

# Risky mate search and male self-sacrifice in redback spiders

Maydianne C. B. Andrade

Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

Male redback spiders twist their abdomens onto the fangs of their mates during copulation and, if cannibalized (65% of matings), increase their paternity relative to males that are not cannibalized. The adaptive male sacrifice hypothesis proposes that this increased reproductive payoff from a single mating outweighs the residual reproductive value of a cannibalized male, because high mortality during mate searching restricts alternative mating opportunities. It has been reported that redback male residual reproductive value is low because males are functionally sterile after one mating—a putative intrinsic constraint that could arguably favor self-sacrifice in the absence of ecological restrictions on multiple mating. However, sterility and self-sacrifice may both arise as aspects of a terminal investment strategy if the probability of multiple mating is sufficiently low. Here I report field data that support the adaptive male sacrifice hypothesis. More than 80% of redback males die without finding a potential mate in nature. Data from two observational field studies and one release experiment suggest that in the absence of cannibalism, male redbacks would expect fewer than one mating opportunity in a lifetime. This expectation was not significantly higher for a large male or one in good condition. A simple quantitative analysis confirms that even if males are assumed to be fertile throughout life, the measured mortality rate during mate search in combination with previously documented paternity benefits of cannibalism is sufficient to ensure that self-sacrifice is adaptive for male redback spiders. *Key words:* constraint, *Latrodectus*, mate searching, redback, self-sacrifice, sexual cannibalism, spider. [*Behav Ecol* 14:531–538 (2003)]

Male redback spiders (*Latrodectus hasselti*) “somersault” during copulation and twist their abdomens directly onto the fangs of their mates (Cariaso, 1967; Forster, 1992). Because most males (65%) are consumed while in this vulnerable posture and because morphologically similar congeners do not somersault (see Kaston, 1970), it has been proposed that the copulatory somersault represents an adaptive male strategy of self-sacrifice in redbacks (Andrade, 1996; Forster, 1992, 1995). Consistent with the adaptive self-sacrifice hypothesis, redback males are at risk of sperm competition but accrue significant paternity benefits if consumed by their mates (Andrade, 1996). Cannibalized redback males copulate longer than do noncannibalized competitors and can double their paternity relative to rivals. Cannibalized males are also less likely to be cuckolded (Andrade, 1996).

The paternity benefits of cannibalism in one mating could result in sexual selection for self-sacrifice only if males have low residual reproductive value after that mating (Buskirk et al., 1984; Elgar, 1992; Parker, 1979). In general, if the probability of finding a mate is sufficiently low owing to ecological factors that constrain success during mate searching, then selection may favor investments in mating that reduce survival (Andrade, 1996; Buskirk et al., 1984; Forster, 1992; Maxwell, 1998; Vollrath, 1998). Data on male reproductive opportunities in nature are thus essential for a quantitative test of the sacrifice hypothesis, but such data are scarce. Although possible cases of male self-sacrifice have been identified in other spiders (Blanke, 1975; Grasshoff, 1964; Knoflach and van Harten, 2000, 2001; Sasaki and Iwahashi, 1995), to date, the net effect of cannibalism on male

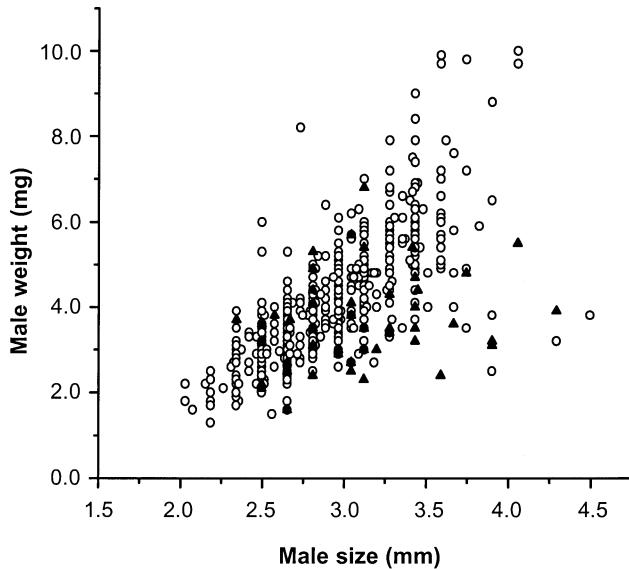
fitness has not been assessed in any sacrificial species (Johns and Maxwell, 1997). Generally, in the absence of a quantitative comparison of costs and benefits, conclusions about the adaptive consequences of cannibalism for males may be premature (see Gould, 1984; Jamieson, 1986). Moreover, studies of a redback congener with a similar life history (*L. riviensis*) suggest that mate-searching males may achieve more than one mating opportunity in nature (Anava and Lubin, 1993), a result that could call into question the adaptive sacrifice hypothesis for redback male mating behavior (Andrade, 1996).

Understanding the evolutionary basis for the unusual behavior of male redback spiders is of interest for several reasons. First, male sacrifice may represent one of the most extreme cases of sexual selection shaping behavior in opposition to selection for survival (see Andersson, 1994). Second, this could be one of few systems in which self-sacrifice is adaptive for the victim as a result of individual selection (e.g., unlike sacrifice in pea aphids; McAllister and Roitberg, 1987). Third, identifying conditions that lead to maximal male investment in a single mating may contribute to our understanding of the resolution of intersexual conflicts over mating investment (see Brown et al., 1997).

Alternatives to the adaptive male sacrifice hypothesis hold that sexual cannibalism is always maladaptive for males and occurs only when predatory females are able to overcome their mates (Arnqvist and Henriksson, 1997; Gould, 1984). Under these hypotheses, male traits that appear to facilitate cannibalism may have arisen in other contexts and now represent intrinsic constraints on adaptive male mating behavior (see Gould, 1984). In the case of redback spiders, the value of multiple mating for males may be low owing to an intrinsic constraint—redback males are functionally sterile after their first mating (Andrade and Banta, 2002). Functional sterility could lead to selection favoring a self-sacrificial strategy. In contrast to this constraint hypothesis, the adaptive male sacrifice hypothesis proposes ecological conditions alone are sufficient to account for male self-sacrifice, and functional sterility arises secondarily as a result of these same conditions.

