Female hunger can explain variation in cannibalistic behavior despite male sacrifice in redback spiders

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Male Australian redback spiders (*Latrodectus hasselti* Thorell: Theridiidae) place their abdomens directly over their mate's mouthparts during copulation, increasing the likelihood of sexual cannibalism. Male sacrifice may be adaptive because cannibalized males increase their paternity relative to those that are not eaten. Despite male sacrifice behavior, however, up to 50% of laboratory matings may end without sexual cannibalism. Here, I report a similar pattern in the field, where males were not cannibalized in 35% of observed matings (6/17). I examined variation in female cannibalistic behavior by evaluating the following three hypotheses for the occurrence of cannibalism from the female perspective: (1) the mistaken identity hypothesis proposes that females sometimes cannibalize males because they mistake them for prey, (2) the mate rejection hypothesis predicts that females cannibalize males who are unacceptable as mates, and (3) the feeding opportunism hypothesis predicts that hungry females are more likely to be cannibalistic. Field observations refuted the first two hypotheses: females recognized males as potential mates (i.e., nonprey), and cannibalized and noncannibalized males were not phenotypically different. The feeding opportunism hypothesis was supported. In staged field matings, cannibalistic females were hungrier than their noncannibalistic counter-parts. Moreover, a logistic regression analysis indicated that hunger was a significant predictor of cannibalism. Because redback males are below the typical prey size that females accept, well-fed females are less likely to consume their mates, despite the vulnerable mating posture. These results indicate that, although males facilitate sexual cannibalism, their fate may depend on the female's physical condition. *Key words:* feeding opportunism, female choice, food limitation, *Latrodectus hasselti*, male sacrifice, redback spider, sexual cannibalism, Theridiidae. *[Behav Ecol 9:33–42 (1998)]*

Sexual cannibalism in invertebrates often occurs as the result of a sexual conflict of interest (Elgar, 1992; Gould, 1984; Johns and Maxwell, 1997; Parker, 1979). For example, male praying mantids and orb-weaving spiders are sometimes consumed by their larger, predatory mates despite behaviors that could promote their escape (Elgar, 1992; Liske and Davis, 1984, 1987). The Australian redback spider (*Latrodectus hasselti* Thorell) may represent an exception to this traditional view of sexual cannibalism: male redbacks have an unusual behavior that appears to facilitate their consumption by the female during copulation (Forster, 1992). During sperm transfer, the male redback moves into a "somersault" posture that places his abdomen over the female's mouthparts (Cariaso, 1967; Forster, 1992), apparently making it easy for the female to consume him (Forster, 1992). Males that are cannibalized obtain paternity advantages compared to males that survive copulation (Andrade, 1996). Even if males survive mating, ecological factors may reduce the likelihood that they could remate (see Andrade, 1996), and thus cannibalism may be adaptive for males. However, not all females eat their mates. Despite the vulnerable somersault posture, males were not consumed in 25–50% of laboratory matings (calculated from Cariaso, 1967; Forster, 1992). In this paper, I evaluate hypotheses for this intriguing variation in female cannibalistic behavior.

Four hypotheses to explain the occurrence of sexual cannibalism in arthropods are outlined in Table 1. Three of these argue that sexual cannibalism is advantageous for females and

usually entails a fitness cost for males. The fourth hypothesis is unique in contending that cannibalism may provide some fitness benefit for the cannibalized male (i.e., the male sacrifice hypothesis). Because fitness effects of sexual cannibalism may be very different for males and females, the behavior of both sexes must be examined to understand variation in the occurrence of cannibalism. Although the male sacrifice hypothesis considers cannibalism from the male perspective and the other three hypotheses address the female perspective, all the female advantage hypotheses are not equally likely if the male sacrifice hypothesis holds. The timing of sexual cannibalism (before, after, or during sperm transfer) can determine which hypotheses are most likely in a given system because it can define the possible fitness effects for females (Newman and Elgar, 1991) and males (Elgar 1992).

For example, the mistaken identity and mate rejection hypotheses would only apply if males are consumed before sperm transfer. Under the mistaken identity hypothesis, females do not recognize males as potential mates and can benefit nutritionally from eating them, and cannibalized males die without reproducing (mantids: Birkhead et al., 1988; Matsura and Morooka, 1983; spiders: Elgar and Nash, 1988). In comparison, the mate rejection hypothesis proposes that females use sexual cannibalism as a mechanism of mate choice. Females recognize male conspecifics as potential mates, but low-quality males are eaten before sperm transfer and thus rejected by the female (Elgar and Nash, 1988). The feeding opportunism hypothesis also proposes that females recognize potential mates, but cannibalistic behavior is determined by hunger level. Males may be consumed during courtship, copulation, or after copulation by hungry females.

The male sacrifice hypothesis proposes that cannibalism occurs because of male facilitation and results in an increase in the proportion of eggs fertilized relative to rival males (mating

Table 1

Hypotheses for the occurrence of sexual cannibalism and their key predictions

Hypothesis[a]	Predictions	Benefit to
Female advantage hypotheses		
Mistaken identity[b]: females sometimes mistake males for prey	(1) Sexual cannibalism is infrequent (2) Precopulatory cannibalism (3) Females do not recognize cannibalized males as potential mates (4) Female behavior toward cannibalized male is indistinguishable from behavior toward prey (5) No explicit prediction about phenotype of cannibalized males	Female: meal Male: none
Mate rejection[c]: Females only cannibalize low-quality males	(1) No prediction about prevalence of cannibalism (2) Precopulatory cannibalism (3) Females recognize males as potential mates (4) Males who are not eaten, but mate successfully, are phenotypically superior to cannibalized males (e.g., with respect to size, mass, courtship vigor)	Female: meal, only high-quality males father young Male: none
Feeding opportunism[d]: hungry females cannibalize males	(1) No prediction about prevalence of cannibalism (2) Pre- or postcopulatory cannibalism (3) Females recognize males as potential mates (4) No explicit prediction about phenotype of cannibalized males (5) Cannibalism is more likely if the female is hungry	Female: meal, increase in number or quality of offspring possible Male: increase in the number or quality of offspring possible
Male advantage hypothesis		
Male sacrifice[e]: cannibalism increases male reproductive success	(1) No prediction about prevalence of cannibalism (2) Cannibalism is during or after copulation (3) Females recognize males as potential mates (4) No explicit prediction about the phenotype of cannibalized males (5) Males do not resist cannibalism (6) Cannibalized males have higher reproductive success than males that are not cannibalized	Female: meal Male: increase in proportion of female's eggs fertilized and/or increase in number or quality of offspring

[a] See Elgar (1992) for a review of these hypotheses.

