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ORIGINAL PAPER

Females reward courtship by competing males in a cannibalistic spider

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Abstract Despite widespread recognition that intersexual interactions shape reproductive strategies, studies of male competition do not typically include effects imposed by females. In cannibalistic redback spiders, escalated fighting between rival suitors is predicted, as males are unlikely to mate with more than one female, and strong first-male sperm precedence favours mating with virgins. In staged competitions for matings between size mismatched rivals, smaller males adopted an alternative sneaking strategy. However, despite initial agonistic interactions, larger males did not pursue or incapacitate smaller males. When inter-male competition occurred, females struck at males frequently, although strikes were rarely seen when males courted in the absence of a rival. After minimal fighting, larger males engaged in significant courtship (3 h) rather than killing inferior rivals. Prolonged courtship was favoured by female behaviour, as males that attempted rapid copulation (smaller, sneaking males) were cannibalised before mating was completed. This premature cannibalism significantly decreases paternity in redback spiders. Thus, significant features of male competitive behaviour (i.e. prolonged courtship by larger males) may be predicted with consideration of the female's response to male reproductive strategies. Although the effect of females may be more subtle in systems without the extreme reversed size-dimorphism of redbacks, these results suggest that female interests should be explicitly considered when studying inter-male interactions.

Keywords Female choice · Male competition · Courtship · Cannibalism

Introduction

Males often compete for access to females, and the resolution of these competitions has a significant effect on male fitness (Trivers 1972; Emlen and Oring 1977; reviewed in Andersson 1994). Contests usually take the form of ritualised displays which are used by males to assess the fighting ability or resource holding potential (RHP) of their opponent (Parker 1974; Maynard Smith 1974, 1976; Parker and Rubenstein 1981; Enquist et al. 1990). If rivals have similar RHP, or the value of the contested resource (often females) is sufficiently high, competitions may escalate beyond displays to fights in which rivals may be injured or killed (Austad 1983; Enquist and Leimar 1990). Models of fight escalation focus on RHP and resource value, but do not explicitly include possible effects of female strategies on inter-male dynamics (e.g. hawk-dove game, war of attrition, 'risk right' models). In general, the interaction of female choice and competition and the effect of females on control and initiation of competitive interactions between males are poorly understood (reviewed in Wong and Candolin 2005, but see Watson 1990; Herberstein et al. 2002; Andrade et al. 2005).

Fatal fighting is more likely when fighting is the only way to secure a contested resource and male residual reproductive value is low (Fromhage and Schneider 2005). However, as larger males typically have higher RHP and win most contests (reviewed in Archer 1988, examples in Andersson

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1994, pp 132–142), smaller males may adopt alternative tactics that avoid combat or bypass female choice (e.g. Wong and Candolin 2005). For example, in some insects, fishes, birds and mammals, larger males guard nests or reproductive females, whilst smaller males (sneakers) attempt to surreptitiously mate females without the investment or risk involved in guarding (Gross and Charnov 1980; Dunbar et al. 1990; Sandell and Liberg 1992; Taborsky 1994; Emlen 1997; Thirgood et al. 1999; Davis 2002). Males who assess themselves to be inferior to their rival and likely to die without mating in an escalated contest may be particularly likely to attempt alternative mating tactics (Jenssen et al. 2005).

Although effects of females on inter-male competition are rarely considered explicitly (reviewed in Wong and Candolin 2005, but see Watson 1990), female mating and fertilisation patterns will ultimately determine the fitness payoff for different competitive strategies (including sneaking behaviour: Van den Berghe et al. 1989; Alonzo and Warner 2000, Smith and Reichard 2005). Interestingly, in some species, females actively instigate competition between males, thereby facilitating indirect mate choice (Watson 1990; Wong and Candolin 2005). However, females might also seek to minimise inter-male competition if it is costly due to the risk of female injury (Thornhill and Alcock 1983; Herberstein et al. 2002) or if traits that maximise male competitive success are not favoured by females (e.g. Moore and Moore 1999; Candolin 2004; Wong 2004a, b). The extent to which females modify male competitive strategies may be difficult to measure when competitively superior males are also physically dominant to females and, thus, able to impose costs if females refuse to mate.