Address correspondence to M.C.B. Andrade, who is now at the Division of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario M1C 1A4, Canada. E-mail: mandrade@utsc.utoronto.ca.

Received 16 April 2002; revised 20 September 2002; accepted 2 October 2002.



**Figure 1**  
Regression of male weight on size for 520 males collected as adults at a field site in Perth, Western Australia, in 1996 and 1997 (open circles). Filled triangles are size and weight of experimental males collected as penultimate instars and used in a male-release study of interweb survivorship.

Here I test the adaptive sacrifice hypothesis by asking whether the paternity benefits of cannibalism (Andrade, 1996) outweigh the lost future reproductive opportunities for redback males if it is assumed males are fertile throughout their lives. I quantify the cost of cannibalism by estimating the expected number of lifetime mating opportunities for an average redback male in the absence of cannibalism. I also examine whether this opportunity cost of cannibalism varies as a function of male size or condition to determine whether the best strategy for a given male varies with phenotype. Finally, I develop and evaluate a simple mathematical model that describes the conditions under which the paternity benefits of cannibalism (Andrade, 1996) will outweigh the value of future mating opportunities to determine whether self-sacrifice is predicted to increase male fitness even in the absence of postmating functional sterility.

#### Natural history

See Forster (1992, 1995) for more details of redback natural history. Redback spiderlings disperse from their natal web by ballooning after emerging from the egg sac (e.g., Suter, 1991). Adult male redbacks have a shorter lifespan than do females (laboratory, a maximum of 8 weeks compared with 2 years for adult females; Andrade, 1996; Forster, 1984). Although females are relatively sedentary as adults, rarely changing the location of their web (Andrade MCB, personal observation), males go through a wandering (mate-searching) phase shortly after their final moult. Like all web-building spiders, males are likely to experience increased vulnerability to predators during mate search because they have relatively poor vision and their vibration-sensitivity may be compromised when they are no longer on a web (Foelix, 1982). In addition, as is common for male web-building spiders (Foelix, 1982), redback males apparently do not eat while searching for a mate, so they use only nutrient stores accumulated as a juvenile during mate search.

## MATERIALS AND METHODS

### Field site

I studied a population of redback spiders on the outdoor grounds of the Western Australia Department of Agriculture (North Perth, Western Australia) during two field seasons that encompassed the height of sexual activity for redbacks (24 November 1995–7 February 1996 [76 days] and 1 December 1996–1 March 1997 [90 days]). The site included maintained lawns, native shrubbery, glass-houses, and outbuildings and is host to a large population of redbacks. I studied the spiders on a roughly rectangular section of the grounds that was surrounded by habitat inhospitable to redbacks (e.g., pavement and other hot exposed areas with no available refuge, dense brush, or heavily watered experimental fields). The site was 75.0 × 40.3 m (3022.5 m<sup>2</sup>) in 1995–1996 and 158.8 × 40.3 m (6399.6 m<sup>2</sup>) in 1996–1997 when heavy watering ceased in an area that was previously a dispersal barrier.

### Web surveys

I marked and numbered every redback web on the site during the first 7 days of each field season (1995–1996 [108 webs], 1996–1997 [273 webs]) and then surveyed the webs each night (redbacks are nocturnal) for the remainder of each season (1995–1996 [68 nights], 1996–1997 [80 nights]) and recorded the identity, sex, and instar of web inhabitants. Every second night, I searched the site for new webs.

### Identifying spiders

Adult males were marked for individual identification with spots of quick-drying Dope modelling paint on the femurs of the first and/or fourth legs in unique color patterns. Males were removed from webs when first seen and marked under a dissecting microscope after brief chilling (1995–1996) or while anesthetized with carbon dioxide (1996–1997), then weighed with a Mettler electronic balance (accurate to .1 mg). In 1996–1997, I also measured male size as the average length of the first two legs (tibia + patella) using an ocular micrometer on a Wild M5 dissecting microscope. Male condition was calculated as the residuals from a regression of male weight on size based on 520 males collected in the field in 1996–1997 ( $R^2 = .53$ ,  $F_{1,418} = 581$ ,  $p < .001$ ; see Jakob et al., 1996) (Figure 1). Marked males were returned to the webs on which they were found within 12 h (1995–1996) or 6 h (1996–1997) of capture. I confirmed that males and other web inhabitants did not abandon the webs within 30 min of male replacement. Individual identification of penultimate (sixth or seventh) instar and adult females was based on estimated body size and abdominal markings (which are very variable; see Kaston, 1970; Levi, 1959, 1969).

Instars were determined by spider size and coloration (Cariaso, 1967; Andrade MCB, unpublished data). Male penultimates (fourth instar) and adults were identified by the distinctive development of the copulatory organs (pedipalps; Kaston, 1970). Variation in female size, coloration, and number of instars before adulthood (Cariaso, 1967; Forster, 1984; Kavale, 1986) makes visual classification of penultimate versus adult females unreliable. Instead, females were classified in two groups: adult/penultimate or early instar (fifth instar or earlier). Although males may mate with females initially found as penultimate instars or as adults, an adult male would be unlikely to survive long enough to mate with an early instar female (Cariaso, 1967; Forster and Kingsford, 1983).

### Controls: marking procedure

There were two groups of control males each season: one group marked using the same procedure as males at the field

site (control marked [CM] males); the other handled similarly but not marked (control unmarked [CU] males). All control males were adult virgins collected from sites in and around Perth during the first 2 weeks of each season. Virgin males were those that showed no abdominal damage from partial cannibalism and had intact pedipalps (pedipalp morphology changes with mating; see Andrade, 1998), and most were collected from webs typical of juvenile males that contained a male moult skin. Males received the CM or CU treatment (assigned randomly) and then were kept in the laboratory in ventilated vials at room temperature until their death. Control males were not fed (typical for adult males in the field; Foelix, 1982) but were given access to water. Longevity of CU and CM males was compared by using survival analysis (SYSTAT 10.2; Steinberg et al., 2002).

