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Novel male trait prolongs survival in suicidal mating

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Male redback spiders (*Latrodectus hasselti*) maximize paternity if they copulate twice with their cannibalistic mate. Facilitating cannibalistic attack during their first copulation yields paternity benefits. However, females have paired sperm-storage organs inseminated during two separate copulations, so males that succumb to partial cannibalism during the first copulation lose at least 50% of their paternity to rivals. In this paper, we describe a novel male trait—an abdominal constriction that appears during courtship—that allows males to survive and mate with females for a second time, despite the substantial cannibalistic damage inflicted during the first copulation. Constricted males that were wounded to simulate early cannibalism had higher endurance, greater survivorship, longer subsequent courtship and higher mating success than wounded males that were not constricted. Constriction was not found in a non-sacrificial congener that rarely survived simulated cannibalism, and the protective effect of constriction in redbacks was specific to the type of damage inflicted by females during the first copulation. Thus, the abdominal constriction allows males to overcome the potential fitness limit imposed by their own suicidal strategy—paradoxically, by prolonging survival across two cannibalistic copulations.

Keywords: sexual cannibalism; redback spider; sexual selection; courtship; male mating success; evolutionary conflict

1. INTRODUCTION

Males of the Australian redback spider (*Latrodectus hasselti*) are cannibalized in 65% of matings after positioning their abdomen above the fangs of their mate during copulation ('copulatory somersault'; Forster 1992; Andrade 1996, 1998). Male facilitation of sexual cannibalism may be an adaptation to increase paternity (Andrade 1996, 2003). Cannibalism is coincident with sperm transfer, and associated with increased copulation duration and decreased female receptivity to rivals (Andrade 1996).

Females typically masticate the posterior dorsum of the male's abdomen during the first copulation (Forster 1992). However, redback mating features two copulations as each of the paired male copulatory organs inseminates independent sperm-storage organs

(Andrade & Banta 2002). Males that survive the substantial damage inflicted by the female and mate for a second time can expect sperm precedence in each female reproductive tract because of the deposition of sperm plugs (Snow 2003; see Andrade & Banta 2002). In contrast, males that die after one copulation (12.5% in nature; Andrade 1998) leave one storage organ empty and can lose 50% or more of their paternity to later-mating rivals (Snow & Andrade 2005). Sacrificial behaviour thus entails an evolutionary conflict for males (e.g. Ramos *et al.* 2004)—sexual selection favours males that facilitate cannibalism at the first copulation, but ensures survival to the second copulation.

A mid-dorsal abdominal constriction, which has been occasionally observed in redback males (figure 1b; Forster 1992), could increase mobility and mating success following partial cannibalism. Abdominal constriction could maintain anterior hydraulic pressure (required for spider locomotion; Foelix 1996) despite the posterior punctures, or may shift essential abdominal organs anterior, to an area not damaged at the first copulation (Forster 1992). To our knowledge, a constriction of this type has not been described in any other spider (e.g. Kaston 1970; Anava & Lubin 1993; Foelix 1996) and so may be unique to sacrificial male redbacks.

If the constriction allows males to survive partial cannibalism, then it should (i) arise in males during courtship, in anticipation of cannibalism during the first copulation; (ii) increase male survivorship following abdominal damage posterior to the constriction (where females typically wound males during the first copulation), but not necessarily anterior to the constriction (an area not usually wounded until the second copulation); (iii) increase male courtship performance and mating frequency following abdominal damage posterior but not anterior to the constriction and (iv) not occur in *Latrodectus hesperus* (the Western black widow), a congener that shows neither male sacrifice nor frequent sexual cannibalism (ca. 2%, Kaston 1970; M. C. B. Andrade, unpublished data). *Latrodectus hesperus* males should rarely survive partial cannibalism. We tested these predictions using laboratory populations of *L. hasselti* and *L. hesperus*.

2. MATERIALS AND METHODS

We used outbred, laboratory-reared descendants of wild-caught spiders from New South Wales, Australia (2000; redbacks—*L. hasselti*) and British Columbia, Canada (2001; *L. hesperus*). Rearing details are given in Snow & Andrade (2004).