Unique opportunities to examine dynamics of male competitive behaviour under the influence of females arise in species where female-biased size dimorphism confers a relatively high level of female control over interactions and where monogyny ensures each copulation is very valuable for males (e.g. Vollrath 1998, Fromhage et al. 2005, see Table 1 in Andrade and Kasumovic 2005). For example, in redback spiders (*Latrodectus hasselti*), fatal fighting should be predicted for males, as they typically achieve only one mating opportunity in their lifetime, resulting in a residual reproductive value close to zero (the mortality rate during mate searching is more than 80%, Andrade 2003). Competition is expected to be particularly intense because strong first-male sperm precedence increases the importance of mating with virgin females (Snow and Andrade 2005), and several males are typically found on webs of single females simultaneously in nature (Andrade 1996). Females might modulate the occurrence of inter-male competition because behaviours necessary for aggressive inter-male competition may be incompatible with typical courtship (e.g. Wong 2004b) or may truncate courtship (Elgar and Bathgate 1996). Physically dominant redback females may significantly constrain coercive male behaviour, as males are only 1–2% the body weight of females (Andrade 1996) and females could impose significant paternity costs on males through the timing of lethal cannibalism (Snow and Andrade 2005).

In this study, we examined the dynamics of inter-male competition and how female behaviour could affect fitness payoffs for male competitive strategies. We staged competitions between rivals with a considerable weight mismatch and compared female behaviour, male behaviour and mating success to matings in which we presented single males to females. We examined whether female response to males depended on context (single-mating males vs competing males), and whether females could impose selection on male competitive behaviour through pre-mating aggression (females use their forelegs to strike at males, Andrade 1996) or the timing of cannibalism (e.g. Snow and Andrade 2005, Snow et al. 2006).

Finally, we were particularly interested in testing two predictions derived from competition theory. First, we predicted that males with relatively low RHP would adopt alternative mating strategies (e.g. Gross and Charnov 1980; Dunbar et al. 1990; Sandell and Liberg 1992; Taborsky 1994; Emlen 1997; Thirgood et al. 1999; Davis 2002; Jenssen et al. 2005; Wong and Candolin 2005). Unlike other systems where males pursuing alternative strategies can retreat from aggressors, in redbacks, all males are confined to the female's web and are unlikely to find other mates if they leave (Andrade 2003). Thus, we also predicted that males with higher RHP would frequently challenge rivals and rapidly escalate interactions until they killed or incapacitated the competitively inferior male (fatal fighting).

Materials and methods

Redback mating

Male redback spiders have paired copulatory organs, each of which inseminates one of the female's paired, independent sperm storage organs during a separate copulation (Snow and Andrade 2005). During copulation, males position themselves above females' fangs by performing a "somersault" (Forster 1992). Male reproductive success depends on mating order, the number of copulations achieved and the timing of cannibalism by females (Snow and Andrade 2005). Cannibalism may include partial or complete consumption of the male, and males may survive the former. To distinguish the types of cannibalism, here, we define *fatal cannibalism* as instances where the male is killed by the female, typically after being wrapped in silk. Fatal cannibalism increases male paternity if it occurs during and after the second copulation (Andrade 1996). However, this must be distinguished from *premature fatal cannibalism* where males are killed after one (rather than two) copulations (Andrade 1996, 1998). Premature fatal cannibalism caps male paternity at about 50% because sperm from the two spermathecae mix at fertilisation (Snow and Andrade 2005). In contrast, if a male is the first to inseminate each spermatheca, he deposits a cuticular sperm plug in each spermatheca and can expect about 89% paternity (Snow and Andrade 2005; Snow et al. 2006).

Typically, a successful single-male mating sequence begins with males engaging in extensive web-based vibratory courtship and web-reduction (Watson 1986) with no direct female contact (stage one; Forster 1992, 1995). The second stage of courtship begins after males first contact the female's legs or abdomen and includes movements on the female's abdomen and on the web. While on the abdomen, males vibrate and move erratically, they then climb back onto the web and continue vibratory courtship movements (see Forster 1995 for details). Some males copulate with the female during this stage. Most males, however, enter a third stage of courtship, during which they largely cease moving on the web and remain on the female's abdomen for long periods. The first copulation typically occurs during this stage, 5.03±0.84 h after the start of courtship, when males insert one of their two copulatory organs into one of the female's two copulatory openings (Forster 1995).

