

Male courtship effort determines female response to competing rivals in redback spiders

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When males compete with rivals in the presence of females, there may be a trade-off between courtship and competition. We examined responses of female redback spiders, *Latrodectus hasselti*, to courtship from rival males under different competitive contexts. We paired size-matched males with females, and assessed correlates of male mating success. We compared these results to published data between females and single males or size-mismatched rivals. Size-matched males attempted copulation after a brief courtship, a strategy similar to smaller, 'sneaker' males in size-mismatched competitions. We also found context-dependent differences in female remating frequency and premature cannibalism. In size-mismatched and single-male trials, females prematurely cannibalized smaller males and males that mated quickly, but this was not the case when rivals were size-matched. However, in both types of competitive trials, males that mated rapidly paid a fitness cost. The courtship duration of the first male to mate was inversely related to the number of copulations that females accepted from that male's rival. Thus, females use premature cannibalism to reduce the paternity of males that minimize investment in courtship if they are clearly distinguishable from their rivals (mismatched context), but they allow males to continue to compete if they are similar in quality (matched context). In both cases, biases in female remating behaviour favoured males that invested in courtship. We conclude that female reproductive behaviour partly depends on the relative size of competing males, but that male fitness depends heavily on investment in courtship.

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Female mating and fertilization preferences are powerful selective forces shaping male sexual behaviour (Andersson 1994; Eberhard 1996). Traits that are important for intrasexual selection may act either in concert or in opposition to those important for intersexual selection (Qvarnström & Forsgren 1998; Moore & Moore 1999). Some studies suggest that competitive interactions between males reinforce female choice (Berglund et al. 1996; Wiley & Poston 1996), while others suggest that traits that ensure male competitive success are not preferred by females (Moore & Moore 1999; Moore et al. 2001). Because intermale competition can affect female fitness (e.g. Wong & Candolin 2005), females may respond directly to competing males and this can influence male tactics in

unpredictable ways (e.g. Watson 1991; Wong & Candolin 2005; Stoltz et al. 2008). Interactions between intrasexual and intersexual selection can thus be complex (Qvarnström & Forsgren 1998; Moore & Moore 1999), and the net effect of this dynamic on the evolution of male strategies is currently unclear (Berglund et al. 1996; Wiley & Poston 1996; Wong & Candolin 2005).

One way in which male competition can affect female choice is through effects on male courtship and thus on the female's ability to assess potential mates. There are a number of systems in which the presence of a rival can affect the rate and frequency of male courtship (blue chromis, DeBoer 1981; sticklebacks, Ridgeway & McPhail 1987; Rowland 1988; Willmott & Foster 1995; sailfin mollies, Travis & Woodward 1989; damselfish, Barnett & Pankhurst 1996; Pacific blue eye, Wong 2004). Similarly, males may decrease their courtship effort at higher population densities (crickets, Cade & Cade 1992; damselfish, Barnett & Pankhurst 1996; guppies, Jir-otkul 1999; but see: crickets, Sadowski et al. 2002), likely factoring in trade-offs between current and future reproductive opportunities, including costs of competition. Females may also respond to intermale competition; the presence of a rival male can change female response to males in many systems (sticklebacks, Ridgeway & McPhail 1987; kestrels, Palokangas et al. 1992; water striders,

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Lauer et al. 1996). In some species, females benefit from inciting male competition, and thus, use competition as an indirect mechanism to select a dominant male partner (Cox & Le Boeuf 1977; Thornhill 1988; Montgomerie & Thornhill 1989; Watson 1991; Oda & Masataka 1995; Semple 1998; Berglund & Rosenqvist 2001). However, competition may also be detrimental to females if it attracts the attention of predators (e.g. guppies: Jakobsson et al. 1995; Kelly & Godin 2001), results in injury to the female (e.g. dung flies, Parker 1970), or if it prolongs the precopulatory period and decreases time available for foraging, oviposition, or other fitness-enhancing activities. In addition, the traits that increase male competitiveness may not be favoured by females (Moore & Moore 1999; Moore et al. 2001). Whether females are able to influence male competitive tactics under these circumstances will depend on the extent to which females are able to restrict the copulatory or fertilization success of undesirable males (even if these are the males that are victorious in competition).

