female experienced was incapable of normal copulation.

In addition, we monitored a subset of guarding only-cohabiting treatments (10/19) using a 24 h digital video system with low-light-sensitive cameras to ensure that males with wax plugs performed all guarding courtship normally. Each camera monitored a maximum of three pairs. No significant differences were observed in the time spent in proximity to and interacting with females (including faux copulation attempts) between guarding-only cohabiting males and intact-cohabiting males ($t_{27,338} = 0.693$, $P > 0.05$). After subadult females in the guarding-only cohabiting treatment matured, we checked the pedipalps of the males to verify the presence of the wax plug.

Statistical Analysis

To determine whether *P. clarus* males produce different vibratory signals during interactions with males, mature females and subadult females/newly mature females in nests, we analysed vibrational signals from cohabiting males and compared them to data from two published studies on the same population, collected using the same equipment (intrasexual signals: Elias et al., 2008; with mature females: Sivalinghem et al., 2010). We first performed a principal components analysis (PCA) on signal duration and peak frequency to calculate new uncorrelated variables for each. Using the PC scores, we then used a discriminant function analysis (DFA) to estimate how well our PC variables predicted signal properties produced in each context. Next, we examined whether presumptive signal types differed in signal attributes. As the various signal attributes were not normally distributed, we used Kruskal–Wallis tests to examine differences in signalling traits between groups. When significant, we used a Wilcoxon two-sample test for subsequent pairwise comparisons to determine which groups differed. Statistical analyses were conducted using JMP 10.0 (SAS Institute Inc., Cary, NC, U.S.A.) and R (R Foundation for Statistical Computing, Vienna, Austria).

To determine whether guarding courtship was costly, we compared oxygen consumption in routine and active (guarding courtship) behaviours. We used an ANOVA with oxygen consumption as the dependent variable, behaviour (routine versus active) as a factor and weight as a covariate to examine whether there were differences in oxygen consumption during routine

activity and courtship. We used male ID as a random factor to control for males being measured twice. Statistical analyses were conducted using JMP 10.0.

In total, we assigned 26 females to the intact-cohabiting treatment. However, because of the limited number of cameras available and near-synchronous female maturation, we were only able to record mating behaviour for the seven individuals that were video-recorded (see above). Because the sample size of individuals examined in the intact-cohabiting treatment differed between the first and subsequent matings, we analysed the results of the first mating interaction between the intact-cohabiting and isolated-control treatments separately from the second and third mating interactions.

To determine whether cohabitation affected mating success, we compared initial mating rates of females with an intact-cohabiting male and with an isolated-control male using a chi-square test. We next examined remating rates of these same females with intact males (second and third mating attempts). We used a log-linear analysis and placed treatment and second and third mating as main effects, as well as their interactions, to examine whether the frequency of successful matings in each mating attempt varied as a consequence of female rearing treatment. We used SPSS v21 (IBM, New York, NY, U.S.A.) for this analysis.

We performed a second analysis to examine whether cohabiting alone (without sperm transfer) was sufficient to reduce female remating rates. For this analysis, we compared the rate of female remating with the second intact male in each treatment using a contingency table. For the intact-cohabiting and isolated-control treatment, this was the first male that each female was paired with. For the guarding-only cohabiting treatments, this was the second male that each female was paired with. Again, we performed a separate analysis of subsequent mating opportunities because of the change in sample size in the intact-cohabiting treatment.

RESULTS

Male Courtship towards Subadult Females

Two principal component scores were calculated and accounted for 84% (PC1) and 16% (PC2) of the variance in signal characteristics. PC1 was positively associated with signal duration (0.71) and negatively associated with peak frequency (−0.71) with an eigenvalue of 1.774. PC2 was negatively associated with signal duration (−0.71) and peak frequency (−0.71) with an eigenvalue of 0.2259. Males produced a unique set of signals when courting subadult females at nests (Fig. 1). A discriminant function analysis was highly significant ($F_{1,48} = 280.33$, Wilks $\lambda = 0.098$, $P < 0.001$) and revealed one error in categorization (Table 1).

Signal types differed significantly in duration (Kruskal–Wallis full model: $\chi^2_{2,45} = 39.33$, $P < 0.0001$). Signals produced while cohabiting with subadult females were longer (mean \pm SD = 0.78 ± 0.14 s) than intrasexual signals (0.091 ± 0.012 s) and adult courtship signals (0.48 ± 0.11 s).