Study animals

Spiders were from an outbred laboratory population of *L. hasselti*, established from field collected individuals from Perth, Western Australia (1999, 2000) and New South Wales, Australia (2002). Spiders were shipped to the University of Toronto Scarborough and reared in a temperature-controlled room at 25°C (12:12 h light cycle). Spiderlings were reared communally with siblings until the fourth instar then separated into individual cages to ensure they were virgins (males mature at the 5th instar, females at the seventh–eighth instar). All spiderlings and males were fed *Drosophila* sp. twice per week, and females were fed house crickets (*Acheta domesticus*) once per week until maturity. Because redbacks are nocturnal, trials were carried out during the dark cycle under red lights.

Mating trials

Females that had become sexually mature within 2 months before the trial were placed in arenas (35 × 30 × 15 cm) for 24 h to construct webs on wooden frames and were randomly assigned to one of two mating treatments: single-male (n=27) or competing size-mismatched males (n=51, male weight difference >1.9 mg, Fig. 1). Weight of laboratory-reared males used in the experiment was not significantly different from 229 field-collected males from Perth, Western Australia (t_{42}=−0.43, p=0.67, Fig. 1). In the field, it is common to

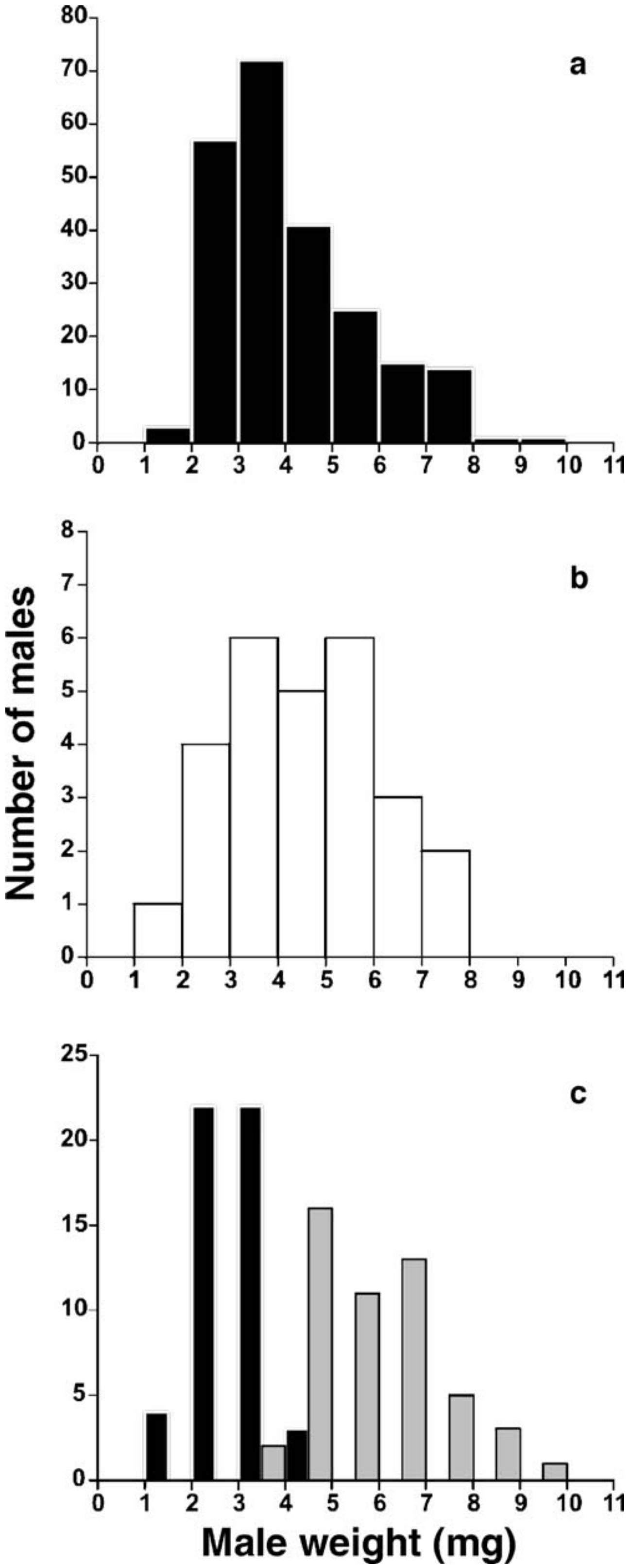

Fig. 1 Weight (milligram) distribution of a sample of: **a** field-caught males (n=229, from Andrade 2003), **b** laboratory-reared males used in single-male matings, (n=27) and **c** laboratory-reared males used in size-mismatched competitive matings (n=51, small males, *black columns*; large males, *grey columns*)

find more than one male on a single female's web (Andrade 1996), and male body weights vary significantly (Fig. 1), so competitive interactions between size-mismatched competitors are not unusual, and the female's web is a common site of inter-male competition. All males were virgins that had moulted within 2 weeks of their use in a trial and were unrelated to the female and rival male (in competition trials). Males were weighed (Ohaus electronic balance accurate to 0.01 mg) 24 h before a trial. Competing males were uniquely marked with a small spot of non-toxic fluorescent paint (Luminous paint, BioQuip Products) on the dorsal abdominal surface while briefly anaesthetised with CO_2. Whenever more than two candidate males were available for a given trial, sequential coin tosses were used to determine which would be used in trials.

Mating trials began when one male (single-male treatment) or two males (competition treatment) were introduced to a web at the furthest point from the female's position. For competition trials, males were placed on opposite edges of the web, but an equal distance from the female. Males were released within ~10 s of their rival. Trials continued for 8 h (mean courtship duration is 5.03±0.84 h, Forster 1995) or until both males were dead.