[b] Robinson (1982), Gould (1984), Elgar (1992), Arnqvist and Henrikkson (1997).

[c] Darwin (1871), Elgar and Nash (1988).

[d] Matsuro and Morooka (1983), Liske and Davis (1984, 1987), Birkhead et al. (1988), Newman and Elgar (1991).

[e] Thornhill (1976), Downes (1978), Parker (1979), Buskirk et al. (1984), Sasaki and Iwahashi (1995), Andrade (1996).

effort; Andrade, 1996; Elgar, 1992; Parker, 1979) or an increase in the absolute number or fitness of offspring through the donation of somatic nutrients from the male (paternal effort; Buskirk et al., 1984; Thornhill, 1976). Male sacrifice can hold only if the cannibalized male fathers offspring, which is not predicted by the mate rejection or mistaken identity hypotheses, but does not necessarily conflict with the predictions of the feeding opportunism hypothesis (Table 1).

Evidence of male sacrifice (Andrade, 1996; Downes, 1978; Forster, 1992; Sasaki and Iwahashi, 1995) and some support for each of the female advantage hypotheses (mistaken identity: Arnqvist and Henriksson, 1997; mate rejection: Elgar and Nash, 1988; feeding opportunism: Birkhead et al., 1988; Kynaston et al., 1994; Liske and Davis, 1984) exists in some species of cannibalistic spiders and praying mantids. However, few of the hypotheses have been tested experimentally (see Elgar, 1992, for a review), and relatively few cannibalism studies have been conducted on field populations (ceratopogonid midges: Downes, 1978; scorpions: Polis and Farley, 1979; spiders: Christenson and Goist, 1979; Jackson, 1980; Sasaki and Iwahashi, 1995; praying mantids: Lawrence, 1992). This is problematic because the frequency or timing of cannibalism may be affected by artificial mating arenas or feeding regimens (Edmunds, 1975; Liske and Davis, 1987; Roeder, 1935, 1962).

In this study, I concentrated on the female advantage hypotheses; the male sacrifice hypothesis has been tested else-

where (Andrade, 1996). First, I addressed key predictions of each hypothesis (Table 1) by watching natural copulations. Second, I tested the feeding opportunism hypothesis directly in a field study in which I supplemented the diet of a subset of females.

Natural history

Australian redback spiderlings emerge from egg sacs (which can contain >300 eggs; Andrade, 1995) throughout the Australian spring and early summer (approximately September–January) and disperse by ballooning (Forster, 1995). Although both sexes emerge at the same time, most males become sexually mature at the fifth instar (after 28–45 days at 25°C) and females at the seventh or eighth instar (after 45–75 days at 25°C; Forster, 1984; Kavale, 1986). All juveniles build webs, but at sexual maturity males cease feeding regularly and abandon their webs to search for females. Adult females construct their webs near the ground and include a partially hidden, dense area of conically shaped webbing (the refuge) as well as an exposed, horizontal portion (the snare; York Main 1964) on which courtship occurs. Although both sexes are the same size at hatching, by adulthood sexual dimorphism is extreme. Male mass (median field mass ± SE = 4.4 ± 0.3 mg, n = 33) is only 1–2% of female mass (256 ± 30 mg; n = 22; Andrade, 1996). Longevity also differs between the sexes: male lifespan

in the laboratory is just 4–8 weeks, compared to up to 2 years for females (Forster, 1984; see Forster, 1995, for a review of *L. hasselti* development and natural history).

Redbacks are primarily nocturnal; females remain inside refuges during the day, occasionally moving onto the snare to capture prey. Any males present on a female's web during the day usually remain stationary near the periphery (Andrade MCB, personal observation; McKeown, 1952). At dusk, females leave the refuge and place themselves on the snare, near the center of the web. In the field, most matings occur between 2200 and 0200 hr (Andrade MCB, personal observation).

During courtship (duration 5.03 ± 0.84 h, Forster, 1995), the female is oriented with her ventral surface up, on the lower surface of her snare. Copulation begins with the male standing on the female's ventral abdominal surface, with both partners facing in the same direction. The female genital openings are located on her venter (on the epigynum), near the point of attachment of the abdomen to the cephalothorax. The male's two intromittant organs, emboli, are located on the palps (the anterior-most appendages), and are inserted in the female's two genital openings during separate copulations. A complete copulation consists of two palpal insertions, each of which inseminates one of the female's two independent spermathecae. During intromission, the male inserts one embolus into one spermatheca, and a few seconds later, moves through 180°, using the inserted palp as a pivot, and comes to rest with the dorsal surface of his abdomen directly over the female's mouthparts (copulatory somersault; Forster, 1992). The male remains in this posture throughout the copulation. In laboratory matings, when cannibalism occurs, it begins during sperm transfer while the male is in this position, when the female extrudes digestive enzymes and may masticate the posterior end of the male's abdomen (Forster, 1992, 1995). After removing the first embolus, the male, even if partially digested, returns to the snare. There he resumes courtship and may remount the female, at which time he inserts his second embolus, and repeats the copulatory somersault. A male may achieve one or two intromissions with his mate (one using each of the pedipalps) and he may be consumed entirely or partially after either (Forster, 1992).