Subadult-directed courtship signals were tonal (mean \pm SD = 71.90 ± 10.60 Hz), much like aggressive signals (118.00 ± 31.78 Hz) and adult courtship signals (68.16 ± 10.38 Hz). Significant differences were observed in peak frequency characteristics (Kruskal–Wallis full model: $\chi^2_{2,45} = 32.77$, $P < 0.0001$) between aggressive and subadult courtship signals ($\chi^2_{1,26} = 19.37$, $P < 0.0001$) as well as between aggressive and adult courtship signals ($\chi^2_{1,35} = 26.86$, $P < 0.0001$) but not between subadult and adult female courtship signals ($\chi^2_{1,29} = 1.15$, $P = 0.28$). In addition, while courtship signals directed towards subadult females were produced using a combination of body shakes and abdominal

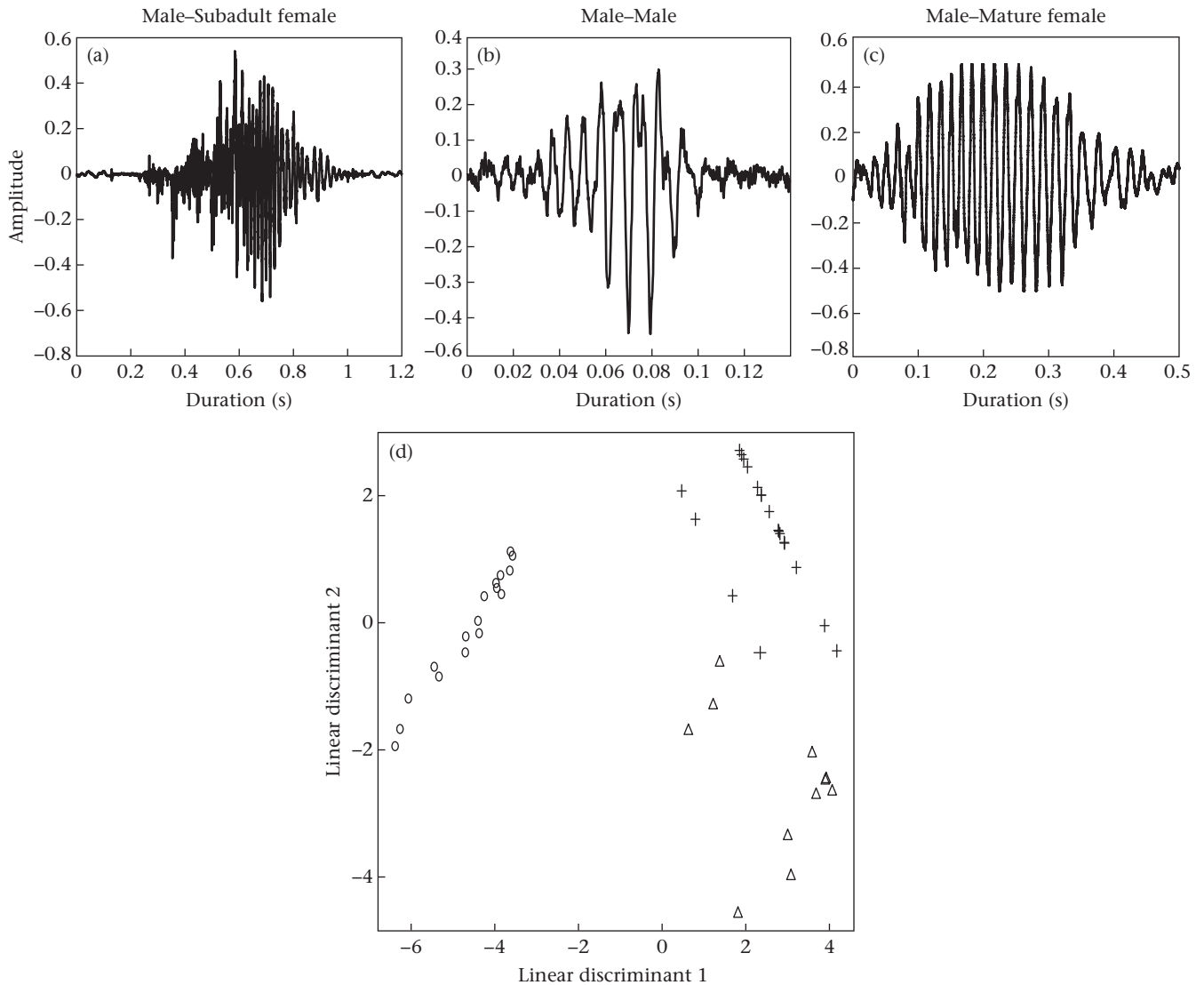


Figure 1. Typical examples of vibratory signals produced by male jumping spiders (*Phidippus clarus*) in three contexts: (a) courting subadult females; (b) aggressive signalling to other males; (c) courting mature females. (d) Linear discriminant function plot of the signalling space for each vibratory signal: Δ : male–subadult female; \circ : male–male; +: male–mature female ($P < 0.001$).

tremulations, aggressive signals and courtship signals directed towards adult females were produced solely by tremulations of the abdomen, and included coordinated visual signals (data not shown). In comparison, males cohabiting with subadult females appeared to grasp silk threads with their tarsal claws and violently shake their bodies to produce vibrations. These shaking behaviours bear a resemblance to descriptions of vibrations in the congener *P. johnsoni* (Jackson, 1977, 1980). A subset of subadult-cohabiting males (4 of 12) produced a series of (5–12) signals in rapid succession along with the typical subadult-directed courtship signals.