Most trials were video-recorded using Panasonic low light black and white cameras with macro zoom lenses and Sony Professional Super® VHS video recorders. In competition trials, black lights were used to confirm male identity. Notes were taken on key behaviours during the first 4–6 h of trials, and detailed behaviours were later scored from videotapes (Observer® Video Pro Version 3.0). Each spider was used in only one trial.

Courtship progress, mating success and sexual cannibalism

We recorded three variables related to courtship duration and copulatory success for each male: (1) latency to abdominal contact (time from start of trial until first contact was made with the female's abdomen, marking the end of the early stage of courtship), (2) latency to copulation (time from start of trial until first copulation) and (3) the number of copulations achieved.

Females may use premature lethal cannibalism where males are killed after a single, rather than two copulations, as a mechanism of cryptic choice (Snow and Andrade 2005). Thus, we recorded whether females killed males after their first copulation.

Intersexual and intra-sexual aggression

We recorded the number of times rival males won the following types of agonistic interactions (1) *Chases* occurred when both males were on the web. These were of two forms: one male would either make a sudden rapid lunge towards his rival (with or without contact) while the second male retreated, or one male would move towards his rival then chase him across the web as the other male retreated. The loser of a chase was the male who retreated. (2) *Scrambles* occurred when both males were on the female's abdomen. These were characterised by rapid erratic movement by both males and sometimes leg-to-leg or leg-to-body contact. The winner of a scramble was the male that remained on the female's abdomen while the loser retreated to the web. If neither male retreated at the end of the scramble (cessation of movement by both males), we scored both males as winners because both remained in close proximity to the female's copulatory openings.

Females sometimes use their forelegs to strike at courting males or at the web adjacent to males. Strikes have been interpreted as rejection behaviour because they can knock males out of webs, often result in cessation of courtship and are associated with decreased mating success (Andrade 1996). We recorded the number of strikes a female made during each trial. We could not reliably distinguish which male was the object of the strike, so we recorded only frequency. Strikes are readily identified, as females otherwise remain largely quiescent throughout courtship (Andrade 1996). In addition, strikes are distinct from predatory behaviour because females chase and rapidly wrap prey in silk (Forster 1995) but do not attempt to chase or wrap males during or after strikes.