### Estimating male interweb mortality

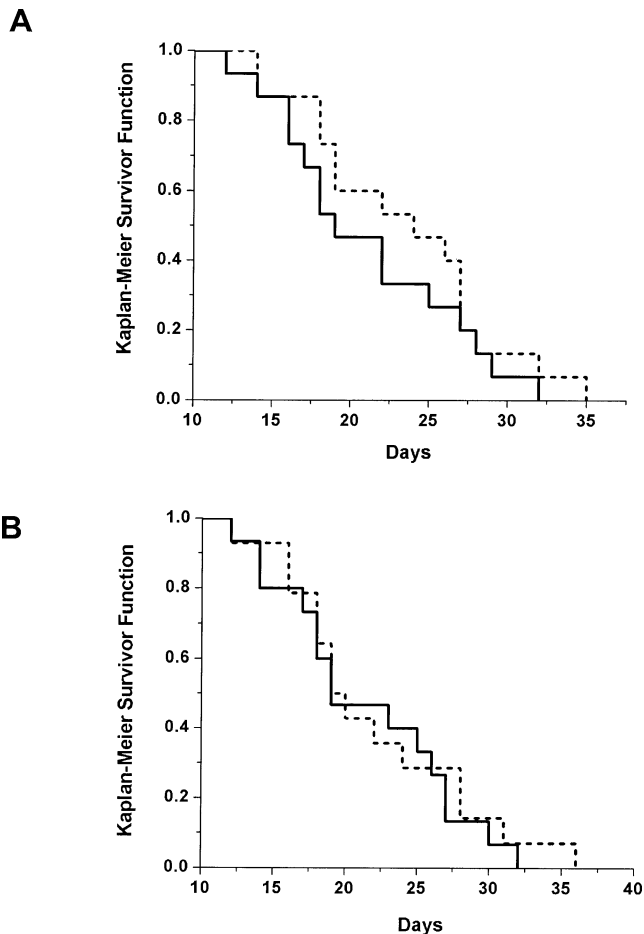
Male survivorship during mate search was assessed as the proportion of newly molted adult males that were later discovered on the web of an adult or penultimate instar female. Males not found on a female's web by the end of the field season were considered to be dead. Males were only included in this study if they were initially marked on an empty web, or on one containing only early instar females, and then disappeared from this web within the first 21 days (1995–1996,  $n = 48$ ) or the first 46 days (1996–1997,  $n = 110$ ) of each field season. This left 50 days in 1995–1996 and 40 days in 1996–1997 during which I searched for marked males on the webs of adult/penultimate females.

The assumption that males that disappear are dead is reasonable given the following three conditions. First, there was no evidence of male emigration out of the field site. I never found webs or marked males outside the boundaries of the site despite weekly searches in the approximately 10-m buffer zone, and long-distance dispersal of adult males is unlikely (see Suter, 1991). This conclusion is supported by the low number of potential adult immigrants to the site (Waser et al., 1994). Most males were initially found as juveniles (1995–1996, 97% of 234 males; 1996–1997, 95% of 520 males). Second, most webs were discovered in the first 2 weeks of the season (92 of 108 webs in 1995–1996; 262 of 273 webs in 1996–1997), despite frequent searches for new webs. Third, the longevity of newly matured adult males was less than my search period (Figure 2).

Using surveys of surviving males to estimate the risk of mate searching is likely to produce accurate estimates not only because male emigration but also because juvenile redback males must disperse to find females and are only successful if they reach the web of a reproductively mature female (see Waser et al., 1994). By observing male molting or finding a moult skin in the web, I confirmed that males disappeared from their juvenile webs only after reaching sexual maturity for 40 of the 48 males I searched for in 1995–1996 and for 100 of 110 males in 1996–1997.

### Male movement and nearest-neighbor distances

Using the interweb mortality of newly matured males to calculate the lifetime expectation of mating assumes that newly-matured males and nonvirgin males have similar mortality rates during mate search. Interweb mortality is likely to be positively related to the distance between webs (all else being equal). I tested this assumption by comparing the distance between adult/penultimate females and their nearest adult/penultimate female neighbor with the distance between the webs of newly-matured males and their nearest adult/penultimate female neighbor (using a  $t$  test,  $n = 108$  pairs of webs; see Clark and Evans, 1954). I also compared



**Figure 2**  
Probability of survival of control males (Kaplan-Meier survivor function) as a function of the number of days after capture. Males were either unmarked controls (CU, solid line) or marked with Dope modeling point (CM, dashed line) in 1995–1996 (A) (CU,  $n = 15$ ; CM,  $n = 15$ ) and 1996–1997 (B) (CU,  $n = 15$ ; CM,  $n = 14$ ).

these distances to the mean nearest neighbor distance for webs marked at a second site ( $n = 23$  webs, 1996–1997, the Lesmurdie Nature Reserve, approximately 25 km east of Perth, a less disturbed habitat than the Agriculture site).

### Male phenotype and survivorship

For survey data, I used  $t$  tests (corrected for multiple comparisons; Rice, 1989) to compare the mean phenotype (weight, size, and condition) of males that reached the web of a potential mate with those that died during mate search.

I also tested the effect of male phenotype by releasing size-mismatched pairs of males from fixed points within the field site and noting their relative success at finding potential mates through web surveys (1996–1997). Males were collected as penultimate instar juveniles and kept in the laboratory until 2 to 4 days after their final molt, when they were individually marked and released. There were five release points at the field site, each of which was 2.46 to 4.40 m from the nearest adult/penultimate female web and at least 10 m from any site boundary. Two males, differing in body weight by at least 0.50 mg, were released at each point at 1-hour intervals on each of five consecutive nights. A coin toss determined which male was released first. I searched for released males in female webs for the following 35 days. I used a Fisher's Exact test to assess whether relative size class (larger or smaller) affected search

outcome (success or death). The release study also provided a third estimate of the mortality rate of mate-searching males that I compared to estimates from the observational study using a  $\chi^2$  test.

### Comparing costs and benefits of cannibalism

Males that facilitate cannibalism and those that avoid cannibalism will gain equal fitness payoffs from a given mating if their mates do not copulate again (cannibalism does not increase female reproductive output; Andrade, 1996). Comparing fitness payoffs for sacrificial and nonsacrificial males requires assessment of expected paternity for males following each strategy under sperm competition, and an estimation of the likelihood of female multiple mating. The simple inequality below captures the nature of the tradeoff for self-sacrificial males (paternity increase versus loss of future reproduction). A more comprehensive analysis, including complexities introduced by variation in female receptivity, will be presented elsewhere (Andrade, 2000).