Table 1

Discriminant function analysis of putative signal types produced by male *Phidippus clarus* in different contexts (actual rows by predicted columns) based on principal component scores incorporating signal duration and peak frequency

	Male–Subadult female	Male–Male	Male–Mature female
Male–Subadult female	10	0	1
Male–Male	0	17	0
Male–Mature female	0	0	20

Respirometric Analyses

Mean oxygen consumption of males was more than three times higher during mate-guarding courtship (mean \pm SE = 1.73 ± 0.11 $\mu\text{mol}/\text{min}$) than during routine activity (0.54 ± 0.11 $\mu\text{mol}/\text{min}$) ($F_{2,37} = 54.71$, $P < 0.001$; Fig. 2). There was no significant association between male mass and oxygen consumption ($F_{2,37} = 1.45$, $P = 0.24$). All males that made contact with an immature female's web produced courtship vibrations (data not shown).

Mating Trials

There was no difference in mating rate between females in the intact-cohabiting (7/8 females mated successfully) and the isolated-control (13/14 females mated successfully) treatments ($\chi^2_1 = 0.17$, $P = 0.68$; Fig. 3). As a result, the mating rate for the first male encountered did not depend on rearing treatment. Remating rates of females in both groups declined similarly to less than 40% during the second and third encounters with males (Fig. 3), such

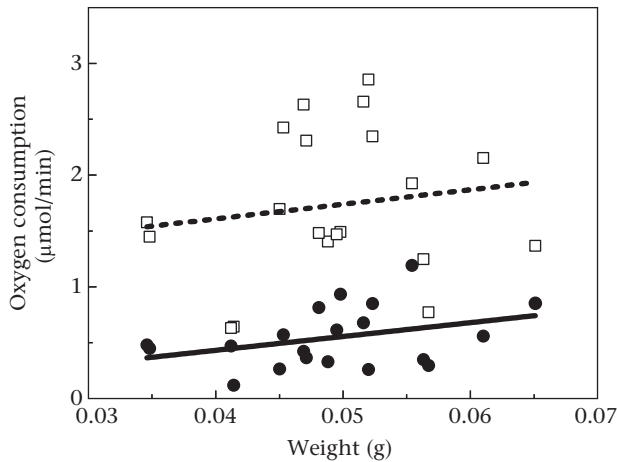


Figure 2. Maximal oxygen consumption of *P. clarus* males during active (open squares, dotted line) and routine (solid circles, solid line) measurement periods.

that remating rates of females did not differ between rearing treatments ($\chi^2_1 = 1.81$, $P = 0.40$; Fig. 3).

Virgin females from the guarding-only cohabiting treatment, paired for the first time with an intact male, had a significantly lower mating rate (<40%) than females from the intact-cohabiting and isolated-control treatments ($\chi^2_2 = 14.40$, $P = 0.0007$; Fig. 4). There was no significant difference between the three rearing treatments in remating rates of females in their second encounter with an intact male ($\chi^2_2 = 3.50$, $P = 0.17$; Fig. 4).

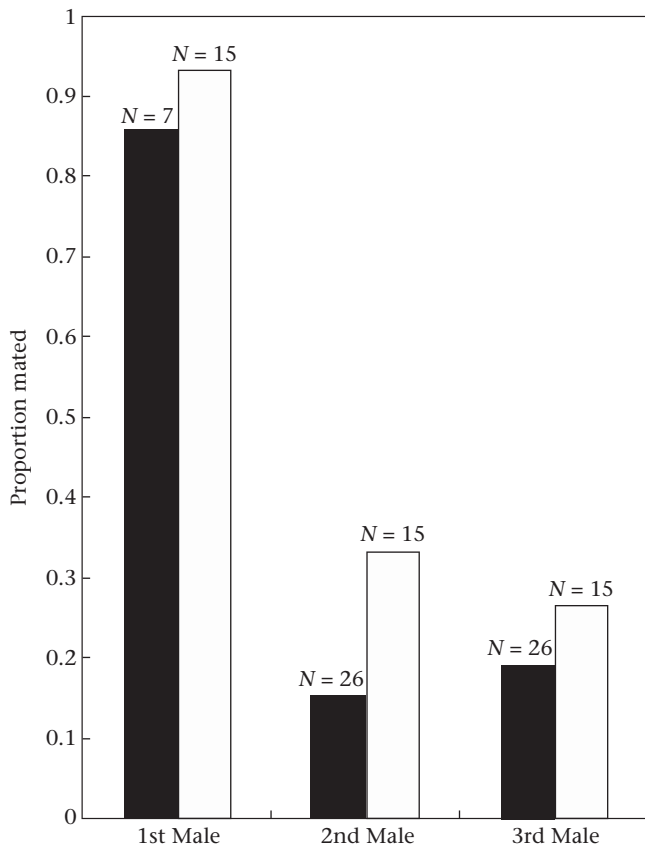


Figure 3. Mating rates of *P. clarus* females that were paired sequentially with three different males after they had cohabited with males (black bars) or were alone (white bars) during their final instar.