Analysis

Statistics were performed with SPSS (version 12.0, with consultation from Sokal and Rohlf 1995). Some data were log-transformed to satisfy the assumption of normality; these are reported as back-transformed means. Non-parametric procedures were used if transformed data were non-normal. Logistic regressions were performed when dependent variables were categorical (e.g. occurrence of cannibalism, number of matings achieved) and model significance tested using the likelihood ratio test (model is significant if $p>0.05$, Hardy and Field 1998). Means are reported ±SE, and all statistical tests are two-tailed. Sample sizes vary for some tests because observations were missed for some trials.

Results

Courtship progress, mating success and sexual cannibalism

The latency to first contact with the female's abdomen was more than 2 h for single-courting males (Fig. 2a), whilst in competitive trials, the latency to abdominal contact was much shorter on average (0.5 h, Mann–Whitney U test: $U=85.0$, $P<0.001$, $n=77$, Fig. 2a). Within competitive trials,

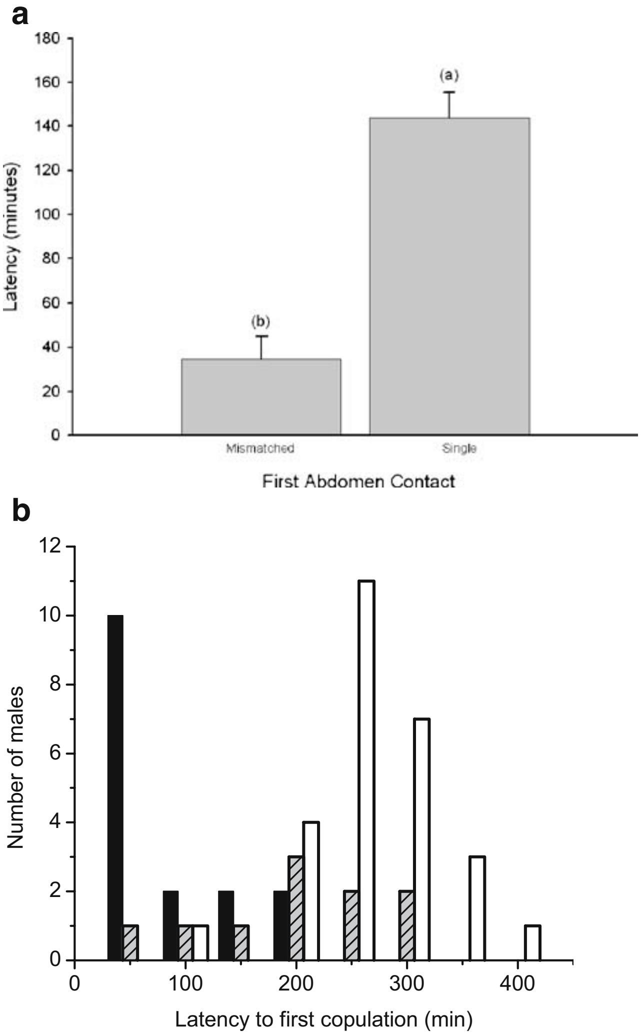

Fig. 2 Latency to **a** first abdomen contact and **b** first copulation in competitive and single-male mating trials. **a** Mean (SE) latency to first abdomen contact was longer in single male compared to competition trials. **b** Frequency histogram of latencies to copulation showing similar latencies for large males (*grey cross-hatched bars*) and single-males (*white bars*, Scheffe post hoc test: $P>0.05$), but significantly shorter latencies for small males that mated first in competition trials (*black bars*, Scheffe post hoc tests: $P<0.05$)

smaller males more frequently made first contact with the female than larger males (67% of trials, $\chi^2=5.7$, $n=51$, $P<0.05$), but latencies were shorter in the cases when first contact was made by larger (24.31±10.87 min) rather than smaller males (39.42±14.52 min; log-transformed data: $t_{48}=6.7$, $P<0.001$).

For single males, first copulations occurred more than 4 h after the start of courtship, which was significantly longer than average latency to first copulation in competition trials (Mann–Whitney *U* test: $U=85.5$, $P<0.001$, $n=70$, Fig. 2b). This difference was driven by a significantly shorter latency in trials where small males mated first, as latency to the first copulation was similar to single-male trials when larger males mated first (Fig 2b). Moreover, smaller males were not observed to engage in the vibration-causing movements typical of courtship in this genus (Forster 1995), but mounted females and attempted copulation when larger males were on a separate portion of the web. In contrast, larger males showed the same courtship behaviours as single-males (see Forster 1995), and despite agonistic interactions with their rivals (see below), continued to engage in web-bound courtship while smaller males often achieved a rapid first mating.