Female responses to male strategies may have particularly large effects in species where females are predacious, possess weaponry, are physically dominant to males, or where cryptic choice occurs. In such systems, females can impose reproductive costs on males engaging in behaviours that reduce female success. For example, female spiders are predacious and often larger than males (Foelix 1996), and several studies suggest that responses of female spiders to male tactics can have significant effects on male fitness (jewel spider, Elgar & Bathgate 1996; golden orb-weaver, Schneider et al. 2000; redback spider: Snow & Andrade 2005; Stoltz et al. 2008).

In this study, we examined the response of females to male competitive strategies in the Australian redback spider, *Latrodectus hasselti*. Redback females are physically dominant to males, which are only 1–2% of the female's body weight (Andrade 1996), and males are therefore unable to force females to copulate. Redback males are often in competition with numerous rivals (Andrade 1996), and this competition occurs only on a female's web. Previous work shows that male competitive tactics, and female responses to those tactics, depend on the relative size of rivals (Stoltz et al. 2008). When pairs of size-mismatched males compete for females, smaller males rush to copulate with females whereas larger males court for the longer durations more typical of single males courting females (4–5 h; Forster 1995; Stoltz et al. 2008). However, brief courtship is costly, as females kill rapidly mating males before normal copulation is complete (Stoltz et al. 2008), and this reduces paternity under sperm competition (Snow & Andrade 2005; Snow et al. 2006). Analysis of competitions between size-mismatched males supports the idea that both courtship duration and male size influence the decision of females to kill a male before the completion of copulation (increased risk to small, brief-courting males, Stoltz et al. 2008). Thus, female behaviour ensures that males adopting the 'rapid mating' tactic suffer fitness costs and that long-courting males are more successful.

Here, we examined the response of female redback spiders to male mating strategies when rival males were size-matched. Since size-matched rivals are likely to have similar resource holding potential (RHP; e.g. Hammerstein & Parker 1982; Enquist & Leimar 1983; Leimar & Enquist 1984), this allowed us to examine behavioural responses of females independently of major competitive differences between males. We examined female behaviours that might affect male fitness as a function of male competitive or courtship behaviours. To help understand the interplay between competitive tactics and female response, we compared data from this study to previously published data on female response to courtship by (noncompeting) single males and pairs of competing size-mismatched males (Stoltz et al. 2008). These comparisons allow a focus on how female behaviours may change in response to variation in the competitive context (i.e. presence or absence of competition, differences in size and tactics of competing males).

METHODS

Mating Behaviour

In the absence of rivals, male redback spiders typically spend several hours ($\bar{X} \pm \text{SE} = 5.03 \pm 0.84$ h) courting a female prior to copulation (Forster 1995). Courtship by single males involves long periods of vibratory signalling on the web. Males then begin a period of movement on and off the female's abdomen, during which vibrational signalling continues, and finally, copulation is attempted while the male is mounted on the female's ventral surface (Forster 1995; Stoltz et al. 2008). Although females are largely quiescent during courtship (Forster 1992, 1995), they sometimes use their forelegs to strike courting males (Andrade 1996). Strikes can knock males off the web, often result in the cessation of courtship, and have been interpreted as rejection behaviour (Andrade 1996).

During copulation, females rest with their ventral surface facing upwards. Males mount females, insert one of their two, paired copulatory organs (palps), then perform a copulatory somersault that positions their abdomen directly above the female's fangs (see Forster 1992, 1995). Males are often injured by cannibalistic females while in this posture, but frequently survive this first copulation and return to the web to court again before attempting a second copulation with their second palp (Andrade 1998; Andrade et al. 2005). Female redback spiders have corresponding, paired, independent sperm storage organs, each of which is inseminated by one of the male's palps (Snow & Andrade 2005).

Females sometimes kill males during their first copulation (=premature fatal cannibalism; males killed by the female after the first copulation and wrapped in silk; Forster 1992; Stoltz et al. 2008). Premature fatal cannibalism caps male paternity at approximately 50% under sperm competition since sperm from the two spermathecae mix at fertilization (Snow & Andrade 2005). In contrast, if a male inseminates each spermatheca his paternity will be approximately 90% compared to any rival mates (Snow & Andrade 2005; Snow et al. 2006).