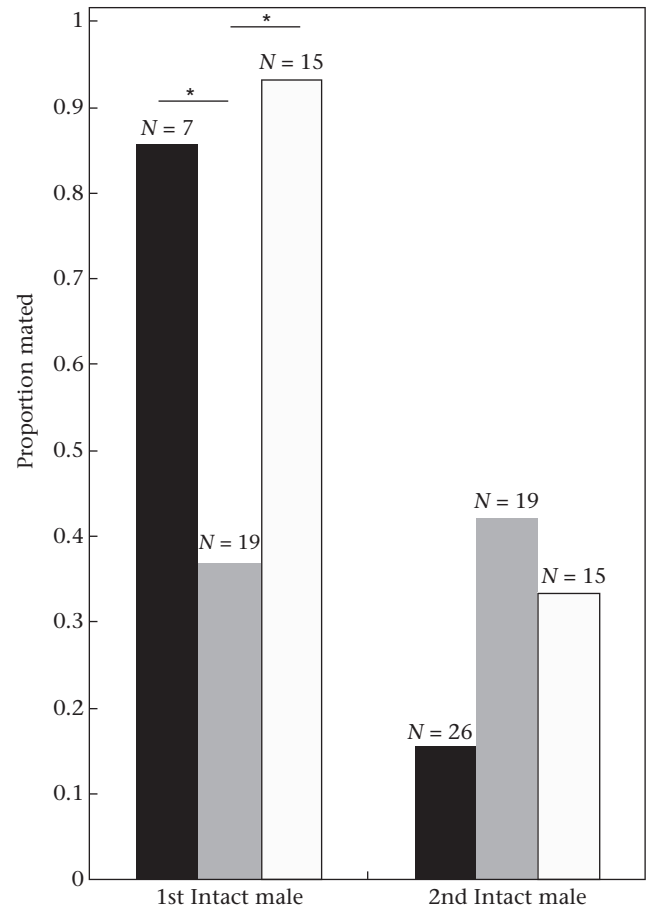


Figure 4. Mating rates for intact-cohabiting (black bars), guarding-only cohabiting (grey bars) and isolated-control (white bars) *P. clarus* females. An asterisk indicates a significant difference in mating success between treatments (* $P < 0.001$).

DISCUSSION

Mate guarding is a common behaviour in a variety of taxa. Our theoretical understanding of mate guarding is based, for the most part, on assumptions of the costs and benefits associated with this behaviour for each sex. For males, costs of female defence (time away from foraging, male aggression) are outweighed by paternity benefits of successful guarding. For females, costs due to the absence of direct mate choice are outweighed by benefits of reduced predation (Cothran et al., 2012; Rodríguez-Muñoz et al., 2011) and male harassment (Davis, 2002), and the costs associated with female choice (Vitousek, Mitchell, Woakes, Niemack, & Wikelski, 2007; Wong & Jennions, 2003). Here we explored other energetic and behavioural costs and benefits that individuals may experience during mate guarding. We found that male *P. clarus* pay additional energetic costs not associated with male–male competition or foraging reduction. We also demonstrate that males can influence female remating rates by guarding behaviours (including time spent in proximity to females in their nests, vibratory signalling, contacting female genitalia, etc.), independent of either sperm transfer or male–male competition.

We found that male *P. clarus* use a unique set of signalling behaviours while interacting with subadult females in nests. Male *P. clarus* thus produce signals in three distinct contexts: aggressive intrasexual signals during male competition, intersexual courtship signals directed at mature females and intersexual courtship signals directed at guarded subadult/newly matured females. Guarding

courtship signals are metabolically costly (this study), which may help explain the reduction in longevity of mate-guarding males (Hoefler, 2008). Males directed much more courtship towards immature females than they did towards mature virgin females (5043 s versus 626 s) even though we found no evidence that these behaviours influenced mating success (Fig. 2). Interestingly, our study suggests that guarding courtship signals may instead function in sperm competition by reducing the receptivity of females to future suitors. This is further supported by our observation that mate-guarding signals were similar for males of different sizes, suggesting that these signals are not condition-dependent ‘handicaps’ used by females to assess potential mates (Andersson, 1982; Zahavi, 1975).

Our results demonstrate that guarding behaviours significantly reduced receptivity to future suitors independent of sperm transfer. This is surprising given that proteins transferred in seminal fluid significantly affect mating in many insects (Avila et al., 2010) and spiders (Aisenberg & Costa, 2005; but see Prokop, 2006). To our knowledge, only one other study has reported a similar result, namely that for the nursery web spider *Pisaura mirabilis*, where the probability of female remating is based on direct transfer of a food item (nuptial gift) and not on sperm transfer (Prokop, 2006). In our system, we propose that males invest in guarding courtship behaviour to manipulate female receptivity. This manipulation could have a large potential cost for females, because male guarding behaviour significantly reduces the likelihood that females will mate with nonguarding males, and females that lose their guarding male may never mate.