The fitness benefit of self-sacrifice is the expected increase in paternity after a cannibalistic compared to a noncannibalistic mating; the cost is equivalent to the expected future paternity of a noncannibalized, once-mated male. If  $P$  is a male's paternity after one cannibalistic ( $P_C$ ) or noncannibalistic ( $P_{NC}$ ) mating, and  $E$  is the expected number of matings in the lifetime of a male for whom mortality only occurs during mate search, and who is on the web of his first potential mate, then self-sacrifice will increase male fitness when

$$P_C - P_{NC} > P_{NC}(E - 1) \quad (1)$$

or

$$P_C > EP_{NC}. \quad (2)$$

Here I assume that mate search mortality is not strategy dependent. Under this assumption, any mortality that occurs before the first encounter with a female is not relevant to a comparison of the fitness effects of the two strategies.

### Calculating the expected number of lifetime mating opportunities

To calculate the expected number of lifetime matings for a male currently on a female's web when there is no risk of cannibalism, I make two conservative assumptions: (1) the probability of a male surviving from one encounter with a female to the next is constant regardless of the number of encounters achieved, and (2) the only source of mortality for males is mortality during mate search. Given these assumptions, by first step analysis (Taylor and Karlin, 1998), the expected number of lifetime encounters for a male currently on a female's web is

$$E = 1/m \quad (3)$$

where  $m$  is the probability of dying during the trip from the web of one female to another.

## RESULTS

### Controls

Paint marking had no effect on male survival in either year (Tarone-Ware Log-rank test: 1995–1996:  $\chi^2 = 0.94$ ,  $df = 1$ ,  $p = .33$ ; mean survivorship  $\pm$  SE: CM =  $23.33 \pm 1.62$ , CU =  $21.00 \pm 1.55$ ; 1996–1997:  $\chi^2 = 0.091$ ,  $df = 1$ ,  $p = .76$ ;

CM =  $21.93 \pm 1.78$ , CU =  $21.40 \pm 1.60$ ) (Figure 2). All control males died within 36 days of collection.

### Male interweb mortality

Few males survived the trip to their first mate. In 1995–1996, only six of 48 males (13%) reached the web of a potential mate after abandoning their juvenile web ( $m = 0.87$ ), and in 1996–1997, 12 of 110 males (11%) reached the web of a potential mate ( $m = 0.89$ ). Similarly, in the male release experiment, seven of 50 released males (14%) were recovered on webs of adult/penultimate females ( $m = 0.86$ ). Estimates of male interweb survivorship did not depend on whether they were derived from either field season or the release experiment ( $\chi^2 = 0.32$ ,  $df = 2$ ,  $p = .85$ ). I directly observed 24 predation events on males by (a) ants ( $n = 4$  observations), (b) heterospecific spiders (including *Achaearanea* sp.,  $n = 15$ ; jumping spiders,  $n = 2$ ); and (c) juvenile *L. hasselti* females (females of fifth instar and younger,  $n = 3$ ).

### Male movement and nearest-neighbor distances

Newly matured males and once-mated males move similar distances to reach the web of an adult or penultimate female. In 1995–1996, the nearest-neighbor distance between newly matured males and adult/penultimate females was 3.40 m (SE = 0.42,  $n = 35$ ), and the interfemale nearest-neighbor distance was 3.64 m (SE = 0.40, Student's  $t$  test:  $t = 0.34$ ,  $df = 68$ ;  $p = .67$ ). In 1996/97, the male-female nearest-neighbor distance was 2.94 m (SE = 0.30 m,  $n = 66$ ) and the interfemale distance was 2.78 m (SE = 0.36; Student's  $t$  test:  $t = -0.43$ ,  $df = 130$ ;  $p = .72$ ). In 1996–1997 experimental release points were 3.21 m (SE = 0.27,  $n = 5$ ) away from the nearest adult/penultimate female web, very similar to the interfemale web distance that year (Mann-Whitney  $U$  test:  $U = 121.0$ ,  $p = .32$ ). Nearest-neighbor distances at the Lesmurdie nature reserve (mean = 2.40, SE = 0.49 m) were also comparable to interfemale web distances that year (Student's  $t$  test:  $t = 0.56$ ,  $df = 87$ ;  $p = .58$ ). On average, successful males moved a distance equivalent to the trip to the nearest female web; however a few males traveled more than 8 m (Figure 3).

### Male phenotype and survivorship

There was no significant effect of size, weight, or condition on male survivorship during mate search. Pairs of males in the experimental release were chosen from throughout the range of observed male body weights and sizes (Figure 1). The mean weight difference of paired large and small males was 1.22 mg (Table 1)—almost 30% of the average body weight of males captured in the field that year (mean, 4.09 mg, SE = 0.06,  $n = 520$  males). Larger males of each experimental pair were slightly less likely to die before reaching the web of a potential mate (20 of 25, 80%) than were smaller males (23 of 25, 92%), but this difference was not significant (Fisher's Exact test,  $p = .42$ ).

Similarly, in the observational study, males that survived the search for a mate tended to be slightly larger than males that died, but none of these differences were significant (Table 1). Because the number of surviving males was small, I pooled data from both field seasons and the release experiment to increase the power of this test. Even with the pooled data, there were no significant differences in the size, weight, or condition of males that survived and those that did not (Table 1), but power of these tests was still relatively low (power: size = 0.50, weight = 0.38, condition = 0.07; G\*Power; Buchner et al., 1997). However, for control males, which had no extrinsic sources of mortality, condition predicted 20% of the variation in survivorship (1996–1997;  $r^2 = .20$ ,  $p = .02$ ,  $n = 28$ ).

**Comparing costs and benefits of cannibalism**

Figure 4 shows the general relationship between the paternity of a male that is cannibalized ( $P_C$ ) and the paternity of a male that is not cannibalized ( $P_{NC}$ ), for which male self-sacrifice yields fitness equal to a strategy of avoiding cannibalism. Each line represents a different expectation of lifetime mating opportunities for a male initially found on a female’s web ( $E$ , from Equation 3). For any given value of  $E$  and  $P_{NC}$ , sacrifice will lead to higher fitness payoffs than avoiding cannibalism when  $P_C$  exceeds the value at the relevant line.