Study Animals

The spiders used in this study were from an outbred laboratory population of *L. hasselti* originally collected from Perth, Western Australia (1999, 2000) and New South Wales, Australia (2002). Spiderlings were reared communally in a temperature-controlled room at 25 °C on a 12:12 h light:dark cycle. Spiderlings were transferred to individual cages at the fourth instar to ensure that they had not mated (males mature at the fifth instar, females at the seventh or eighth instar). Males were fed fruit flies (*Drosophila* sp.) twice per week and females were fed crickets (*Acheta domesticus*) once per week. Since *L. hasselti* are nocturnal, all mating trials were conducted under the dark cycle illuminated by red light.

Mating Trials

Females that had matured within 2 months of the trial date were placed in mating arenas (35 × 30 × 15 cm) for 24 h and allowed to build webs on wooden frames before the introduction of males for the competitive mating trials. Trials were filmed for 8 h, or until both males died, using Panasonic low-light black and white cameras with macro zoom lenses and Sony Professional Super VHS recorders. Male spiders were weighed (Ohaus Explorer electronic balance) and marked with a small spot of nontoxic paint (BioQuip Products, Inc., Rancho Dominguez, CA, U.S.A.) 24 h before each trial. We randomly chose unrelated males of similar weight (mean weight difference = 0.2 mg, 4.9% of average body weight of 229 males collected in the field; see Figure 1A in Stoltz et al. 2008) from

among all males of appropriate size that matured within the previous 14 days. Trial males weighed 1.7–5.9 mg. We randomly chose one male from each pair and introduced him to the web from a dragline at the furthest point from the female. We introduced the second, size-matched male approximately 10 s later on the opposite side of the web, also as far as possible from the female. Each spider was used in only one trial. Recordings were analysed using Observer Video Pro Version 3.0 (Noldus Information Technology, Wageningen, The Netherlands).

To determine whether male or female mating behaviour was affected by competitive context, we compared behaviour of spiders in these size-matched competition trials with data from previously published, but concurrently run, competitive trials with size-mismatched rival males ($N = 51$; Stoltz et al. 2008) and noncompetitive, single-male mating trials ($N = 27$; Stoltz et al. 2008). Size-mismatch trials were run as described above except that the mean weight difference of males was 2.6 mg (64% of average body weight of 229 males collected in the field; see Figure 1A in Stoltz et al. 2008). Size-mismatched males weighed 1.4–8.8 mg (see Stoltz et al. 2008). Single-male (noncompetitive) trials were run as described except that only one male was introduced to each virgin female's web. Results of size-mismatched and single-male trials are described in Stoltz et al. (2008), but data are reproduced here for statistical comparison to results from the size-matched trials. We broadly compare mating success, agonistic interactions and female receptivity in matched matings and in mismatched and noncompetitive matings, then focus on predictors of mating success in the new matched-competition trials.

Courtship progress and mating success

In all trials we recorded (1) the time at which contact was first made with the female's abdomen (by either male) and (2) the latency to the first copulation (by either male = precopulatory courtship duration), as this was negatively correlated with female aggressive behaviour and male mating success in single and mismatched-competition trials (Stoltz et al. 2008). In competitive trials (matched and mismatched), we also recorded mating patterns (whether the female mated with one male or both males, or remained unmated).

Within size-matched competition trials we recorded three variables that might predict which male obtained the first copulation: (1) which male made first abdomen contact, (2) the number of precopulatory visits by each male to the female abdomen and (3) the time that each male was mounted on the female before the first copulation. We recorded the total number of copulations obtained by each male because this can affect paternity (Snow & Andrade 2005).

Agonistic interactions and female receptivity

We scored two types of agonistic interactions between males, referred to as chases and scrambles. Chases occurred when both males were on the web and one male made a rapid lunge towards the other male, which retreated to the opposite side of the web. The loser of a chase was the male that retreated from the lunge. Scrambles occurred when both males were on the female's abdomen and both males made rapid, erratic movements. The loser of a scramble was the male that left the female's abdomen and retreated to the web. If both males remained on the female's abdomen when the males' movements ceased, both were scored as winners since both remained in close proximity to the female's copulatory openings (Stoltz et al. 2008). Within matched-competition trials we tested whether male success in agonistic interactions predicted mating success.

Female receptivity was measured through the occurrence of strikes at the males and the occurrence of premature fatal cannibalism. We tested whether the number of strikes by females was

related to (1) the time that the first abdomen contact was made, (2) the time of first insertion, or (3) the number of agonistic interactions between males. In addition, to determine whether females lethally punish short-courting males in size-matched competition trials (as they do in size-mismatched and single-male trials, Stoltz et al. 2008), we examined whether courtship duration predicted premature cannibalism.