Alternatively, the reduction in mating rate without sperm transfer could reflect an adaptive response by females if females assess male quality/availability based on the males that guard them. In this scenario, females that have been guarded by a male could either reject subsequent, relatively inferior males, or shift their preference function. In wolf spiders, for example, courtship directed at subadult females has direct effects on mating patterns after maturation (Hebets, 2003; Rutledge et al., 2010). In addition, the presence of guarding males affects mate choice, specifically precopulatory sexual cannibalism, in pirate spiders (Johnson, 2005). Although our sample size was too small to test for this specifically, our observation that nearly all males copulated with their guarded female makes it unlikely. Future work is necessary to evaluate this possibility.

Previous research has demonstrated that selection in the breeding season for *P. clarus* occurs in two distinct bouts: one driven by male–male competition early in the breeding season and the other driven by female choice late in the breeding season. The most important traits in each selective episode differ, with selection on faster maturation earlier in the breeding season and larger sizes (and longer legs, in particular) later in the breeding season (Elias et al., 2008; Elias, Sivalingham, et al., 2010; Hoefler, 2007, 2008; Kasumovic et al., 2009, 2010, 2011; Sivalingham et al., 2010). Our results demonstrate that the traits associated with successful cohabitation (early maturation, larger size/weight) are directly related to reproductive success, as more than 85% of males mated with their cohabiting female. Interestingly, the mating rates were the same whether a male courted a virgin female or cohabited with a subadult female, suggesting that males could follow two reproductive strategies: mature earlier and compete for access to mates, or mature later and court virgin females. This is especially possible as males are very short-lived as adults (Hoefler, 2007). We observed higher mating rates for isolated virgin females in our study (85% successful) compared with an earlier study on virgin females (66% successful; Sivalingham et al., 2010). These results may be a function of the time between maturation and the first male encountered (1–2 days: this study; 1–5 days: Sivalingham

et al., 2010). In the present study, we wanted to standardize the time that females in the isolated-control and guarding-only cohabiting treatments encountered their first intact male. Future work will investigate patterns of mate choice and maturation timelines in the field and in the laboratory.

We suggest that partitioning of selection has a secondary effect of promoting the evolution of multiple signals (Andersson, Pryke, Ornborg, Lawes, & Andersson, 2002; Hebets & Papaj, 2005), a topic that is currently under much debate (Bro-Jørgensen, 2010; Candolin, 2003; van Doorn & Weissing, 2004, 2006; Hebets & Papaj, 2005; Iwasa & Pomiankowski, 1991, 1994; Johnstone, 1996; Rowe, 1999; Schluter & Price, 1993). One hypothesis is the ‘multiple receivers’ hypothesis, which posits that multiple signals are maintained because different signals are evaluated by inter- and intrasexual conspecifics (Andersson et al., 2002; Guindre-Parker, Gilchrist, Baldo, Doucet, & Love, 2013). We propose that *P. clarus* demonstrates a variation of the multiple receiver hypothesis. In this case, we posit that multiple signals are maintained because signals are evaluated by conspecifics in different contexts. In our case, however, the multiple receivers do not vary in space, but rather in time. A comparative study or meta-analysis examining the diversity in signals and the temporal and/or spatial distribution of receivers may provide insight into the evolution of multiple signals.

Our results provide a unique perspective into the potential costs that males and females encounter during mate guarding. Placed in the context of the life history and reproductive biology of *P. clarus*, our results highlight the ongoing sexual conflict between males and females. Early in the breeding season, cohabitation, as well as the signals and behaviours produced during cohabitation, reduce female receptivity, making male–male competition the dominant selective force and limiting the role of female mate choice. Male mate choice is also thought to be important during this period in the breeding season (Hoefler, 2007). Females may limit the costs in this ‘male-centred’ portion of the breeding season by undergoing near-synchronous maturation, thereby shifting selection to favour female mate choice. This type of interplay between male competition and female mate choice is likely an important aspect in many mating systems (Hunt, Breuker, Sadowski, & Moore, 2009).

Acknowledgments

We thank David Punzalan and Madeline B. Girard for moral and intellectual support. We also thank Aiswaraya Baskaran and Andrade lab undergraduate assistants for assisting in spider maintenance and experiments. In addition, we thank the anonymous referees for their helpful comments. This work was supported by the National Science Foundation (IOS-1021385 to D.O.E.), an Australian Research Council DECRA Fellowship to M.M.K. (DE120100214), a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to A.C.M. and M.C.B.A., and a Canadian Foundation for Innovation (CFI) infrastructure grant to M.C.B.A. We declare no conflicts of interest.