METHODS

I studied wild redbacks in and around an outdoor courtyard on the campus of the University of Western Australia (UWA) and around the outbuildings of the Western Australia Department of Agriculture (WA-Ag) in Perth, Western Australia, during December 1993 and January 1994. I observed undisturbed copulations at the WA-Ag site and noted the following factors, which allowed a preliminary evaluation of the three female advantage hypotheses (Table 1): (1) the prevalence of sexual cannibalism, (2) the timing of sexual cannibalism with respect to copulation, (3) whether there was qualitative evidence of mate recognition by females (i.e., whether female behavior toward males differed from behavior toward prey), and (4) whether cannibalized males differed phenotypically (in size, mass, or condition) from males that were not cannibalized.

Unmanipulated matings

In December 1993, I surveyed webs at WA-Ag to determine whether males typically associated with females before copulation and whether cannibalism ever occurred during web cohabitation (before courtship). I surveyed the webs of 28 adult or subadult females on 4 days during the last 2 weeks of December, estimated female developmental stage, noted the presence of egg sacs and/or males, and the mating status of

any males present. Female instar was determined by comparison to descriptions of laboratory-reared females of known instar (Andrade MCB, unpublished data; Cariaso, 1967; Kavale, 1986;). Male mating status (i.e., virgin or previously mated) was determined by examining the paired male emboli, which are visibly changed by copulation. Each embolus is a tightly coiled, sclerotized tube filled with sperm at maturity and borne on the pedipalp (Bristowe, 1958; Foelix, 1982; Gertsch, 1949). The embolus uncoils when inserted through the female genital opening during copulation, but does not completely recoil after removal. In addition, during courtship, a mid-dorsal constriction appears in the male's abdomen and his posterior abdomen shrinks slightly (Forster, 1992). This abdominal constriction is visible after copulation. Thus, I could determine if a male had mated previously and had not been cannibalized if he had an abdominal constriction in combination with one or two uncoiled emboli.

In early January 1994, 19 of the 28 webs were free of egg sacs and contained adult females and apparently virgin adult males (i.e., no abdominal constriction or damage, coiled emboli). I observed these webs on two consecutive nights and recorded the occurrence and outcome of any mating activity to determine the natural frequency of sexual cannibalism. Webs were inspected on a rotating basis between 1900 and 2400 h, at least twice every hour, for 1–5 min per visit, with the exception of those in which no courtship activity occurred within the first half hour. I excluded webs with no early activity to maximize observation time on active webs. Webs were illuminated with red light during observations (using a headlamp and flashlight with red photographic filters attached) to reduce disturbance to the spiders.

I collected spiders after mating was observed and weighed them with a Mettler AE50 balance (accurate to 0.1 mg). Males were preserved in 75% ethanol, and females were returned to the laboratory at the University of Western Australia, where each was housed alone and fed one katydid (*Requena verticalis*) each week until she produced an egg sac that was reared to hatching (to ensure that the mating had been successful). Females were then preserved in 75% ethanol.

I determined size from measurements of leg length (patella and tibia; average of left and right first leg) and cephalothorax width and length made on preserved spiders using an ocular micrometer. In addition, I examined males with a hand lens or dissecting microscope and classified them on a scale of 1–4 based on abdominal damage each time they were observed on the web during a mating interaction and immediately after copulation (Table 2). I considered sexual cannibalism to have occurred if a female had partly or completely consumed the male's abdominal contents by the end of the final intromission (classes 3 or 4 in Table 2). Cannibalized males (classes 3 and 4) could be distinguished from males that were undamaged (class 1), or that had been affected by digestive enzymes, but not punctured with the female chelicerae (class 2) by examination. Males without punctures in the abdominal integument were not considered to have been cannibalized because theridiids feed by puncturing their prey, regurgitating digestive enzymes into the body, then consuming the externally digested food through puncture wounds.

I dissected preserved females to determine their mating history and thus whether they had been virgins before the observed copulation. A sclerite at the tip of the male's embolus breaks off inside the female spermatheca during copulation (Abalos and Baez, 1963; Bhatnagar and Rempel, 1962; Breene and Sweet, 1985; Eberhard, 1985; Kaston, 1970). Although the embolic sclerite does not appear to prevent the female from remating (Breene and Sweet, 1985; Kaston, 1970), female mating history can be conservatively estimated by the number of sclerites present inside the spermathecae and coiled ducts

Table 2

Postcopulatory classification of males based on abdominal injury after first and second palpal insertions in field matings

| | | | No. males in each class after[b] | |
Class	Male abdominal condition	Canniba-lized?[a]	1st insertion	2nd insertion
1	Alive, undamaged integument	No	8	3
2	Alive, some digestion of abdominal integument, no puncture wound	No	12	7
3	Alive, advanced digestion of abdominal integument, abdomen shrunken, puncture wound present	Yes	1	2
4	Dead, abdomen completely shrunken	Yes	3	8

[a] Males were considered to have been cannibalized if the abdominal integument was punctured by the female (i.e., class 3 or 4).

[b] Includes data from the 24 mating interactions observed (i.e., unmanipulated and experimental matings). Four males did not complete two palpal insertions: 3 were killed during the first insertion and 1 courted the female, but did not copulate a second time.

(Kaston, 1970). For example, if I saw a female receive two palpal insertions from one male, but dissection revealed three sclerites inside her spermathecae, that female had already mated once before the observed mating.

Feeding opportunism experiment

I tested the feeding opportunism hypothesis in a field experiment at the UWA site in which I introduced males to the webs of virgin females that had fed normally or been diet supplemented for the previous 5 weeks. Webs of 39 adult or subadult female redbacks were marked in mid-December 1993. I examined each web daily for 5 weeks and removed males found on the webs to ensure that females remained virgins (actual mating status was confirmed later by dissection). Females found as adults (7 of the 39) had an unknown mating history, but were initially considered virgin because no egg sacs were visible in their webs and they did not produce any egg sacs during the 5-week observation period. The remaining females were in their penultimate instar when found (and thus virgin), but all moulted and were sexually mature by the first week of January 1994.