Mating after a brief courtship was costly for males. Across all trials, males that copulated quickly suffered an increased risk of premature fatal cannibalism by females (Fig. 3). During premature fatal cannibalism, males were wrapped in silk and incapacitated as they dismounted the female after their first copulation. This behaviour is distinct from cannibalism that occurs across two copulations. Males that copulate twice are never wrapped in silk after the first copulation (see Andrade et al. 2005). In single-male trials, although most males achieved two copulations, premature fatal cannibalism occurred in matings that had shorter latencies to the first copulation ($n=3$ killed, 191.00±36.68 min vs $n=24$ survived, 271.38±10.75 min $G_1=9451$, $n=27$, $p<0.001$). In competitive trials, males with brief latencies to the first copulation were more likely to be killed prematurely by females ($G_1=5.145$, $n=27$, $p<0.05$, Fig. 3). As smaller males more commonly attempted earlier mating, premature cannibalism of smaller first mates was more common than for larger first mates (67% of smaller first mates killed vs 22% of larger first males killed; $\chi^2=4.75$, $n=27$, $P=0.03$). This result is due to differences in pre-copulatory courtship duration as well as male size per se. For first-mating males, copulatory success (one or two copulations) increased with latency to copulation ($G_1=10.721$, $n=43$, $p<0.01$) and with male weight (milligram; $G_1=5.97$, $n=43$, $p<0.05$). The final logistic model, which included latency to copulation and male weight, was also significant (overall fit: $D_{50}=46.213$, $p>0.05$).

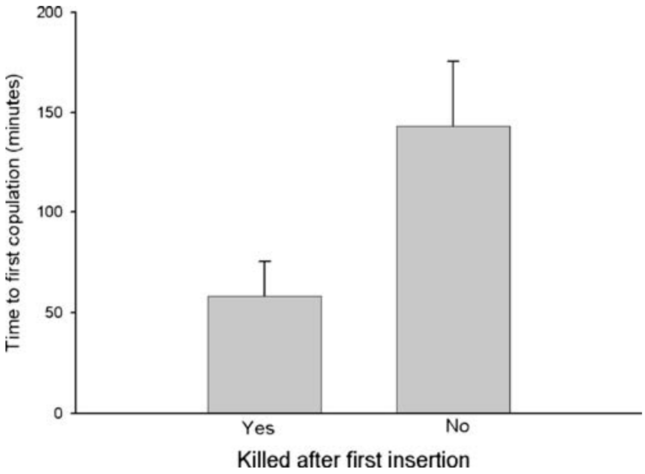

Fig. 3 Mean (SE) latency to first copulation for males killed by females after their first insertion ($n=13$) compared to those that survived ($n=14$) their first insertion in size-mismatched competition trials

Intersexual and intra-sexual aggression

The prolonged courtship typical of larger males was particularly interesting because it occurred despite aggressive interactions with (and thus awareness of) smaller males with lower RHP. Competing males engaged in both agonistic chases (0.84±0.16/h) and scrambles (0.48±0.13/h) in 50 of 51 trials, suggesting males were typically aware of their rivals. The difference in the number of scrambles won by smaller (1.42±0.53) compared to larger males (2.4±0.74) was not significant (Wilcoxon Z test: $Z=-1.4$, $P=0.16$, $n=50$). However, larger males won far more chases, suggesting they were physically dominant to small males (5.42±1.18 compared to 0.98±0.45; Wilcoxon Z test: $Z=-4.0$, $P<0.001$, $n=50$).

The low rate of competitive interactions and lack of escalation may be the result of female aggression. Although females struck at males during single-male trials (0.59±0.40 strikes/trial, $n=27$), the frequency of strikes was much higher when males were competing (13.29±2.99 strikes/trial, $n=51$; Mann–Whitney U test: $U=34.0$, $P<0.001$). Moreover, within competitive trials, the frequency of female strikes tended to increase as the latency to first abdomen contact decreased ($r_s=-0.29$, $P=0.06$, $n=44$), and strikes increased significantly as the number of inter-male scrambles increased ($r_s=0.30$, $P=0.05$, $n=44$). We found no relationship between female strikes and (1) the total number of chases in a trial ($r_s=-0.01$, $P=0.10$, $n=44$) or (2) latency to first copulation ($r_s=-0.14$, $P=0.40$, $n=37$).