References

- Aisenberg, A., & Costa, F. G. (2005). Females mated without sperm transfer maintain high sexual receptivity in the wolf spider *Schizocosa malitiosa*. *Ethology*, *111*, 545–558.
- Alcock, J. (1994). Post-insemination associations between males and females in insects: the mate-guarding hypothesis. *Annual Review of Entomology*, *39*, 1–21.
- Andersson, M. (1982). Sexual selection, natural-selection and quality advertisement. *Biological Journal of the Linnean Society*, *17*, 375–393.
- Andersson, S., Pryke, S. R., Ornborg, J., Lawes, M. J., & Andersson, M. (2002). Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist*, *160*, 683–691.
- Avila, F. W., Siro, L. K., LaFlamme, B. A., Rubinstein, C. D., & Wolfner, M. F. (2010). Insect seminal fluid proteins: identification and function. *Annual Review of Entomology*, *56*, 21–40.

- Bennett, V. J., Smith, W. P., & Betts, M. G. (2012). Evidence for mate guarding behaviour in the Taylor's checkerspot butterfly. *Journal of Insect Behavior*, 25, 183–196.
- Benton, T. G. (1992). Determinants of male mating success in a scorpion. *Animal Behaviour*, 43, 125–135.
- Benvenuto, C., & Weeks, S. (2011). Mate guarding behaviour in clam shrimp: the influence of mating system on intersexual conflict. *Behavioral Ecology and Sociobiology*, 65, 1899–1907.
- Benvenuto, C., & Weeks, S. C. (2012). Intersexual conflict during mate guarding in an androdioecious crustacean. *Behavioral Ecology*, 23, 218–224.
- Birkhead, T. R., & Møller, A. P. (1998). *Sperm competition and sexual selection*. San Diego, CA: Academic Press.
- Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology & Evolution*, 25, 292–300.
- Calbacho-Rosa, L., Cordoba-Aguilar, A., & Peretti, A. V. (2010). Occurrence and duration of post-copulatory mate guarding in a spider with last sperm precedence. *Behaviour*, 147, 1267–1283.
- Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews*, 78, 575–595.
- Cothran, R. D. (2008). Phenotypic manipulation reveals sexual conflict over precopula duration. *Behavioral Ecology and Sociobiology*, 62, 1409–1416.
- Cothran, R. D., Chapman, K., Stiff, A. R., & Relyea, R. A. (2012). 'Cryptic' direct benefits of mate choice: choosy females experience reduced predation risk while in precopula. *Behavioral Ecology and Sociobiology*, 66, 905–913.
- Davis, E. S. (2002). Female choice and the benefits of mate guarding by male mallards. *Animal Behaviour*, 64, 619–628.
- Dodson, G. N., & Beck, M. W. (1993). Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes*. *Animal Behaviour*, 46, 951–959.
- van Doorn, G. S., & Weissing, F. J. (2004). The evolution of female preferences for multiple indicators of quality. *American Naturalist*, 164, 173–186.
- van Doorn, G. S., & Weissing, F. J. (2006). Sexual conflict and the evolution of female preferences for indicators of male quality. *American Naturalist*, 168, 742–757.
- Edwards, G. B. (2004). Revision of the jumping spiders of the genus *Phidippus* (Araneae: Salticidae). *Occasional Papers of the Florida State Collection of Arthropods*, 11, 1–156.
- Elgar, M. (1992). Sexual cannibalism in spiders and other invertebrates. In M. Elgar, & B. Crespi (Eds.), *Cannibalism: Ecology and evolution among diverse taxa* (pp. 128–155). Oxford, U.K.: Oxford University Press.
- Elias, D. O., Andrade, M. C. B., & Kasumovic, M. M. (2011). Dynamic population structure and the evolution of spider mating systems. *Advances in Insect Physiology*, 41, 65–114.
- Elias, D. O., Botero, C. A., Andrade, M. C. B., Mason, A. C., & Kasumovic, M. M. (2010). High resource valuation fuels 'desperado' fighting tactics in female jumping spiders. *Behavioral Ecology*, 21, 868–875.
- Elias, D. O., & Kasumovic, M. M. (2012). [Vibratory courtship of *Phidippus clarus*]. Unpublished raw data.
- Elias, D. O., Kasumovic, M. M., Punzalan, D., Andrade, M. C. B., & Mason, A. C. (2008). Assessment during aggressive contests between male jumping spiders. *Animal Behaviour*, 76, 901–910.
- Elias, D. O., Sivalinghem, S., Mason, A. C., Andrade, M. C. B., & Kasumovic, M. M. (2010). Vibratory communication in the jumping spider *Phidippus clarus*: substrate-borne courtship signals are important for male mating success. *Ethology*, 116, 990–998.
- Elwood, R. W., & Dick, J. T. A. (1990). The amorous *Gammarus*: the relationship between precopula duration and size-assortative mating in *G. pulex*. *Animal Behaviour*, 39, 828–833.
- Fahey, B. F., & Elgar, M. A. (1997). Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneidae, Araneae). *Behavioral Ecology and Sociobiology*, 40, 127–133.
- Fernandez-Montraveta, C., & Cuadrado, M. (2003). Cohabitation between an adult male and a subadult female in a burrowing wolf spider (Araneae, Lycosidae). *Journal of Arachnology*, 31, 135–138.
- Forster, L. (1982). Visual communication in jumping spiders (Salticidae). In P. N. Witt, & J. S. Rovner (Eds.), *Spider communication: Mechanisms and ecological significance* (pp. 161–212). Princeton, NJ: Princeton University Press.
- Grafen, A., & Ridley, M. (1983). A model of mate guarding. *Journal of Theoretical Biology*, 102, 549–567.
- Guindre-Parker, S., Gilchrist, H. G., Baldo, S., Doucet, S. M., & Love, O. P. (2013). Multiple achromatic plumage ornaments signal to multiple receivers. *Behavioral Ecology*, 24, 672–682.
- Hardling, R., Kokko, H., & Elwood, R. W. (2004). Priority versus brute force: when should males begin guarding resources? *American Naturalist*, 163, 240–252.