(a) Development of constriction

We photographed lateral abdominal profiles (figure 1a,b) of virgin males restrained in glass tubes under a dissecting microscope and randomly placed them into control (redbacks, $n=21$; *L. hesperus*, $n=10$) or courtship treatments (redbacks, $n=36$; *L. hesperus*, $n=12$). Courtship males were allowed to court on the newly made web of an unrelated conspecific virgin female (female removed); control males were placed in identical but web-free, ethanol-washed arenas. *Latrodectus* males court in response to web-bound pheromone alone (Kaston 1970; Ross & Smith 1979). We confirmed this for courtship males. Trials lasted for 18 h with additional photographs of males taken after 2 h and at the end of the trial.

An observer unaware of treatment classified pretrial and 2 h images of males as visibly 'constricted' or 'non-constricted'. Constriction was also measured on digital images as a decrease in the ratio of abdominal width : length (figure 1b). Abdomen length

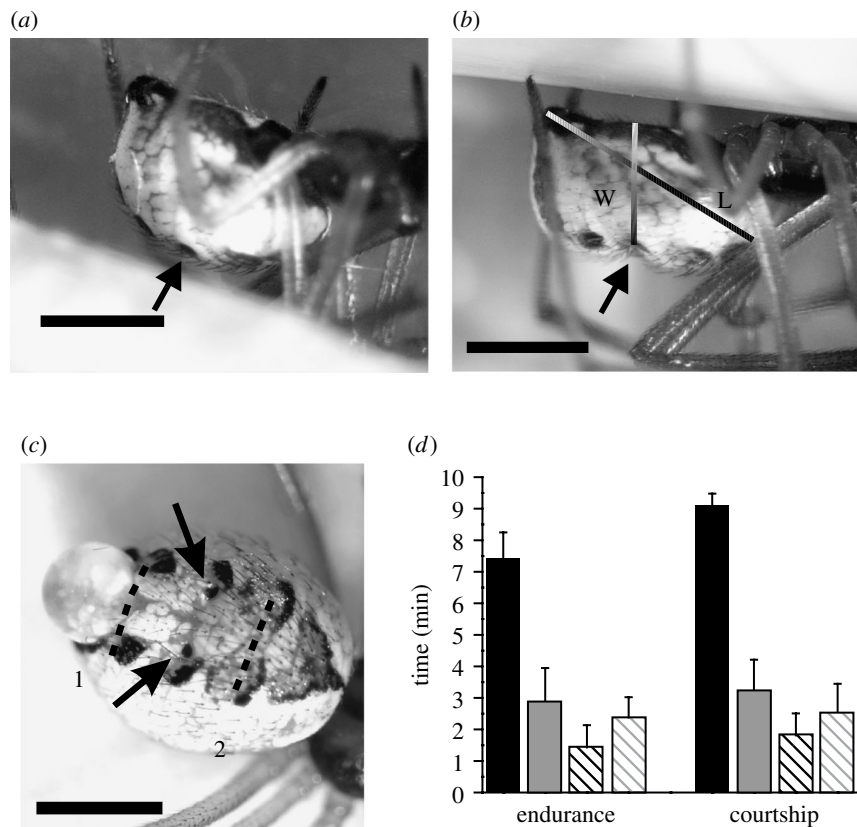


Figure 1. (a), (b) Lateral and (c) dorsal abdominal images of male redback spiders (scale bars, 1 mm; arrows indicate the mid-dorsal apodemes, location of constriction) and (d) effect of constriction on endurance and courtship following abdominal wounding. (a) Prior to courtship, males show no constriction. (b) After courtship, an abdominal constriction results in a reduction in abdominal width (line 'W') to length (line 'L') ratio. (c) Dotted lines show the locations of simulated first copulation (line 1, posterior to apodemes) and second copulation (line 2, anterior) cannibalism. This posterior-wounded male is leaking haemolymph (typical location and magnitude seen with first copulation cannibalism). Constricted males (black bars) had longer endurance and courtship than non-constricted males (grey bars) in 10 min trials following posterior (solid bars) but not anterior wounding (hatched bars). Graph shows means and standard error.

was the distance between the base of the spinnerets and anterior-most point of abdomen, and width was the length of a line starting at a right angle to the ventral abdominal surface and ending at the dorsal surface at the mid-dorsal apodemes (figure 1b). Abdominal dimensions were measured three times independently for each image; analyses use mean values.