Discussion

In this study, courtship behaviour of male redback spiders shifted with context. When alone with a female, a male's first copulation was preceded by prolonged courtship, but courtship essentially disappeared for smaller rivals in competitive contexts. Larger males, however, still engaged in significant courtship, more than 3 h on average (Fig. 2b), and did not kill or incapacitate their rivals despite initial aggressive interactions. Although inter-male aggression occurred, it was relatively rare, did not escalate and was correlated with female aggressive behavior. Aggressive strikes at males by females occurred infrequently in single-male trials, but were common when rival males were present. The most prominent response of females to the behaviour of competing males was premature sexual cannibalism, which was triggered when males did not provide sufficient courtship before attempting copulation (i.e. brief pre-copulatory latency). Thus, despite factors that favour escalated fighting (monogyny and first male sperm precedence, Andrade 2003; Snow and Andrade 2005; see Fromhage and Schneider 2005), these data show that male competitive behaviour cannot be understood without considering the effect of the behaviourally dominant female.

Competition between males may not have escalated for reasons other than female aggression or reward for prolonged courtship. First, males could use ritualised fights (e.g. chases in which larger males were dominant) to determine relative RHP after which individuals adopt the strategies most likely to maximise their success (Whitehouse 1991). For example, in a kleptoparasitic spider (*Argyrodes antipodiana*), male interactions on female's webs did not escalate, but inferior rivals obtained copulations by sneaking after initial interactions (Whitehouse 1991), as we saw here. Similar alternative strategies were observed in golden orb-web spiders (*Nephila edulis*) where larger males are more conspicuous to cannibalistic females, so essentially attempted 'sneak' copulations (Schneider et al. 2000). While small males approached the female directly, mated quickly and copulated for longer, large males attempted to mate through a hole cut in the web, which protected them from the female but decreased mating success (Schneider et al. 2000). This may not be surprising in polygynous *A. antipodiana* or in *N. edulis* where larger males are at elevated risk of pre-copulatory cannibalism; it is remarkable for monogynous redback males. While smaller males could increase their success by sneaking rather than fighting, larger males risk significant paternity loss so should aggressively exclude or kill inferior rivals. This is particularly true because any smaller males that mate successfully could deposit mating plugs that would decrease or eliminate paternity of later-mating rivals (Snow et al. 2006).

Second, fatal fighting may not be a viable option for larger males if smaller males are sufficiently difficult to detect. If considerable time would be required to find and subdue small males, a fatal fighting strategy might entail a significant reduction in the time and energy available for courtship and an increased risk of other rivals arriving at the web. In our trials, smaller males' reduced movement and lack of typical courtship could have rendered them vibrationally cryptic, and hence difficult to find, as web-building spiders rely mainly on vibrational information for detecting and localising objects in the web (Landolfa and Barth 1996). In this study, however, in almost every trial, larger males interacted with smaller males on the web, but other than brief chases, did not pursue aggressive attacks against their rivals. This suggests that detection problems alone cannot explain this behaviour.

In contrast, there are indications that the lack of fatal fighting may be favoured by female behaviours that yield benefits for males that engage in courtship rather than inter-male aggression. Inter-male agonistic interactions were associated with elevated aggression by females. Particularly when rivals were physically mounted on the female, fights (i.e. scrambles) were related to an increase in female strike behaviour. Perhaps because of female interference, there was no significant effect of male size on the outcome of scrambles, rather, male retreat was often determined by female strikes. In contrast, there was no correlation between female strikes and chases (male competition on the web), and in these, larger males were more often victorious. Strikes can impose significant costs as males are often knocked off webs (Andrade 1996), which will delay courtship, may cause injuries and increase predation risk for males. Although physiological or male-imposed injury costs of fighting are often invoked as factors that militate against the escalation of agonistic interactions, our data suggest that female-imposed costs could also be significant determinants of male competitive strategies. This conclusion would be consistent with existing game theory models in which female-imposed reductions in the payoff for fighting would have strong effects. However, in practice, such effects are rarely incorporated in studies of inter-male contests (reviewed in Wong and Candolin 2005). An alternative interpretation of our data is that female strike behaviour is of minimal importance to male aggression, as female strikes were correlated only to the occurrence of scrambles, and these competitive interactions may not be critical to the outcome of male competition (as larger males were not dominant in these competitions). Our study cannot distinguish these interpretations, so it remains unclear whether strike behaviour of females suppresses escalation of male fights; additional studies combined with manipulation will be necessary to clarify this point.