Paternity effects of cannibalism were estimated from a laboratory study:  $P_C = 0.92$ ;  $P_{NC} = 0.45$  (Andrade, 1996). Using these empirically derived estimates of  $P_C$  and  $P_{NC}$ , Expression 2 becomes

$$0.92 > E(0.45). \tag{4}$$

So the benefit of being cannibalized by the female will exceed lost reproductive opportunities for redback males whenever

$$E < 2.04, \tag{5}$$

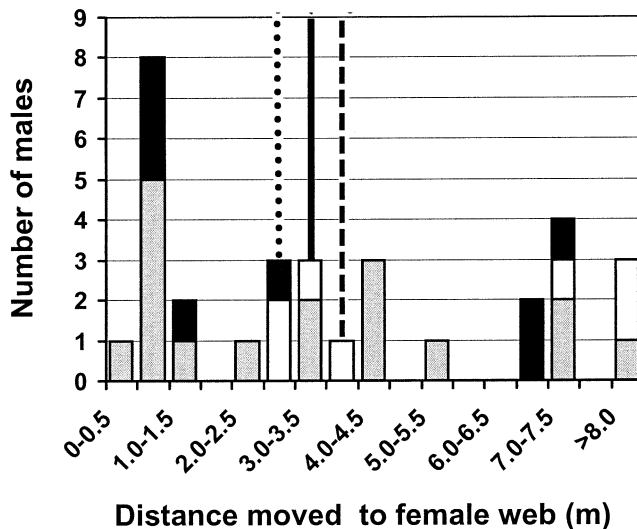
which, by Equation 3, corresponds to an interweb mortality rate of 0.49.

**Expected lifetime mating opportunities**

The probability of mortality for males moving between webs ( $m$ ) is between 0.80 (large release males) and 0.92 (small release males). Using the lowest estimate of male mortality and Equation 3, the total expected number of encounters for a large male currently on a female’s web (with no risk of cannibalism) is

$$E = 1/0.80 = 1.25 \text{ encounters} \tag{6}$$

and at the highest estimate of male mortality, small males can expect



**Figure 3**  
Distances (m) moved to new webs by surviving males in the release study (empty bars), and by males that were marked as newly matured adults in 1995–1996 (solid bars) and 1996–1997 (shaded bars). Vertical lines show the average distance to the nearest adult/penultimate female web in each field season (dotted line, 1996–1997; dashed line, 1995–1996) and for experimentally released males (solid line).

$$E = 1/0.92 = 1.09 \text{ encounters.} \tag{7}$$

Data from both field seasons yields an average interweb mortality rate of  $m = 133/158 = 0.84$ . Thus the best estimate of the expected number of lifetime encounters for a male found with a female is

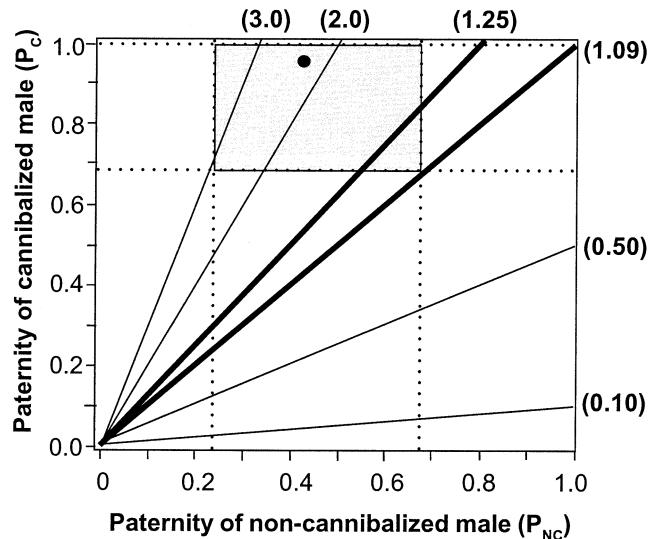
**Table 1**  
**Comparison of newly matured males that survive the trip to find a mate and those that perish**

Phenotype	Survived	Perished	T	$p$	$p_b$
<b>Field survey 1</b>					
$n$	8	40			
Weight (mg)	4.35 (0.64)	3.83 (0.22)	-0.91	.37	—
<b>Field survey 2</b>					
$n$	17	93			
Weight (mg)	5.05 (0.48)	4.34 (0.16)	-1.67	.10	.29
Size (mm)	3.05 (0.10)	2.89 (0.04)	-1.52	.13	.40
Condition <sup>a</sup>	0.367 (0.27)	0.113 (0.10)	-0.97	.34	.34
<b>Male release experiment</b>					
$n$	7	43			
Weight (mg)	3.74 (0.23)	3.60 (0.17)	-0.31	.75	.75
Size (mm)	2.98 (0.16)	2.80 (0.05)	-1.38	.52	1.00
Condition <sup>a</sup>	-0.23 (0.21)	0.04 (0.13)	0.82	.42	1.00
<b>Pooled data</b>					
$n$	24	136			
Weight (mg) <sup>b</sup>	4.60 (0.31)	4.04 (0.11)	-1.89	.18	.36
Size (mm)	3.03 (0.08)	2.86 (0.03)	-2.01	.05	.14
Condition <sup>a</sup>	0.19 (0.21)	0.09 (0.08)	-0.50	.62	.62

Values are mean (SE).  $p$  indicates uncorrected  $p$  values;  $p_b$ , sequential Bonferroni adjusted  $p$  values (Rice, 1989) from a pooled-variance  $t$  test for differences between means.

<sup>a</sup> Residuals from a regression of male weight on size. Weight/size regressions were highly significant (field season 2:  $r^2 = .52$ ,  $p < .001$ ; release experiment:  $r^2 = .45$ ,  $p < .001$ ).

<sup>b</sup> Sample sizes for pooled weights: 32 survived, 176 perished.