Analysis

Statistical analysis was performed using SPSS version 13.0 (SPSS, Chicago, IL, U.S.A.). Data that violated the assumption of a normal distribution were log transformed. If the log-transformed data did not produce a normal distribution, nonparametric statistics were used. Statistical tests were two tailed with mean \pm SE reported. Sample sizes varied for some tests because not all observations for each trial were recorded.

RESULTS

Competitive Behaviour

We found no significant difference in the number of chases between matched (0.009 ± 0.002 per min) and mismatched trials (0.013 ± 0.003 per min; Mann–Whitney U test: $U = 834$, $N_1 = 33$, $N_2 = 51$, $P = 0.94$). In contrast, size-matched males engaged in almost twice as many scrambles (0.013 ± 0.003 per min) as size-mismatched rivals (0.008 ± 0.002 per min; Mann–Whitney U test: $U = 557$, $N_1 = 33$, $N_2 = 51$, $P < 0.05$). There was no fatal fighting in size-matched competitions, and the few injuries that occurred were inflicted by males while their rivals were in copula. Injuries typically involved one male biting or pulling the leg of the male that was copulating, and occasionally resulted in leg autotomy, but was too infrequent for meaningful analysis.

Contextual Variation in Mating Behaviour

Males in the noncompetitive (single-male) trials courted for more than 2 h before first contact with the female, whereas when males were competing (matched and mismatched), the female was typically first contacted (by either male) within 1 h (Kruskal–Wallis test: $H_3 = 51.82$, $P < 0.001$; Table 1). The latency to the female's first copulation (with either male) was briefest and similar for size-matched males and smaller males that mated first in mismatched trials, whereas the latency to the female's first copulation was significantly longer when the first-mating male was a larger mismatched male and longest for single males (Kruskal–Wallis test: $H_3 = 76.68$, $P < 0.001$; Table 1).

We asked whether females discriminated against male competitive behaviour by examining female strike behaviour. In the combined data set, strikes by females towards males were more common overall in competitive trials than in noncompetitive trials

Table 1

Mean \pm SE time until first contact with the female's abdomen and time to the female's first copulation when male redback spiders, *Latrodectus hasselti*, were under competitive or noncompetitive contexts

Time (min)	Competitive context			Noncompetitive*
	Mismatched*		Matched	
	Larger male first	Smaller male first		
First abdomen contact†	24.3 \pm 10.86	39.42 \pm 14.5	15.27 \pm 2.45	143.8 \pm 11.86
Female's first copulation†	207.94 \pm 25.56	47.28 \pm 9.2	83.03 \pm 10.72	262.44 \pm 11.27

* As reported in Stoltz et al. (2008).

† Mean latency for the first male only in each trial.

(Kruskal–Wallis test: $H_2 = 33.44$, $P < 0.001$; Fig. 1). In size-mismatched trials, female strikes increased with the number of scrambles (Stoltz et al. 2008), but strike behaviour was not related to the number of competitive interactions in matched trials (Spearman rank correlation: scrambles: $r_s = 0.064$, $N = 24$, $P = 0.765$; chases: $r_s = 0.203$, $N = 22$, $P = 0.365$), although scrambles were far more common overall in these trials (see above).

Another potential means of discrimination by females is premature cannibalism, which we investigated with a logistic regression with premature cannibalism as the dependent variable, courtship duration and the form of competition (none, matched or mismatched) as the independent variables and male size as a covariate. Male size had no effect on cannibalism, but there was a significant interaction between the form of competition and latency to the first copulation (Wald test: $W_1 = 3.83$, $P = 0.050$; Fig. 2). The interaction was due to the lack of an effect on premature cannibalism for size-matched males (Wald test: $W_1 = 0.84$, $P = 0.772$; Fig. 2) in contrast to the other groups (Stoltz et al. 2008). This result could have arisen if most matched trials had short latencies to copulation and a high rate of premature cannibalism, but this was not the case. The rate of premature cannibalism varied with competitive context (chi-square test: $\chi^2_2 = 10.3$, $P = 0.006$) and was intermediate in matched-male trials (35%, $N = 23$) relative to mismatched (52%, $N = 27$) and single-male trials (11%, $N = 27$).