A more critical effect of female behaviour in this study was the limitation of male competitive strategies by female-derived fitness benefits of prolonged courtship. Female behaviour could limit escalation in groups where males have to choose between competitive behaviour and courtship (e.g. Whitehouse 1991), particularly if males who court rather than compete increase their paternity. In some species, the presence of a rival male accelerates courtship (e.g. Elgar and Bathgate 1996); in others, there may be female-imposed costs of reduced courtship. This has seldom been explored, but has been suggested in the European bitterling (*Rhodeus sericeus*) where aggression of dominant males towards other males interrupts courtship and increases the time until females spawn (Candolin and Reynolds 2002). In redbacks, female punishment of males that truncate courtship is more direct (Fig. 3). Males that attempt mating too quickly are fatally cannibalised after one copulation and cannot inseminate both sperm storage organs (as is common for longer-courting males). In contrast, males that copulate twice after a longer courtship could expect higher paternity on average than males that copulate once even if one of the spermathecae is previously inseminated (Snow and Andrade 2005). Thus, female cannibalistic behaviour determines the profitability of the competitive strategies available to dominant males and reduces the benefit of fighting rather than courting.

We argue that the premature death of rapid-mating males is due to variation in female cannibalistic behaviour. An alternative explanation is that these males mate so quickly that there is insufficient time for them to develop protection against the partial cannibalism that normally occurs as part of the first copulation (Andrade et al. 2005). However, there is good evidence that the premature death of males is due to female behaviour. In matings with two copulations, females masticate but do not incapacitate males after their first copulation. In contrast, premature cannibalism involved females wrapping males in silk then consuming them at the end of the first copulation.

Premature cannibalism as a mechanism of female discrimination in redbacks was suggested in a sperm competition study (Snow and Andrade 2005) in which males that were killed after their first copulation were smaller than males that survived. Given that competing larger males typically court for longer than smaller rivals, our results could be explained if females simply prefer larger males. However, in our study, copulatory success (one or two copulations) increased with increased latency to copulation independent of the effect of increased male size. Similarly, in our single-male trials, the few cases of premature cannibalism occurred with males that mated relatively rapidly. Thus, male size and latency to copulation may both factor into female decisions regarding premature cannibalism. Females might seek prolonged courtship as an assessment trial for males, as courtship is energetically costly to sustain (Vehrencamp et al. 1989; Andrade 2000). Alternatively, conflict over mating may have lead to resistance to stimulation by less elaborate displays (Thornhill and Alcock 1983; Eberhard 1985; Holland and Rice 1998). It is not yet clear why females permit smaller sneaker males to mate and presumably achieve some paternity (e.g. Candolin and Reynolds 2002). Nor it is clear how male interactions might play out when neither rival is dominant (e.g. size-matched competitors). These questions are the subject of ongoing work.

Our data suggest that costs imposed by females could have dramatic and otherwise unpredictable effect on male decisions with respect to courtship and competitive interactions. Female-imposed costs may be similarly important in systems where considerable sexual size dimorphism gives females a physical advantage over males (e.g. Head 1995; Holland and Rice 1998; Vollrath 1998; Elgar et al. 2000; Persons and Uetz 2005) or where females can manipulate paternity (e.g. via cryptic choice, Eberhard 1996; Elgar et al. 2000). These results suggest that it may be informative to explicitly consider female interests in models for understanding male competitive behaviours. Although influences of females may be more subtle in other systems, they could nonetheless have strong cumulative effects (e.g. Eberhard 1985). The extreme nature of courtship and mating in redback spiders may provide a valuable opportunity for probing general rules governing the complex interplay between optimal male strategies and female choice.

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