- Harts, A. M. F., & Kokko, H. (2013). Understanding promiscuity: when is seeking additional mates better than guarding an already found one? *Evolution*, 67, 2838–2848.
- Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 13390–13395.
- Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, 57, 197–214.
- Hoefler, C. D. (2007). Male mate choice and size-assortative pairing in a jumping spider, *Phidippus clarus*. *Animal Behaviour*, 73, 943–954.
- Hoefler, C. D. (2008). The costs of male courtship and the potential benefits of male choice for large mates in *Phidippus clarus* (Araneae, Salticidae). *Journal of Arachnology*, 36, 210–212.
- Hoefler, C. D., & Jakob, E. M. (2006). Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons. *Animal Behaviour*, 71, 109–116.
- Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of Evolutionary Biology*, 22, 13–26.
- Iwasa, Y., & Pomiankowski, A. (1991). The evolution of costly mate preferences 2: the handicap principle. *Evolution*, 45, 1431–1442.
- Iwasa, Y., & Pomiankowski, A. (1994). The evolution of mate preferences for multiple sexual ornaments. *Evolution*, 48, 853–867.
- Jackson, R. R. (1977). Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Animal Behaviour*, 25, 953–957.
- Jackson, R. R. (1978a). Life-history of *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology*, 6, 1–29.
- Jackson, R. R. (1978b). Mating strategy of *Phidippus johnsoni* (Araneae, Salticidae) 1: pursuit time and persistence. *Behavioral Ecology and Sociobiology*, 4, 123–132.
- Jackson, R. R. (1980). The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology*, 8, 241–249.
- Jackson, R. R. (1986). Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. *Journal of Natural History*, 20, 1193–1210.
- Johnson, J. C. (2005). Cohabitation of juvenile females with mature males promotes sexual cannibalism in fishing spiders. *Behavioral Ecology*, 16, 269–273.
- Johnstone, R. A. (1996). Multiple displays in animal communication: 'backup signals' and 'multiple messages'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 329–338.
- Jormalainen, V. (1998). Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. *Quarterly Review of Biology*, 73, 275–304.
- Jormalainen, V., Tuomi, J., & Yamamura, N. (1994). Intersexual conflict over precopula duration in mate guarding Crustacea. *Behavioural Processes*, 32, 265–283.
- Kasumovic, M. M. (2013). The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype. *Animal Behaviour*, 85, 1049–1059.
- Kasumovic, M. M., Elias, D. O., Punzalan, D., Mason, A. C., & Andrade, M. C. B. (2009). Experience affects the outcome of agonistic contests without affecting the selective advantage of size. *Animal Behaviour*, 77, 1533–1538.
- Kasumovic, M. M., Elias, D. O., Sivalinghem, S., Mason, A. C., & Andrade, M. C. B. (2010). Examination of prior contest experience and the retention of winner and loser effects. *Behavioral Ecology*, 21, 404–409.
- Kasumovic, M. M., Mason, A. C., Andrade, M. C. B., & Elias, D. O. (2011). The relative importance of RHP and resource quality in contests with ownership asymmetries. *Behavioral Ecology*, 22, 39–45.
- Kasumovic, M. M., & Seebacher, F. (2013). The active metabolic rate predicts a male spider's proximity to females and expected fitness. *Biology Letters*, 9, 20121164.
- Kokko, H., & Johnstone, R. A. (2002). Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357, 319–330.
- Land, M. F. (1985). The morphology and optics of spider eyes. In F. G. Barth (Ed.), *Neurobiology of arachnids* (pp. 53–78). Berlin, Germany: Springer-Verlag.
- Land, M. F., & Nilsson, D. E. (2002). *Animal eyes*. Oxford, U.K.: Oxford University Press.
- Miller, G. L., & Miller, P. R. (1986). Pre-courtship cohabitation of mature male and penultimate female *Geolycosa turricola* (Araneae, Lycosidae). *Journal of Arachnology*, 14, 133–134.
- Neff, B. D., & Svensson, E. I. (2013). Polyandry and alternative mating tactics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120045.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, 45, 525–567.
- Parker, G. A. (1974). Courtship persistence and female-guarding as male time investment strategies. *Behaviour*, 48, 157–184.
- Parker, G. A. (1979). Sexual selection and sexual conflict. In M. S. Blum, & N. A. Blum (Eds.), *Sexual selection and reproductive competition in insects* (pp. 123–166). New York, NY: Academic Press.
- Parker, D., & Vahed, K. (2010). The intensity of pre- and post-copulatory mate guarding in relation to spermatophore transfer in the cricket *Gryllus bimaculatus*. *Journal of Ethology*, 28, 245–249.
- Prenter, J., Elwood, R., & Montgomery, W. (2003). Mate guarding, competition and variation in size in male orb-web spiders, *Metellina segmentata*: a field experiment. *Animal Behaviour*, 66, 1053–1058.
- Prokop, P. (2006). Insemination does not affect female mate choice in a nuptial feeding spider. *Italian Journal of Zoology*, 73, 197–201.
- Pruitt, J. N., Burghardt, G. M., & Riechert, S. E. (2012). Non-conceptive sexual behaviour in spiders: a form of play associated with body condition, personality type, and male intrasexual selection. *Ethology*, 118, 33–40.
- Pruitt, J. N., & Riechert, S. E. (2011). Nonconceptive sexual experience diminishes individuals' latency to mate and increases maternal investment. *Animal Behaviour*, 81, 789–794.
- Robinson, M. H. (1982). Courtship and mating behaviour in spiders. *Annual Review of Entomology*, 27, 1–20.
- Rodríguez-Muñoz, R., Bretman, A., & Tregenza, T. (2011). Guarding males protect females from predation in a wild insect. *Current Biology*, 21, 1716–1719.