I randomly assigned females to one of two groups: unfed (natural diet, n = 19) or fed (supplemented diet, n = 20). All females were allowed to feed on prey they captured naturally, but because female spiders are generally food limited in nature (Wise, 1975, 1993), I expected that many females on a natural diet would be in poor condition. Thus, I supplemented the diet of fed females with two large calliphorid flies (with wings clipped) or 1 medium-sized katydid (*Requena verticalis*) twice a week from December 27 until January 22 (i.e., eight feedings over a 4-week period). The supplementary feeding protocol was as follows. I grasped the live prey by the hind legs or abdomen with a pair of forceps, and held it so its front legs and head touched the web. I released the prey when the female began to wrap it in sticky webbing (this usually precedes consumption, Forster, 1995). To control for the disturbance caused by feeding, I lightly touched the webs of

unfed females with forceps until the female moved toward them (on the same schedule as the fed females' feedings).

I collected males from webs not involved in mating observations at the WA-Ag site during December 1993 and early January 1994, examined them to ensure that they were virgins, and held them in the laboratory under natural photoperiod at approximately 22°C until mating trials. They were not fed during this time; male redbacks rarely eat after maturity (Kavale, 1986). I conducted mating trials during 3 nights at the end of January and randomly assigned each female to 1 night. Trials were initiated between 2100 and 2200 h by placing a single, haphazardly chosen virgin male on the periphery of each web. If a male did not commence courtship movements within 5 min, he was removed and a second male was introduced. Interacting pairs were observed at intervals of 35 min or less, and each observation period lasted at least 5 min. I recorded details of behavior until the end of an interaction or 0500 h, then removed any pairs I had observed copulate and those in which examination of the male's emboli indicated that a mating had occurred. Because the duration of redback copulation is often shorter than 35 min (Andrade, 1996; Forster 1992, 1995), I did not always see the spiders in copula.

I collected, weighed, preserved, and measured spiders after they had mated and confirmed female mating status by dissecting preserved spermathecae and counting male embolic sclerites. For all matings, I report data for only those cases in which the number of sclerites found exactly matched the number of palpal insertions I had observed or inferred (total n = 24, 9 unmanipulated and 15 experimental matings). Females that produced egg sacs during the mating trial period (n = 11) were excluded from the analysis, since they obviously had mated previously, but their behavior toward courting males was noted.

Calculating condition

I compared the relative condition of cannibalistic and noncannibalistic experimental females. Relative condition is an index that compares the condition (mass/size) of each female to an estimate of her minimum and maximum possible condition (Figure 1). Experimental females were compared to laboratory females (n = 34) reared from egg sacs collected in Perth and held under a 12h :12 h light:dark photoperiod at 23°C and 80% relative humidity. Spiderlings were fed small flies (*Drosophila* spp.) and immature house crickets (*Acheta domesticus*) approximately twice weekly until maturity. I then withheld food from the laboratory-reared adult females for 3 months, after which they were in poor condition and close to starvation (mean mass ± SE = 132 ± 8 mg; see Forster and Kavale, 1989). These females were weighed, then fed one or two house crickets (*A. domesticus*, mean total mass ± SE = 316 ± 5 mg) every 24 h for 4 consecutive days. After the fourth feeding, females were considered to be satiated and in good condition because they attacked the crickets they were given, but did not feed extensively within the 24 h following its introduction, and had more than tripled their starvation mass (mean mass after fourth feeding ±SE = 438 ± 17 mg). These females were weighed, euthanized, preserved in 75% ethanol, and measured.

To produce the relative condition index, I first used principal components analysis (Wilkinson et al. 1992) to calculate a composite variable that incorporated all measurements of body size for laboratory-reared females (size; see Table 3). Mass and size were correlated for laboratory-reared females in good and poor condition (Figure 1A). The relative condition of a field-mated female was calculated by comparing her mass and size to these two lines (Figure 1B). Using this measure, a female with a relative condition rating of 1.0 or more is in very good condition and satiated, whereas one with a
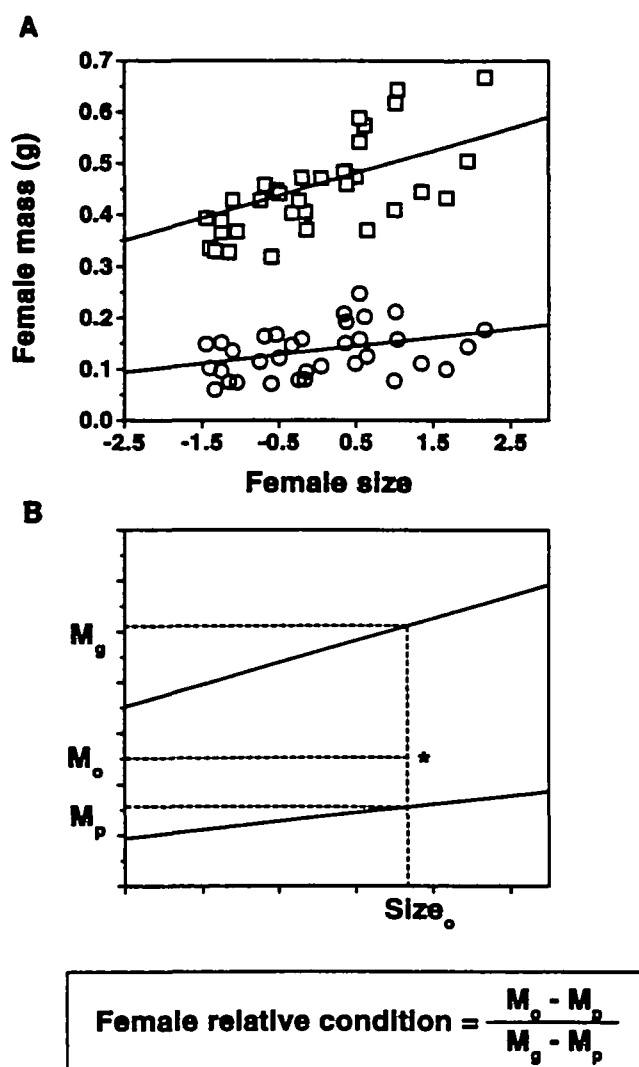
A