(b) Effect of constriction

We assessed the effect of constriction on male performance by simulating cannibalistic in constricted or non-constricted males. To simulate cannibalistic damage, we made a transverse incision (0.65–0.70 mm deep) on the dorsal abdominal surface of CO₂-anaesthetized males using a razor blade fragment (figure 1c). Wounding resulted in haemolymph loss (figure 1c), as seen during cannibalism (Forster 1992). Wounding was posterior to the mid-dorsal apodemes (area typically pierced and masticated by females during first copulations) or anterior to the apodemes (area only damaged during and after the second copulation; figure 1c). Some males did not recover from anaesthetic, so sample sizes vary in some groups.

(i) Survival and leg curling

A second group of black widow ($n=40$) and redback males ($n=40$) were allowed to court on a web or placed in an empty arena (as above) for 2 h. We noted the presence or absence of visible constriction, and then performed anterior or posterior wounding and placed males in cages for recovery. One hour later, we looked for a 'curled-leg' posture, which indicates fatal haemolymph loss in spiders (e.g. Foelix 1996). After 24 h, we assessed male survivorship.

(ii) Performance

In redbacks, second matings occur only after a 10–15 min inter-copulatory courtship (Forster 1992). As most redback males

constrict during courtship (§3), observational study cannot determine whether constriction increases second mating success. Instead, we measured performance and mating success of a third group of non-constricted ($n=30$) and constricted virgin redback males ($n=30$) after anterior or posterior wounding. 'Constricted' males had a visible constriction after 2 h courtship on an empty web. Each 'non-constricted' male was weight-matched to a constricted male (within 0.4 mg) and left in an empty arena for 2 h. Males were wounded as outlined above. Immediately after males recovered from anaesthetic, we noted the number that showed a curled-leg posture.

As a proxy for courtship effort, wounded males were subjected to a 10 min endurance trial by an experimenter unaware of treatment group. Males were forced to run continuously in a circular arena in response to touches from a paintbrush (e.g. Ramos *et al.* 2004). We recorded the time at which males failed to respond to 10 consecutive touches.

After endurance trials, males were each placed on a web with a virgin female. We noted courtship activity for 10 min then left males with females for 15–18 h. Successful copulation was observed on videotapes or inferred by examination of male copulatory organs (palps are permanently altered by mating; see Andrade 1996).

3. RESULTS

(a) Development of constriction

A dorsoventral abdominal constriction was visible in 78% of courting redback males, but only a few control males (19%, Pearson $\chi^2_1=18.58$, $p<0.001$, $n_1, n_2=36, 21$; figure 1a,b) after 2 h. Constrictions always arose between the mid-dorsal apodemes (figure 1b,c). Abdominal width : length ratios

(figure 1b) decreased by 6.9% on average relative to controls after 2 h of courtship (repeated measures GLM; time \times treatment $F_{2,54}=4.702$, $p=0.013$). Most courtship males (83%) developed a measurable constriction (width : length ratio less than pretreatment ratio). Unlike redbacks, black widow males showed no visible constrictions (0 of 20 males classified as 'constricted') and no change in width : length ratio relative to controls (repeated measures GLM; time \times treatment $F_{2,19}=1.904$, $p=0.176$).

(b) Effect of constriction

(i) Survival and leg curling

Constriction increased mobility and survival of male redback spiders after simulated partial cannibalism. One hour after wounding posterior to the apodemes (figure 1c,d), 89% of control males (8/9) but only 22% of courtship males (2/9) showed a 'curled-leg posture' (Fisher's exact test $p=0.015$, $n_1, n_2=9, 9$). The two courtship males with leg curling did not have a visible constriction prior to wounding, and were the only two courtship males to die within 24 h. In comparison, most control males (89%) died in the same period (Fisher's exact test $p=0.02$, $n_1, n_2=9, 9$).