- Rowe, L. (1994). The costs of mating and mate choice in water striders. *Animal Behaviour*, 48, 1049–1056.
- Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, 58, 921–931.
- Rutledge, J. M., Miller, A., & Uetz, G. W. (2010). Exposure to multiple sensory cues as a juvenile affects adult female mate preferences in wolf spiders. *Animal Behaviour*, 80, 419–426.
- Schluter, D., & Price, T. (1993). Honesty, perception, and population divergence in sexually selected traits. *Proceedings of the Royal Society B: Biological Sciences*, 253, 117–122.
- Schroder, T. (2003). Precopulatory mate guarding and mating behaviour in the rotifer *Epiphanes senta* (Monogononta: Rotifera). *Proceedings of the Royal Society B: Biological Sciences*, 270, 1965–1970.
- Simmons, L. W. (2001). *Sperm competition and its evolutionary consequences in the insects*. Princeton, NJ: Princeton University Press.
- Sivalinghem, S., Kasumovic, M. M., Mason, A. C., Andrade, M. C. B., & Elias, D. O. (2010). Vibratory communication in the jumping spider *Phidippus clarus*: polyandry, male courtship signals, and mating success. *Behavioral Ecology*, 21, 1308–1314.
- Suter, R. B., & Walberer, L. (1989). Enigmatic cohabitation in bowl and doily spiders, *Frontinella pyramitela* (Araneae, Linyphiidae). *Animal Behaviour*, 37, 402–409.
- Uhl, G. (2002). Female genital morphology and sperm priority patterns in spiders (Araneae). In S. Toft, & N. Scharff (Eds.), *European arachnology* (pp. 145–156). Aarhus, Denmark: Aarhus University Press.
- Vitousek, M. N., Mitchell, M. A., Woakes, A. J., Niemack, M. D., & Wikelski, M. (2007). High costs of female choice in a lekking lizard. *PLoS One*, 2, e567.
- Weir, L. K., Grant, J. W. A., & Hutchings, J. A. (2011). The influence of operational sex ratio on the intensity of competition for mates. *American Naturalist*, 177, 167–176.
- Wong, B. B. M., & Jennions, M. D. (2003). Costs influence male mate choice in a freshwater fish. *Proceedings of the Royal Society B: Biological Sciences*, 270(Suppl.), S36–S38.
- Yamamura, N. (1987). A model on correlation between precopulatory guarding and short receptivity to copulation. *Journal of Theoretical Biology*, 127, 171–180.
- Yamamura, N., & Jormalainen, V. (1996). Compromised strategy resolves intersexual conflict over pre-copulatory guarding duration. *Evolutionary Ecology*, 10, 661–680.
- Zahavi, A. (1975). Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, 53, 205–214.
- Zeiss, C., Martens, A., & Rolff, J. (1999). Male mate guarding increases females' predation risk? A case study on tandem oviposition in the damselfly *Coenagrion puella* (Insecta: Odonata). *Canadian Journal of Zoology*, 77, 1013–1016.