B

$$\text{Female relative condition} = \frac{M_o - M_p}{M_g - M_p}$$

Figure 1
Calculation of relative condition of females. (A) The relationship between size (measured by the first principal component of a factor analysis incorporating three linear measures of body size) and mass (g) for 32 laboratory-reared females in poor condition (circles; near starvation; mass = $0.132 + 0.016$ size; $p = .045$, Spearman correlation coefficient = $.349$) and the same females in good condition (squares; satiated; mass = $0.449 + 0.061$ size; $p < .001$, Spearman correlation coefficient = $.701$). The slopes of these two lines are significantly different (t test, $t = 3.372$, $p < .002$). (B) A diagrammatic representation of the calculation of relative condition based on the two regression lines in panel A. The observed size (size$_o$) of a field-caught female is used in each regression equation to calculate the expected mass of a female of same size in poor (M_p) and good (M_g) condition. The relative position of the observed mass (M_o) between these two extremes is equal to the condition of that female relative to an approximation of her mass at starvation (M_p) and satiation (M_g).

rating of 0.0 or less is in very poor condition and close to starvation. Because the endpoints of this scale are estimates of female condition at starvation and satiation, the relative condition index should reflect female hunger level. I use the terms "relative condition" and "hunger level" interchangeably in the remainder of the paper.

To examine the mate rejection hypothesis, I compared the phenotypes of cannibalized males with those that were not cannibalized. Females have ample opportunity to assess males

Table 3
Results of a principal components analysis of measures of body size

Factor[a]	n	Mean (mm)	SE	Coefficient[b]	% Variance[c]
Females					
Cephalothorax width	34	3.145	0.049	.346	
Cephalothorax length	34	3.282	0.037	.370	
Leg	34	6.122	0.061	.363	
					85.9
Males					
Cephalothorax width	24	0.978	0.013	.531	
Leg	24	2.709	0.046	.531	
					88.5

[a] Cephalothorax width was measured at the widest point of the dorsal surface and length from the anterior tip to the point of pedicel attachment. Leg is the average total length of the patella and tibia of the first legs of each individual.

[b] Only the coefficients of each factor for the first principal component (used as a measure of overall size) are shown. The size of each individual is a composite measure calculated by summing the products of each standardized factor and its coefficient.

[c] Percentage of total variance in the measurements accounted for by the first principal component.

during the extensive vibratory courtship, which involves male movements on the web and on the female's venter (Forster, 1992, 1995). It is likely that females can use vibrations produced by males during courtship to detect small differences in male size or mass. Another web-building spider, *Zygiella x-notata*, is able to detect particles as small as 0.05 mg using vibrational information transmitted through the web (Klärner and Barth, 1982).

Measures of size (calculated as described above for females, Table 3), mass, and absolute condition (mass/size) were used as possible indicators of male quality, and cannibalized and noncannibalized males were compared on this basis. Although size, mass, and condition are expected to be correlated, I examined each independently because they could represent independent criteria for female choice. In most spiders, adult body size reflects juvenile foraging success and is constant throughout adult life (Vollrath, 1987; Arnqvist and Henrikkson, 1997). Females may prefer larger males with better foraging skills. In comparison, females may use male mass or condition (mass/size) as an indicator of male age. There is a strong positive relationship between male size and mass at final moult (Andrade MCB, unpublished data), but because male redbacks eat little after maturity (Forster, 1995; Kavale, 1986), their mass and condition are expected to decrease over time. Age might be a relevant criteria for females if (1) the quality of male sperm degrade over time (male redbacks transfer sperm to their emboli from the gonads at maturity and then carry it there until they mate) and/or (2) the age of a suitor reflects a heritable ability to find a mate quickly.

Because of small sample sizes, most of the data were analyzed using the Mann-Whitney test (Systat version 5.0; Wilkinson et al., 1992) and corrected for multiple comparisons with a sequential Bonferroni procedure (Rice, 1989) where appropriate. Other statistical procedures are specified where used.

RESULTS

Web cohabitation

Male redbacks often remained on the webs of females for several days before initiating courtship (= web cohabitation).

Table 4

A comparison of the phenotypes of males involved in cannibalistic and noncannibalistic field matings

Factor	Cannibalism			No cannibalism			Mann-Whitney
	n	Median	Range	n	Median	Range	p
Unmanipulated matings							
Leg (mm)[a]	6	2.717	2.295–2.851	3	2.795	2.708–2.882	0.496
Cephalothorax width (mm)[b]	6	0.965	0.900–0.986	3	0.979	0.950–1.014	0.564
Mass (g)	6	0.004	0.003–0.007	3	0.005	0.003–0.007	0.197
Condition[c]	6	0.003	−0.006–0.018	3	0.004	0.002–0.031	0.439
Experimental matings							
Leg (mm)[a]	7	2.746	2.286–3.040	8	2.677	2.371–3.185	0.728
Cephalothorax width (mm)[b]	7	0.985	0.899–1.118	8	0.965	0.838–1.043	0.418
Mass (mg)	7	0.003	0.003–0.007	8	0.005	0.002–0.008	0.345
Condition[c]	7	0.002	−0.003–0.038	8	−0.001	−0.162–0.005	0.298

[a] Leg is the average total length of the patella and tibia of the first legs of each individual.
[b] Cephalothorax width was measured at the widest point of the dorsal surface.
[c] Condition = (mass/size); see Table 3 and text for calculation of size.