**Figure 4**  
Theoretical relationship between the paternity achieved by a male that avoids cannibalism in each mating ( $P_{NC}$ ) compared to a male that is cannibalized when he mates ( $P_C$ ) at which the fitnesses of males following each strategy are equal. Solid lines show the equal-fitness values of  $P_C$  and  $P_{NC}$  at different expectations of future mating opportunities for males ( $E$ , numbers in brackets adjacent to each line, from Equation 3). For a given expected paternity for a  $P_{NC}$  male, and value of  $E$ , male self-sacrifice will be favored whenever the paternity of a cannibalized male falls above the relevant line. The two bold lines are the maximum and minimum field-derived estimates of  $E$  for redback spiders. The filled circle shows an empirical estimate of ( $P_{NC}$ ,  $P_C$ ) for redback spiders, and dotted lines are 95% confidence intervals around the estimate (see Andrade, 1996: 70).

$$E = 1/0.84 = 1.19 \text{ encounters.} \quad (8)$$

Thus, any male that reaches the web of a female can expect only the mating in which he is currently engaged—the likelihood of reaching a second female is small. Figure 4 shows that at the empirically-derived values of  $P_C$  and  $P_{NC}$  for redback males (mean, solid circle; 95% confidence limits for each estimate, dotted lines; Andrade, 1996), self-sacrifice will yield higher fitness than a multiple-mating strategy whether  $E$  is at the minimum (Equation 7) or maximum (Equation 6) value derived here (bold lines).

This analysis also suggests that most males will die without ever encountering a female. The expected number of lifetime encounters for a male that starts out on his juvenile web is equal to

$$E - 1. \quad (9)$$

Given the best estimate of  $E$  (Equation 8), a typical male redback can expect only 0.19 encounters in his lifetime.

## DISCUSSION

Male redback spiders (*L. hasselti*) are unlikely to have the opportunity to mate more than once in their lifetimes. Estimates of mortality rates were very similar for both replicates of the observational study and for the experimental release—at least 80% and up to 92% of males died during the search for a potential mate. These data suggest that very few males achieve an encounter with a female before death (see Equations 6 and 7). In addition, although condition is a strong predictor of survival for males with no extrinsic sources of mortality, this advantage is lost during mate searching. I could

find no significant effect of male condition, size, or weight on the likelihood of survival for searching males. Observations suggest that much of male mortality during mate search may be owing to predation by larger animals that are unlikely to be deterred by relatively small differences in male size or condition. Although there was a trend for larger males to be more likely to reach female webs, even males in larger size classes could expect only 0.25 encounters in their lifetime (Expression 4 and Equation 7). Thus, the conclusion that males rarely encounter females does not change significantly as a function of male phenotype. The quantitative analysis of the fitness effects of sacrificial behavior suggests that self-sacrifice is the best strategy for all redback males (Figure 4).

The number of matings achieved by a male is likely to be even lower than calculated here if interweb mortality rates increase as males age and if intermale competition ensures copulation is not the inevitable result of every encounter. The average number of rival males per web is two, but at least 30% of females may mate with only one male in nature (Andrade, 1996). Thus, when a male redback is mating, his residual reproductive value is likely to be close to zero. This will lead to strong selection on males to use strategies that maximize their reproductive output from that single mating.

Selection favoring self-sacrifice would be weakened if there were significant individual variation in the expectation of future mating. Although I found no evidence of variation in mortality risk as a function of male phenotype, tests for phenotypic effects were of low power and may have been unable to detect small differences between males that survived and those that perished. Nevertheless, given the paternity benefits of cannibalism for males, the expectation of future mating would have to be greater than 2.04 (Expression 5), equivalent to a mate search mortality risk lower than 0.49, to alter the conclusion that self-sacrifice is the best strategy. This is a much lower mortality risk than 0.80, the lowest rate measured here ( $\chi^2 = 4.37$ ,  $df = 1$ ,  $p = .04$ ). Moreover, even with a relatively small sample of 25 release males (large males, Table 1), the power to detect a difference between a measured mortality rate of 0.80 and the rate at which the best strategy would no longer be self-sacrifice (0.49) is 91% (Systat power analysis for single proportions; Dallal et al., 2002). Finally, aging patterns of male redbacks in the laboratory suggest life history adaptations to high extrinsic mortality (see Austad, 1993); adult males experience rapid senescence relative to adult females, even under ideal conditions (male longevity, Figure 2; female longevity: Andrade and Banta, 2002). Thus, the available data support the conclusion that mortality risk is high for all males and will have a strong effect on mating strategies.

One apparent response to these ecological conditions is male self-sacrifice. With the measured mortality rates during mate searching, the paternity benefits of being cannibalized (Andrade, 1996) will always outweigh the reproductive opportunities lost by cannibalized males (Figure 4). Consistent with this interpretation, the copulatory somersault may be fixed in the species. Every copulation described to date (Andrade, 1996, 1998; Cariaso, 1967; Forster, 1992, 1995) involves a somersault by the male onto the female's fangs, whereas this behavior has not been reported in other black widows (see Kaston, 1970). Variation in the outcome of mating for male redbacks (i.e., death or survival) is apparently owing to variation in female cannibalistic behavior rather than to variation in male somersault behavior (Andrade, 1998).

Although high mortality rates can affect selection on male strategies, this alone is not sufficient to favor self-sacrifice (Buskirk et al., 1984). Among invertebrates, male encounter rates with predatory conspecific females have been monitored or estimated in an eresid spider (Schneider and Lubin, 1996)

and in praying mantis (Maxwell, 1998). Males of these species do not show behaviors consistent with self-sacrifice, despite relatively low encounter rates with females. Male eresid spiders can expect to encounter and mate with 1.2 females on average (Schneider and Lubin, 1996). However, some males of this species encounter three, four, or more than five females, and less than 30% of males die without encountering a female (Figure 2; Schneider and Lubin, 1996). This is very different from redbacks (Figure 4). Male praying mantis may have a distribution of encounter rates more similar to redbacks—in one study, only four, 19% of males, were observed to interact with more than one female in a season (Maxwell, 1998). However, there is no evidence that male mantis engage in self-sacrifice (Maxwell, 1998, 1999). Despite the high mortality rates, this is expected (Buskirk et al., 1984) because there is little evidence of a reproductive benefit for cannibalized males (Maxwell, 1998). These studies suggest that (1) the probability of male remating must be consistently low to favor self-sacrifice, and (2) the benefit of sexual cannibalism, which in redbacks arises as a result of female reproductive biology, is also essential for the evolutionary maintenance of self-sacrifice. Given that male mating opportunities are apparently limited in other systems in which sacrifice is absent (see Breene and Sweet, 1985; Maxwell, 1998; Vollrath and Parker, 1992), it would be interesting to focus on the question of male self-sacrifice from the perspective of the female; i.e., why do females of some species cede reproductive benefits to males that they cannibalize (see Andrade, 1996; Elgar et al., 2000).