In contrast, most redback males wounded anterior to the apodemes showed leg curling within 1 h (constricted: 89%, non-constricted: 78%; Fisher's exact test $p=1.0$, $n_1, n_2=9, 9$), and died within 24 h (constricted: 100%, non-constricted: 89%, Fisher's exact test $p=1.0$, $n_1, n_2=9, 9$). Similarly, most black widow males showed leg curling and died within 24 h of wounding, regardless of courtship experience or location of wounding (courtship, 80% mortality, $n=10$; no courtship, 90% mortality, $n=10$, Pearson $\chi^2_1=0.392$, Fisher's exact test $p=1.00$).

(ii) Performance

Immediately after posterior wounding, 60% of non-constricted but only 7% of constricted redback males had curled legs ($\chi^2_1=9.60$, $p=0.002$, $n_1, n_2=15, 15$). Wounded, non-constricted males ceased responding earlier than constricted males in our endurance test (GLM $F_{1,28}=11.992$, $p=0.002$; figure 1d), and almost half of the non-constricted males (47%) collapsed and died after less than 1 min of courtship, whereas all constricted males courted for at least 5 min (courtship duration: GLM $F_{1,28}=28.903$, $p<0.001$; figure 1d). Constricted males were significantly more likely to mate (73% compared with 13% mated, Fisher's exact test $p=0.003$).

When wounded anterior to the apodemes, redback males succumbed quickly regardless of constriction. Leg curling was common (constricted: 53%, non-constricted: 67%; $\chi^2_1=0.556$, $p=0.456$, $n_1, n_2=15, 15$), endurance was poor, males rarely courted virgin females (figure 1d; GLM: endurance $F_{1,24}=0.996$, $p=0.328$; courtship $F_{1,24}=0.403$, $p=0.531$), and few mated (constricted: 20%; non-constricted: 20%).

4. DISCUSSION

Our data show that a prominent constriction arises in most redback males during their first courtship, and

this does not require contact with females. Constriction was not simply an effect of dehydration or loss of mass with courtship effort as the constriction was discrete, its location consistent across males (figure 1b), and it was never seen in courting *L. hesperus* males. Contraction of dorsoventral musculature attached to the apodemes (Foelix 1996) probably causes the observed pinching in of the dorsal cuticle. Although similar muscles are present in other spiders (Foelix 1996), constriction of the exoskeleton as a regular part of courtship has not, to our knowledge, been described in any other invertebrate, including the most probable sister species of redbacks (Garb *et al.* 2004), *Latrodectus katipo* (Kavale 1986). The constriction may thus be a derived trait of self-sacrificial redback males.

Constriction increases the likelihood of males surviving partial cannibalism and achieving a second copulation. Constricted males had higher endurance, survivorship, courtship duration and mating success following abdominal wounding that mimicked first copulation cannibalism. The mechanistic basis of this effect is unclear, but protection from lethal effects of partial cannibalism was probably due to the constriction itself, rather than another effect of courtship. First, males that courted but did not constrict were more likely to develop curled legs and die within 24 h of wounding than were males with visible constrictions. Second, the location of wounding relative to the constriction was critical. There was no effect on survival or any measure of performance for wounding anterior to the constriction (figure 1d), a location not usually damaged during the first copulation.

The specificity in the protection provided by constriction suggests it is tuned to the effect of female cannibalistic behaviour on male fitness. Decreased performance and death following the second copulation would not affect male lifetime reproductive success (Andrade 2003). In contrast, death after the first copulation would lead to significant paternity loss (Snow & Andrade 2005). Constriction is necessary because males promote female cannibalism (Forster 1992; Andrade 1996), apparently because of the benefits of partial consumption (Andrade 1996, 2003). The constriction allows redback males to overcome a potential optimization conflict between different stages of their mating behaviour by prolonging survival, despite facilitation of repeated cannibalistic attack by females.

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