Although premature cannibalism of the first male to mate was more common when precopulatory latency was short in mismatched and single-mating trials (Stoltz et al. 2008), it was unclear what triggered premature cannibalism in matched trials. There was no significant relationship between the likelihood of premature lethal cannibalism after the first mating and (1) the time that first abdomen contact was made (Wald test: $W_1 = 0.22$, $P = 0.64$), (2) the number of scrambles ($W_1 = 0.10$, $P = 0.75$) or (3) the number of chases/lunges ($W_1 = 2.24$, $P = 0.13$).

We asked whether female remating behaviour varied with context. In single-male trials, most females allowed the male to achieve two copulations (also see Andrade 1998), whereas in the majority of competitive trials (matched and mismatched), the first-mating male achieved only one copulation despite repeated attempts to approach and mount the female (chi-square test: $\chi^2_2 = 20.90$, $P < 0.001$; Table 2), and in about half of the competitive trials, the female was polyandrous (Table 2).

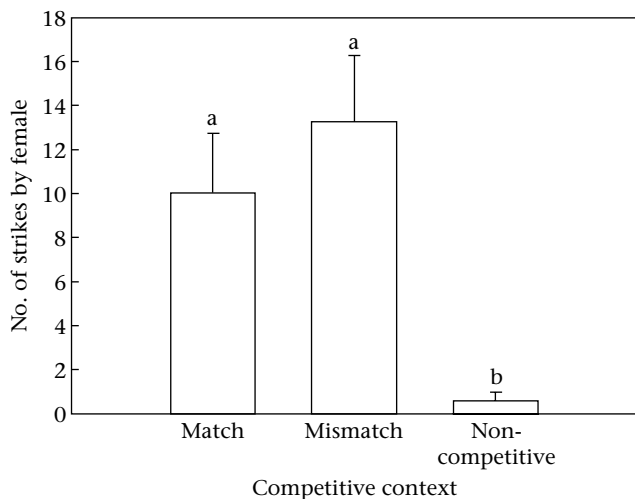


Figure 1. Mean + SE number of strikes by females at male redback spiders, *Latrodectus hasselti*, in noncompetitive and competitive trials (match = size-matched rival males; mismatch = size-mismatched rival males, noncompetitive = no rival). Different letters above bars denote a significant difference between the mean number of strikes (one-way ANOVA, Tukey HSD post hoc test: $P < 0.05$).

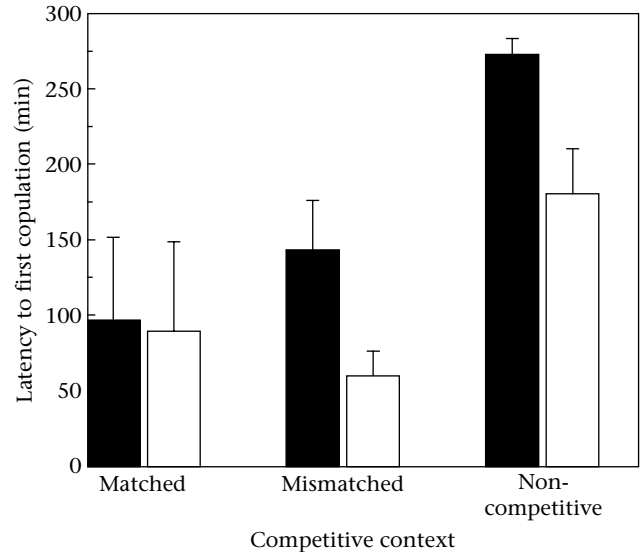


Figure 2. Mean + SE latency to the female's first copulation for matings in which the male survived the first copulation (■) and those in which the female fatally cannibalized the male after one palp insertion (=premature cannibalism, □) as a function of context (match = size-matched rival males; mismatch = size-mismatched rival males, noncompetitive = no rival).