A second striking aspect of redback male reproductive behavior is the functional sterility that ensues after mating. The data presented here demonstrate that functional sterility after one mating is not reproductively costly for males. Although there is no known benefit derived from sterility, it might result from a male allocation strategy that involves maximal investment in one mating. Thus, it is plausible that both sacrifice and sterility are maintained as part of a male terminal investment strategy that is favored by ecological factors (Andrade and Banta, 2002). This is contrary to hypotheses positing that intrinsic constraints on male multiple mating lead to vulnerability to cannibalism (see Gould, 1984). Mechanistically, functional sterility in redbacks may arise from damage that occurs to male palps during mating (see Berendonck and Greven, 2002; Bhatnagar and Rempel, 1962). Gould (1984) proposed that *Latrodectus* males might frequently succumb to sexual cannibalism because mechanistic damage to the palps would weaken them and leave them unable to escape predatory females after copulation. He argued that complicity in sexual cannibalism was unlikely to ever be favored by selection, and would instead arise only as a maladaptive consequence of other traits (Gould, 1984). This was in contrast to the model of Buskirk et al. (1984), which predicted that selection imposed by costly mate searching, rather than constraint, might lead to males facilitating their own consumption by their mates. The data presented here are consistent with the Buskirk et al. model (1984). Sterility in redbacks—a putative intrinsic constraint on multiple mating—is not necessary to explain male self-sacrifice. This conclusion is also consistent with comparative data. Palpal damage associated with mating has been reported in many species of *Latrodectus* (see Berendonck and Greven, 2002; Bhatnagar and Rempel, 1962; Foelix, 1982) and in *Nephila* spiders (Christenson, 1989; Schneider et al., 2001) among others, but male self-sacrificial behavior, or even male behavior that is neutral with respect to potential female attacks, has not been reported in any of these species. This result is interesting because the relative importance of intrinsic constraints in the evolution of behavioral strategies

has been controversial in general (see Brooks and McLennan, 1991; Reeve and Sherman, 1993), as well as in the case of male self-sacrifice in particular (see Alcock, 1998; Buskirk et al., 1984; Gould, 1984). A phylogenetic test of these hypotheses would complement this study by providing insight into the importance of ecology versus constraint in the origin of self-sacrifice. However, the data presented here demonstrate that consistent with theory (Buskirk et al., 1984), ecological factors could combine with female reproductive biology to favor the copulatory sacrifice in male redback spiders.

This work was funded by the National Science Foundation (Doctoral Dissertation Improvement Grant to M.C.B.A. and P. W. Sherman), the Leon fellowship fund, and the Olin foundation (Cornell University), and I was supported by a Natural Sciences and Engineering Research Council 1967 Science and Technology fellowship and an Olin fellowship during different phases of this work, which was completed in partial fulfillment of the requirements for a Ph.D. in the Department of Neurobiology and Behavior at Cornell University. I thank D. Cook and F. Berlandier of Agriculture Western Australia; W. Bailey, D. Edwards, and especially I. Dadour of the University of Western Australia for help with collecting permits and/or for providing research space and equipment in Australia; and F. Berlandier and I. Dadour for generously providing accommodation in Australia. F. Berlandier, M. Kolybaba, and A. C. Mason helped in the field. R. R. Hoy, K. Adler, and R. Booker provided research space or equipment at Cornell University. This paper was improved by comments from P. Biston, R. B. Cocroft, M. E. Hauber, A. C. Mason, S. Kain, the “shemlens” group, and behavior “lunch bunch” (Cornell University, 1996–2000). I am grateful for helpful suggestions from my PhD committee: P. W. Sherman, S. T. Emlen; R. R. Hoy, B. N. Danforth, and H. K. Reeve.

## REFERENCES

- Alcock J, 1998. Unpunctuated equilibrium in the natural history essays of Stephen Jay Gould. *Evol Hum Behav* 19:321–336.
- Anava A, Lubin Y, 1993. Presence of gender cues in the web of a widow spider, *Latrodectus revivensis*, and a description of courtship behaviour. *Bull Br Arachnol Soc* 9:119–122.
- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Andrade MCB, 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science* 271:70–72.
- Andrade MCB, 1998. Female hunger can explain variation in cannibalistic behavior despite male sacrifice in redback spiders. *Behav Ecol* 9:33–42.
- Andrade MCB, 2000. Constraints on mating success and selection for male sacrifice in redback spiders (PhD dissertation). Ithaca, New York: Cornell University.
- Andrade MCB, Banta EM, 2002. Value of remating and male functional sterility in redback spiders. *Anim Behav* 63:857–870.
- Arnqvist G, Henriksson S, 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evol Ecol* 11:253–271.
- Austad SN, 1993. Retarded senescence in an insular population of Virginia opossums (*Didelphis virginiana*). *J Zool* 229:695–708.
- Berendonck B, Greven H, 2002. Morphology of female and male genitalia of *Latrodectus revivensis* Shulov, 1948 (Araneae, Theridiidae) with regard to sperm priority patterns. In: European arachnology 2000 (Toft S, Scharff N, eds). Aarhus: Aarhus University Press; 157–167.
- Bhatnagar RDS, Rempel JG, 1962. The structure, function, and postembryonic development of the male and female copulatory organs of the black widow spider *Latrodectus curacaviensis* (Muller). *Can J Zool* 40:465–510.
- Blanke VR, 1975. Untersuchungen zum Sexualverhalten von *Cyrtophora cicatrosa* (Stoliczka) (Araneae, Araneidae). *Z Tierpsychol* 37:62–74.
- Breene RG, Sweet MH, 1985. Evidence of insemination of multiple females by the male black widow spider, *Latrodectus mactans* (Araneae, Theridiidae). *J Arachnol* 13:331–335.