Males were not active during the day and stayed motionless, usually on the periphery of the female's web. At the WA-Ag site, adult females without egg sacs (n = 23) had between zero and six males on their webs each day (median = 2). Females were never seen attacking or consuming males during web cohabitation.

Mating behavior

In the 24 matings (9 unmanipulated and 15 experimental) I observed, redback courtship and copulation behavior was similar to detailed descriptions of laboratory interactions published elsewhere (Forster, 1992, 1995). Males initiated courtship from the periphery of the web and engaged in a complex sequence of courtship movements, the main characteristics of which are similar to those described for other Latrodectus species (see Cooke, 1973; D'amour et al., 1936; Kaston, 1970; McCrone and Levi, 1964; Ross and Smith, 1979). During every intromission, the copulatory somersault occurred a few seconds after embolus insertion and the male remained in the somersault posture until he removed his embolus. Following the first intromission, the male resumed courtship on the snare, usually repeating all the earlier courtship behaviors. The second intromission and somersault appeared identical to the first.

Prevalence and timing of sexual cannibalism

Cannibalism occurred frequently: 65% of the females on a natural (i.e., unsupplemented) diet cannibalized their mates (total = 11/17; unmanipulated = 6/9; experimental unfed = 5/8). In most of the matings (20/24, 83%, experimental and unmanipulated), two successful intromissions occurred (Table 2). Although the female sometimes pierced, masticated, or extruded enzymes onto the male's abdomen during the first palpal insertion, only 3/24 males were killed during the first insertion. The other 21 males returned to the web and resumed courtship, and although 13 of them showed evidence of partial digestion of the abdominal integument (Table 2), it did not appear to affect their ability to court the female. In most matings where the male was killed by the female, cannibalism (i.e., consumption of abdominal contents) was completed during and immediately following the second palpal insertion. The female did not always extrude digestive enzymes during copulation; 12.5% (3/24) of the males accomplished two intromissions without any abdominal damage. (Table 2).

Evidence for mate recognition

Every instance of sexual cannibalism was initiated while the male was in the somersault position. Females did not attack males when they first entered the web (observed naturally on three occasions), nor during courtship. Redback females remained quiescent in the web throughout successful courtships (i.e., those that ended in copulation). In comparison, females quickly oriented toward and then attacked prey items shortly after they contacted the web. Female rejection behavior was observed in 11 instances (7 unmanipulated, 4 experimental) with females that produced new egg sacs during the mating trial period and that were apparently nonreceptive. They actively discouraged courtship by striking at the males with their forelegs, sometimes knocking males out of the web. However, even these nonreceptive females never attempted to wrap males in webbing, or to eat them.

There was no evidence of discrimination among males. Cannibalized and noncannibalized males did not differ statistically with respect to their size (i.e., cephalothorax width, leg length), mass, or condition (Table 4).

Feeding opportunism

Female redbacks may feed on males opportunistically. In the feeding experiment, females with supplemented diets were less likely to cannibalize their mates. Two of the seven (29%) fed females that eventually mated were cannibalistic compared to five of eight (62%) unfed females, although this difference was not significant (p = .315, Fisher's Exact test). However, this comparison is complicated by considerable overlap between the relative condition of fed and unfed females (relative condition range; fed: 0.234 to 1.366; unfed: −0.032 to 0.594). Some fed females were not satiated at the time of the trial (e.g., a relative condition of 0.234 is close to the starvation level); mainly because they did not consume all experimental prey due to natural disturbances.

Because the diet supplementation failed to adequately separate the females in the fed and unfed groups with respect to condition, I pooled the data from all the experimental matings (n = 15) to determine whether cannibalism is related to female condition. From the pooled data, it is clear that noncannibalistic females (median relative condition = 0.748, n = 8) were in better condition than cannibalistic females (median = 0.073, n = 7, Mann Whitney U = 8.0, p = .021).
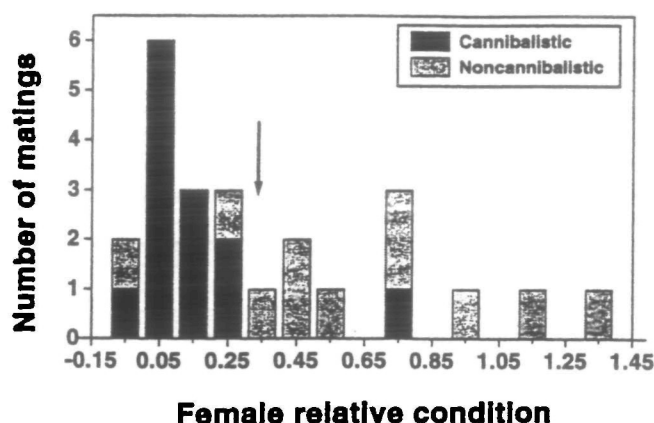
Female relative condition

Figure 2
Relative condition of cannibalistic and noncannibalistic females from 24 field matings. Values on the x-axis represent midpoints of bins that encompass 0.1 units on the relative condition scale. A logistic regression analysis (see text) identifies 0.31 (arrow) as the relative condition at which female behavior is predicted to switch from cannibalistic to noncannibalistic.

Using data from all observed matings ($n = 24$; Figure 2) allows an estimation of the point at which female behavior might be expected to switch from cannibalistic to noncannibalistic. The relationship between relative condition and cannibalism was examined using logistic regression analysis (Systat version 5.0; Wilkinson et al., 1992; Hosmer and Lemeshow, 1989). Female relative condition was a significant predictor of cannibalism [probability(cannibalism) $= e^a/(1 + e^a)$; where $a = -6.01*$(relative condition) $+ 2.11$; G test for inclusion of variable: $G = 13.02$, df $= 1$, $p < .003$, $n = 24$; Hosmer-Lemeshow goodness of fit test: $C = 10.53$, df $= 8$, $.25 > p > .1$; Hosmer and Lemeshow, 1989]. A reasonable first estimate of the female behavioral switch point, where the logistic model predicts the probability of cannibalism to be 50%, corresponds to a female relative condition of 0.351. This decision rule would have correctly predicted the behavior of 21/24 females (87%; Figure 2).