We examined whether latency to the first copulation explained variation in the number of copulations achieved by the first male to mate, or the number of copulations achieved by the rival, second-mating males in competitive trials. For each analysis, we used a multinomial logistic regression model with number of copulations (of first or second male) as the dependent variable, competitive context as the independent factor, precopulatory latency as the covariate, and a context*latency interaction term. For the number of copulations achieved by the first male to mate (model likelihood ratio: $\chi^2_3 = 11.949$, $P = 0.008$), there was a significant interaction between competitive context and latency to copulation (likelihood ratio: $\chi^2_1 = 5.365$, $P = 0.021$). This interaction arose because there was a positive relationship between latency and the number of matings achieved for first-mating mismatched males (Wald test: $W_1 = 8.101$, $P = 0.004$), but not for first-mating matched males (Wald test: $W_1 = 0.655$, $P = 0.418$; Fig. 3a). However, latency to the first copulation affected the mating success of the rival male (the male that did not mate first) in both types of competitive trials (model likelihood ratio: $\chi^2_4 = 20.54$, $P < 0.001$). The rival male achieved more copulations when precopulatory latency of the first-mating male was lower in both matched and mismatched competitions (likelihood ratio: $\chi^2_2 = 17.414$, $P < 0.001$; Fig. 3b). This analysis excludes a single case where a second male achieved three copulations (in size-mismatched trials). We exclude this datum since three copulations would not increase sperm transfer in

Table 2

Female mating decisions and the number of matings that the first male to mate achieved in competitive and noncompetitive matings

	Number of male mates				Total matings achieved by the female's first mate (and her only mate in noncompetitive trials)		
	0	1	2	N	1	2	N
Matched	6%	43%	51%	35	71%	29%	33
Mismatched	14%	39%	47%	51	61%	39%	44
Noncompetitive	—	100%	—	—	15%	85%	27

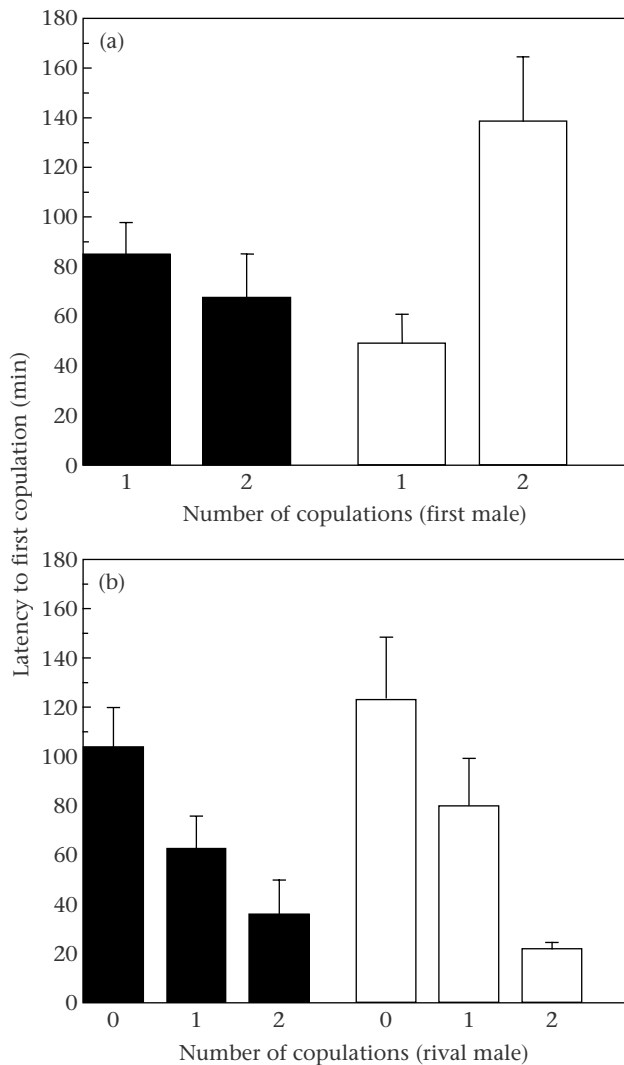


Figure 3. Mean \pm SE latency to the female's first copulation (i.e. courtship duration of the first male to mate) and (a) number of copulations achieved by the first male to mate and (b) number of copulations achieved by the rival male (male that did not mate first) in competitive trials with size-matched (■) and size-mismatched males (□).

redback spiders (Andrade & Banta 2002), and inclusion makes the statistical model unreliable. Latency to the first copulation in this single case was 47.38 min, which is consistent with the pattern in the rest of the data (Fig. 3b).