- Brooks DR, McLennan DA, 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. Chicago: University of Chicago Press.
- Brown WD, Crespi BJ, Choe JC, 1997. Sexual conflict and the evolution of mating systems. In: The evolution of mating systems in insects and arachnids. (Choe J, Crespi B, eds). Cambridge: Cambridge University Press; 352–378.
- Buchner A, Erdfelder E, Faul F, 1997. How to use G\*Power. [http://www.psych.uniduesseldorf.de/aap/projects/gpower/how\\_to\\_use\\_gpowers.htm](http://www.psych.uniduesseldorf.de/aap/projects/gpower/how_to_use_gpowers.htm).
- Buskirk RE, Frohlich C, Ross KG, 1984. The natural selection of sexual cannibalism. *Am Nat* 123:612–624.
- Cariaso BJ, 1967. Biology of the black widow spider, *Latrodectus hasselti* Thorell (Araneida: Theridiidae). *Philipp Agric* 51:171–180.
- Christenson T, 1989. Sperm depletion in the orb-weaving spider *Nephila clavipes* (Araneae: Araneidae). *J Arachnol* 17:115–118.
- Clark P, Evans F, 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- Dallal GE, Pechnyo M, Marcantonio R, 2002. Power analysis. In: *Systat 10.2, statistics II*. Richmond, California: Systat Software; 311–393.
- Elgar MA, 1992. Sexual cannibalism in spiders and other invertebrates. In: *Cannibalism: ecology and evolution among diverse taxa* (Elgar M, Crespi B, eds). Oxford: Oxford University Press; 128–155.
- Elgar MA, Schneider JM, Herberstein ME, 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proc R Soc Lond B* 267:2439–2443.
- Foelix R, 1982. Biology of spiders. Cambridge: Harvard University Press.
- Forster LM, 1984. The Australian redback spider (*Latrodectus hasselti*): its introduction and potential for establishment and distribution in New Zealand. In: *Commerce and the spread of pests and disease vectors* (Laird M, ed). New York: Praeger; 273–289.
- Forster LM, 1992. The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae), the Australian redback spider. *Aust J Zool* 40:1–11.
- Forster LM, 1995. The behavioural ecology of *Latrodectus hasselti* (Thorell), the Australian redback spider (Araneae: Theridiidae): a review. *Rec West Aust Mus Suppl* 52:13–24.
- Forster LM, Kingsford S, 1983. A preliminary study of development in two *Latrodectus* species (Araneae: Theridiidae). *N Z Entomol* 7: 431–438.
- Gould SJ, 1984. Only his wings remained. *Nat Hist* 9:10–18.
- Grasshoff M, 1964. Die Kreuzspinne *Araneus pallidus*—ihr Netzbau und ihre Paarungsbiologie. *Nat Mus* 94:305–314.
- Jakob EM, Marshall SW, Uetz GW, 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77:61–67.
- Jamieson IG, 1986. The functional approach to behavior: is it useful? *Am Nat* 127:195–208.
- Johns P, Maxwell M, 1997. Sexual cannibalism: who benefits? *Trends Ecol Evol* 12:127–128.
- Kaston BJ, 1970. Comparative biology of American black widow spiders. *San Diego Soc Nat Hist Trans* 16:33–82.
- Kavale J, 1986. The comparative biology of two *Latrodectus* species. In: *Zoology*. Dunedin: University of Otago.
- Knoflach B, van Harten A, 2000. Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). *J Nat Hist* 34:1639–1659.
- Knoflach B, van Harten A, 2001. *Tidarren argo* sp. nov. (Araneae: Theridiidae) and its exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug and sexual cannibalism. *J Zool* 254:449–459.
- Levi HW, 1959. The spider genus *Latrodectus* (Araneae, Theridiidae). *Trans Am Microsc Soc* 78:7–43.
- Levi HW, 1969. Notes on American Theridiid spiders. *Psyche March*: 68–73.
- Maxwell M, 1998. Lifetime mating opportunities and male mating behaviour in sexually cannibalistic praying mantids. *Anim Behav* 55:1011–1028.
- Maxwell M, 1999. The risk of cannibalism and male mating behaviour in the Mediterranean praying mantid, *Iris oratoria*. *Behaviour* 55:1011–1028.
- McAllister MK, Roitberg BD, 1987. Adaptive suicidal behaviour in pea aphids. *Nature* 328:797–799.
- Parker GA, 1979. Sexual selection and sexual conflict. In: *Sexual selection and reproductive competition in insects* (Blum M, Blum N, eds). New York: Academic Press; 123–166.
- Reeve HK, Sherman PW, 1993. Adaptation and the goals of evolutionary research. *Q Rev Biol* 68:1–32.
- Rice WR, 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Sasaki T, Iwahashi O, 1995. Sexual cannibalism in an orb-weaving spider *Argiope aemula*. *Anim Behav* 49:1119–1121.
- Schneider JM, Lubin Y, 1996. Infanticidal male cressid spiders. *Nature* 381:655–656.
- Schneider JM, Thomas ML, Elgar MA, 2001. Ectomised conductors in the golden orb-web spider, *Nephila plumipes* (Araneoidea): a male adaptation to sexual conflict? *Behav Ecol Sociobiol* 49:410–415.
- Steinberg D, Preston D, Clarkson D, Colla, P. 2002. *Survival analysis. In: Systat 10.2: statistics II*. Richmond, California: Systat Software; 533–580.
- Suter R, 1991. Ballooning in spiders: results of wind-tunnel experiments. *Ethol Ecol Evol* 3:13–25.
- Taylor HM, Karlin S, 1998. *An introduction to stochastic modeling*, 3rd ed. New York: Academic Press.
- Vollrath F, 1998. Dwarf males. *Trends Ecol Evol* 13:159–163.
- Vollrath F, Parker G, 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature* 360:156–159.
- Waser PM, Creel SR, Lucas JR, 1994. Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behav Ecol* 5:135–141.