A sample of virgin females ($n = 22$) collected from a variety of locations in and around Perth were generally in poor condition, with an average relative condition of 0.349 (SE = 0.086). Sixty-eight percent (15/22) of the virgin females had a hunger level lower than 0.351, a proportion similar to the 65% of females found to be cannibalistic in this study.

DISCUSSION

Mistaken identity hypothesis

The mistaken identity hypothesis predicts that females cannot distinguish males from prey and thus attack an approaching male as they would any potential prey item. However, females that consistently consume rather than copulate with males that approach them would risk remaining unmated. High levels of sexual cannibalism through mistaken identity should result in strong selection on females to develop sensory capabilities that would allow them to recognize males (Elgar, 1992). Most spiders have a highly developed vibrational sense which is used extensively for detecting and localizing prey (e.g., Bleckmann, 1985; Bleckmann and Barth, 1984; see Barth, 1982, 1985, for reviews). Thus female spiders potentially have the sensory tools for distinguishing males from prey, and mate recognition is expected to be the norm, particularly in species in which males have vibratory courtship displays.

The mistaken identity hypothesis does not account for sex-

ual cannibalism in the redback for two reasons. First, the high frequency of cannibalism (65%) is inconsistent with this hypothesis. Second, cannibalism always occurs during and after copulation and differs qualitatively from normal predatory behavior. This indicates that females distinguish males from prey. Kleptoparasitic theridiids use web vibration information to assess the activity of their hosts (Vollrath, 1979), and it is likely that *Latrodectus* also perceive web vibrations (D'amour et al., 1936). The movements of male redbacks during their extended courtship (Forster, 1995) probably produce characteristic vibrations that allow females to identify them as conspecifics (see Barth, 1982; Robinson, 1982).

Arnqvist and Henriksson (1997) found support for sexual cannibalism by mistaken identity in the fishing spider, *Dolomedes fimbriatus*, where females attempt precopulatory cannibalism in >90% of mating attempts, and most of these attacks are identical to their behavior toward prey. They conclude that female aggression during courtship is nonadaptive (also see Johns and Maxwell, 1997) and results in underinsemination in the field, but is maintained by pleiotropic gene effects combined with strong selection for indiscriminate juvenile aggression and predatory ability. However, *D. fimbriatus* males produce vibratory signals during courtship (Arnqvist, 1992) which females may be able to recognize. Moreover, female aggression toward courting males may have a functional explanation. Arnqvist and Henrikkson (1997) found males that avoided cannibalism were significantly larger than males that were eaten and excluded from paternity. If, in natural populations, this results in a bias in the size of males who are able to mate successfully, sexual cannibalism in D. fimbriatus may be consistent with the mate rejection hypothesis (Table 1).

Mate rejection hypothesis

If females use sexual cannibalism as a mechanism of precopulatory mate rejection, it is expected that (1) females will recognize males as potential mates and assess them during courtship, (2) rejected males will be consumed before sperm transfer, and (3) males that are not cannibalized will differ from cannibalized males with respect to some phenotypic characteristic desired by females. Although redback females did recognize males as potential mates, I found no evidence for the other two predictions. Cannibalized males fathered offspring because cannibalism always occurred while the male was transferring sperm. Although females are sometimes not receptive to male courtship, rejection behavior does not involve cannibalism. Finally, males that were cannibalized were not detectably different (i.e., in size, mass, or condition) from those that survived.

Female choice and the timing of sexual cannibalism

A modification to the mate rejection hypothesis may be more relevant for species such as redbacks in which sexual cannibalism only occurs during or after copulation. While females of these species may not exclude males from mating via sexual cannibalism, the timing of cannibalism may be used to reduce the paternity of some males relative to others (e.g., Eberhard, 1996). If sexual cannibalism represents a postcopulatory mechanism of female choice, (1) there should be variation in the timing of sexual cannibalism, (2) this variation should affect the male's paternity, and (3) the probability of sexual cannibalism should depend on some phenotypic characteristic of the male.

Redback females appear to take one of four options when a male approaches, each of which may result in different patterns of male fertilization success. First, the female might reject the male outright. Second, she might cannibalize the

male during the first palpal insertion. Such a male will trans-
fer a maximum of half as many sperm as a male who is able
to copulate with both palps. Third, she might cannibalize the
male during the second palpal insertion, and fourth, she
might allow the male two palpal insertions and not cannibal-
ize him. A male who achieves two palpal insertions and is not
cannibalized may fertilize more eggs than a male who is can-
nibalized after one insertion. However, cannibalized redback
males copulate longer than males who are not cannibalized,
and females are more likely to become sexually nonreceptive
after cannibalistic matings (Andrade, 1996). Therefore, a
male who completes two palpal insertions but is not con-
sumed will have lower paternity than a male who is cannibal-
ized after two insertions. By cannibalizing a male during his
second insertion, the female is choosing him as the father of
the majority of her young, regardless of her past mating his-
tory. All of these female behavior patterns were seen in this
study (Table 2), but statistical comparisons of the phenotypes
of males in these different categories were not possible be-
cause of small sample sizes.

The timing of sexual cannibalism may also be affected by
female mating status. Females that cannibalize before the sec-
ond palpal insertion may risk underinsemination (i.e., one
empty spermatheca). This risk may explain why the majority
of cannibalistic females in this study (11/14) consumed their
mate after two complete palpal insertions. Observations indi-
cate that a small percentage of females may remain underin-
seminated in the field. The male was eaten before his second
insertion in 21.4% (3/14) of the cannibalistic copulations ob-
served here, and in another study (Andrade 1996), 30.4%
(7/23) of redback females collected near the end of the mat-
ing season may have received only one palpal insertion. Fur-
ther work is needed to determine whether the fertility of red-
back females is limited by the number of palpal insertions
received, as it is in fishing spiders (Arnqvist and Henriksson,
1997), and whether this might represent a cost of "prema-
ture" cannibalism for females.