Predictors of Mating Success

For size-matched rivals, we sought variables that might predict which male achieved the first mating. There were no predictors of male mating success in courtship progress or female aggressive behaviour. We found no significant relation between female strikes and (1) time that first abdomen contact was made (Spearman rank correlation: $r_s = 0.066$, $N = 24$, $P = 0.761$) or (2) latency to copulation ($r_s = 0.278$, $N = 24$, $P = 0.189$). Similarly, matched males that obtained the first copulation were neither those that had made first abdominal contact with the female, nor those that had made more visits to the female abdomen or spent more time mounted on the female (all $P > 0.1$; Table 3). Agonistic interactions were also unrelated to mating success. Males that achieved the first mating were not those that had won more chases or scrambles (Table 3).

DISCUSSION

Here we confirm that competitive contexts affect male and female mating behaviour in redback spiders (also see Stoltz et al. 2008), and we show that courtship behaviour of one male can affect the mating success of his later-mating rival by altering female receptivity to future mating attempts. Although sole-courting male redback spiders typically copulate twice, females restrict most competing males to a single copulation when they mate first, regardless of the relative size of the male's rival (Table 2). The mating success of competing males, mediated by female receptivity (this study) or premature cannibalism (Stoltz et al. 2008), depends not only on their own precopulatory courtship, but also on the courtship behaviour of their rival, as we show here (Fig. 3b).

Male mating behaviour also changed with context, suggesting that males assess the presence and relative size of their rivals. If males are smaller than their rivals (Stoltz et al. 2008) or similar in size (this study), courtship is abbreviated or nonexistent, and males attempt to rapidly mount and copulate with females (Table 1). In contrast, if males court females in the absence of a rival, or if males are larger than their rival, courtship is prolonged (Table 1; Stoltz et al. 2008). This suggests that males may be assessing the quality of their rivals (mutual assessment) as opposed to assessing their own quality (self- and cumulative assessment) (Payne 1998; Taylor & Elwood 2003). The majority of empirical studies of contests between males have shown that self- and cumulative assessment mechanisms are common (Taylor & Elwood 2003; Prenter et al. 2006; Elias et al. 2008). Contests in redbacks differ from those in these other systems in that males are only likely to face rivals in one competitive bout. In this case, one would predict that mutual assessment would be favoured as a way to adjust male mating behaviour. Future studies will look at this possibility.

The response of female redbacks to abbreviated courtship (i.e. a 'sneaker' or 'scramble' tactic) from competing males is context dependent. While premature cannibalism apparently functions as a 'punishment' for abbreviated courtship when lone males court, or when rival males are mismatched in size (Stoltz et al. 2008), this was not the case when competing males were matched for size. When rivals were similar in size, there was a decrease in premature cannibalism overall, and no relationship with intermale aggression or precopulatory courtship duration. The first male to mate could thus continue to compete with his rival for subsequent copulations. In contrast, when competitors were size-mismatched, the female killed the first-mating male in more than half of trials; thus, competition over mating often ceased after the first copulation. Although the first-mating male was more frequently alive and able to compete in size-matched contests, if the first copulation occurred rapidly, that male usually achieved fewer matings than his rival (Fig. 3b), despite continuous attempts by both males to mate. It is possible that decreased courtship reflects competitive inferiority of males that are thus less likely to win in direct competition for the female. However, we found no evidence for this in our data. Moreover, competitive inferiority could not explain the higher relative success of second males in the size-mismatched trials (Fig. 3), where the first male was often dead when the second male mated. Thus, the increased success of second males probably reflects a female bias against short-courting first mates. Together with previous results (Stoltz et al. 2008), this study supports the idea that courtship duration, mediated by context-dependent variation in females' response to the courting males, is a strong determinant of male mating success in redback spiders.

When rivals were size-matched, redback males courted for only brief periods before the first copulation, adopting a similar tactic to smaller 'sneaker' males in size-mismatched trials. Whereas females prematurely cannibalized these brief-courting 'sneaker' males when rivals were size-mismatched (Snow & Andrade 2005; Snow

Table 3Comparison of male redback spiders, *Latrodectus hasselti*, that achieved and that did not achieve the first copulation in matched-size competitive trials

	Achieved first copulation	Did not achieve first copulation	Statistic	P
Achieved first abdominal contact	53% (N=8)	47% (N=7)	Pearson $\chi^2=0.427$	P=0.513
Did not achieve first abdominal contact	35% (N=6)	65% (N=11)		
Visits to abdomen	10.82±2.21 visits	14.79±3.79 visits	Paired $t_{34}=0.459$	P=0.694
Time mounted	40.95±6.86 min	54.43±12.44 min	Paired $t_{24}=-0.866$	P=0.395
Scrambles won	3.59±1.19 scrambles	2.65±0.87 scrambles	Wilcoxon Z=-1.035 (N=64)	P=0.301
Chases won	1.88±0.51 chases	2.63±0.80 chases	Wilcoxon Z=-0.435 (N=60)	P=0.664
Achieved 1 copulation	70% (N=33)	44% (N=33)	Fisher's exact test	P=0.50
Achieved 2 copulations	30% (N=32)	10% (N=32)		

et al. 2006), there was no evidence that females prematurely cannibalized size-matched rivals that provided similarly brief courtship. Although this result could simply reflect insufficient power in our design for size-matched trials, our sample sizes were similar to those used in size-mismatched trials where a strong effect was found (Stoltz et al. 2008). The existence of a link between courtship duration and premature cannibalism in mismatched but not matched trials could suggest that females discriminate against small males (which most frequently mated first in size-mismatched trials), rather than against brief courtship. This is unlikely because the size distribution of relatively smaller males in the previous study (range 1.4–4.9 mg, Stoltz et al. 2008) was very similar to that of the matched males used in this experiment (range 1.7–5.9 mg). Thus, the data suggest that females may be less likely to kill males that mate rapidly if they detect the presence of a similarly sized rival rather than a larger rival. Moreover, although premature cannibalism was not linked to courtship duration in this study, courtship duration of the first-mating male did predict the mating success of his rival. Mating access is apparently controlled by females in this size-dimorphic species (Andrade 1996), and the number of matings achieved by each male can have strong effects on paternity (Snow & Andrade 2005). Thus, the available evidence strongly suggests that the female's response to competing males varies as a function of the relative size of rivals and their investment in courtship. Variation in female responses to males (premature cannibalism and/or remating behaviour) will strongly affect male fitness, and thus could impose selection on male mating behaviour.

Understanding the mating strategy of female redback spiders is integral to predicting the strategies of males (Stoltz et al. 2008). However, several aspects of females' strategies are unclear: such as, why would female discrimination focus on courtship duration of competing males, and why does the effect of courtship on the female's strategy vary with the relative size of competitors? In species like redbacks, where males provide no parental care and consumption of the male apparently does not affect female reproductive output (Andrade 1996; also see Fromhage et al. 2003), female preferences should focus on heritable traits of males that are likely to increase offspring fitness (Andersson 1994). Elaborate courtship is thought to provide the opportunity to evaluate a potential partner, and may provide information about endurance and vigour of courting males (Bastock 1967; Andersson 1994). Prolonged courtship, in particular, may serve as an endurance test for courting males, particularly in species such as redbacks where males rarely eat as adults and thus have limited energy reserves. Preference for prolonged courtship may ensure higher paternity for males that survive an arduous mate search period (Andrade 2003) with energy reserves sufficient to maintain hours of activity. Such males may be those that have high energy reserves at maturity (reflecting successful foraging during juvenile instars) and/or are able to find females rapidly.

If this is the case, why would female response to variation in courtship duration depend on the relative weight of rival males? Male weight could be a proxy for condition, which reflects both juvenile resource acquisition and adult energy expenditure during mate search for redbacks. Larger males are favoured by females in a number of species (reviews: birds: Nowicki et al. 1998; Ohlsson et al. 2002; Naguib et al. 2008; crickets: Scheuber et al. 2003; scorpionflies: Engels & Sauer 2007). If brief courtship and small size suggest a poor-quality male, females may allow the first copulation from a relatively small male (Stoltz et al. 2008) to ensure sperm stores, or perhaps for genetic benefits (such as bet hedging, genetic diversity of offspring, or as part of a 'trading up' strategy; Watson 1991, 1998; Pitcher et al. 2003; reviewed in Jennions & Petrie 2000). If females can easily distinguish these males from their longer-courting, larger rivals, premature cannibalism may increase female fitness by biasing paternity to the superior male (Snow & Andrade 2005). In contrast, when weight differences of rivals are small and males scramble to attempt mating on the same timescale (these trials), females may not be able to resolve differences between males. Under these circumstances, it may be better to allow males to continue to compete, but to adjust mating frequency relative to courtship effort of the first male, as we found here. Ongoing work will examine benefits of multiple mating for females and the relative importance of male weight and courtship in female mating decisions.

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