Feeding opportunism

Newman and Elgar (1991) modeled the cannibalism decision
from the female perspective and found that virgin females
should be less likely to attempt precopulatory cannibalism
than should mated females and that decreased mean or in-
creased variance in food availability would lead to increased
cannibalism in all females (see Arnqvist and Henriksson,
1997, for a test of this model). Thus, females of some species
may balance a male's value as a mate versus his value as food
when deciding whether to cannibalize an approaching male
(Newman and Elgar, 1991). The Newman–Elgar model in-
cludes several assumptions not satisfied in the redback system.
However, the logic of their model, combined with empirical
results from other systems (see Birkhead et al., 1988; Liske
and Davis, 1984, 1987; Matsuro and Morooka, 1983) suggests
the predictions of the feeding opportunism hypothesis out-
lined in Table 1.

Differences in female mating status cannot explain the vari-
ation in cannibalism found in this study because I confirmed
that all females were virgins before the observed matings. In
addition, in redback spiders, cannibalism never occurs before
sperm transfer (Forster, 1992; 1995; this study), so female mat-
ing status should not have a large effect on the cannibalism
decision. However, female hunger is apparently an important
factor in determining cannibalistic behavior in redback spi-
ders. Females that are in poor condition take advantage of
the male's vulnerable posture during copulation. Although a
male's paternity may be strongly influenced by the timing of
cannibalism, the results presented here (Figure 2) indicate

that the ultimate fate of a redback male (i.e., whether he is
eaten at all) is largely determined by the female's condition
rather than by some aspect of his phenotype. Such opportu-
nistic feeding by females suggests that the frequency of can-
nibalism might vary with food availability in different locations
or at different times (Birkhead et al., 1988). But it is likely
that sexual cannibalism is always prevalent in field populations
of redbacks because female spiders are generally food limited
in nature (Anderson, 1974; Kessler, 1973; Wise, 1975, 1993).
A sample of virgin females collected from a variety of sites in
Western Australia had a median relative condition (0.394)
that was less than half their estimated condition at satiation
(1.0), and most of them (15/22) would be predicted to be
cannibalistic based on the condition-dependent decision rule
proposed here (Figure 2).

The putative switch point from cannibalistic to noncanni-
balistic behavior (Figure 2) requires experimental confirma-
tion, but the available data suggest that it is a reasonable first
approximation. It is desirable to identify such a point because
(1) it would allow prediction of a female's mating behavior
from measurements of her size and mass, and (2) it may be
possible to connect this pivotal hunger level to some female
physiological requirement and thus gain insight into the
mechanistic reasons for the change in female behavior.

This study suggests that, although redback females recog-
nize males as conspecifics, they consider the value of a male
as potential prey after sperm transfer has commenced. As with
other small prey, females ignore males unless they are food
stressed. Males are 1–2% of female body mass (Andrade 1996)
and may not provide much nutritional value (e.g., Darwin,
1871; Elgar, 1992; Robinson and Robinson, 1980) or may be
far below the average prey size that females accept (see
Gertsch, 1949, Reichert and Luczak, 1982). Congeneric fe-
males (L. mactans) often do not attack prey <15% their own
size (cited in Forster, 1992). Similarly, redback females in
good condition most commonly ate prey several times their
size (large orthopterans and cockroaches), but disregarded
small prey similar in size to males (small homopterans, flies,
and ants; Andrade MCB, personal observation). In compari-
son, small prey were readily consumed by females in poor
condition. This shift is consistent with a prediction from op-
timal foraging theory: increased predator hunger levels are
expected to lead to increased diet width (Emlen, 1966; Nu-
utinen and Ranta, 1986).

Even given their usual diet choice, however, it is somewhat
puzzling that males were not always consumed by females. The
somersault places the male in an extremely vulnerable posi-
tion and probably reduces handling time for females, possibly
increasing the profitability of the male as a food source rela-
tive to other small prey. However, the necessary costs of re-
gurgitating enzymes, waiting for them to predigest the abdom-
inal contents, and of wrapping the male in silk may balance
the reduced cost of capturing the male. In the field, even
when small prey had become entangled in the web and were
largely immobile, they were not attacked by satiated females
(Andrade MCB, personal observation), although this might
similarly reduce handling costs. Unless the female is food
stressed, the small net benefit of consuming a male may not
be worth the time spent in eating him. In other work, I was
unable to find any direct benefit to females who consumed
their mates (no difference in female mass following canni-
balism, nor number or mass of eggs produced, nor hatching
time of those eggs; Andrade, 1996).

Variation in the occurrence of cannibalism is unlikely to be
the result of different male mating strategies. Males that cop-
ulate but are not cannibalized probably have a low probability
of remating (see Andrade, 1996; Forster, 1992), partly because
males experience a high mortality rate when moving between

female webs in the field (approximately 90%, Andrade MCB, unpublished data). Moreover, for male redbacks, the somersault behavior, and thus their attempted sacrifice, appears fixed (Forster, 1992, 1995; Kavale, 1986). Facilitating sexual cannibalism may always be the best strategy for a male because of the benefits of increased paternity (Andrade, 1996). In comparison, cannibalism may or may not yield a net fitness benefit for the female, depending on several factors (e.g., her physical condition and the nutritional value of the male), including the timing of cannibalism. Therefore, unlike other cannibalistic mating systems (Elgar, 1992; Gould, 1984; Parker, 1989), sexual cannibalism in redbacks does not occur when a conflict of interest is "won" by the female; rather, cannibalism appears to occur when the interests of the male and female coincide.

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