Sexual cannibalism and mate choice decisions in wolf spiders: influence of male size and secondary sexual characters

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Sexual cannibalism may influence expression of elaborate male traits by either reinforcing or opposing sexual selection. Male *Schizocosa ocreata* (Hentz) wolf spiders (Lycosidae) have tufts of bristles on the first pair of legs that may function as a condition-indicating signal trait. We paired virgin and previously mated adult females with males under seminatural conditions (laboratory containers with leaf litter). For males encountering virgin females, probability of attempted premating cannibalism varied with male size, body condition, tuft size, fluctuating asymmetry of tufts (FA) and female size (larger females attacked smaller males and males in poor condition with smaller, more asymmetrical tufts). Probability of successful cannibalism varied with the relative size of both sexes and female body condition, but not male tuft size (smaller males were cannibalized by larger females in better condition). Males with larger tufts (relative to body size) were more likely to mate, but no other traits (male or female) were associated with mating success. Postmating cannibalism risk was associated with female size and age, and male size, body condition and tuft size (larger, older females cannibalized smaller males in poor condition with smaller tufts). For males paired with previously mated females, probability of cannibalism was influenced by size of both sexes and male tuft size (larger females cannibalized smaller males with smaller tufts). While no morphological characteristics (male or female) influenced the probability of second matings, recently matured females were more likely to mate twice. Results suggest that both mate choice and sexual cannibalism can impose reinforcing directional selection on male size and secondary sexual characters.

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Sexual cannibalism may be defined as the killing and consumption of an actual or potential mate before, during, or after copulation, but always in the context of courtship and mating (Elgar 1992). Consequently, it is a potentially powerful selective agent since it has direct and immediate effects on both male survival and subsequent mating opportunities. Conspicuous male secondary sex traits are generally favoured by sexual selection and counteracted by other natural selection (Endler 1988; Andersson 1994). Traits selected by female mate choice often favour greater elaboration (e.g. male size, Gatz 1981; length of tail, Basolo 1990; male song repertoire size, Searcy et al. 1982), whereas increased metabolic costs, predation risk (reviewed in Burk 1982; Magnhagen 1991) and foraging difficulty (Møller 1989) constrain further elaboration of the trait. These counteracting selection pressures on conspicuous ornaments are likely to be common, but the phenomenon of sexual cannibalism may create novel predictions about the relationship between sexual selection and some forms of natural selection acting on secondary sex traits.

Because sexual cannibalism may occur before, during, or after copulation (reviewed in Elgar 1992), the timing of male consumption relative to mating is critical to understanding the fitness benefits and costs for males and females as well as the intensity and direction of selection acting on male traits (Newman & Elgar 1991). If sexual cannibalism occurs primarily before copulation rather than after, and/or males have multiple mating opportunities, exaggerated male traits may be selected by either mate choice or cannibalism or both. If cannibalism occurs only after mating, and males are unlikely or unable to mate multiply, cannibalism may have a minimal effect on selection of male ornaments. This is particularly true if the energetic value of the male as a prey item is not great enough to significantly affect female fecundity (Andrade 1998).

Premating cannibalism has been considered as a foraging decision (Dong & Polis 1992), a by-product of selection for aggressiveness (Arnqvist & Henriksson

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1997), a case of mistaken identity, or 'mate choice with extreme prejudice' (Elgar 1992; Johnson 2001). Among the latter two cases, females may follow a simple decision rule: if the male is not recognized or is unacceptable as a mate, then eat him. However, cannibalism and mating are not mutually exclusive behaviours, since females may choose to mate and then cannibalize a male afterwards. Therefore, the relation between female mate choice and natural selection through cannibalism risk may not be static, but contingent upon the shifting value of the male as a mate or a prey item (Buskirk et al. 1984; Andrade 1998). Understanding differences between pre- and post-mating cannibalism is important for understanding the relationship between mate choice and sexual cannibalism criteria.

Male spiders show diverse courtship displays and secondary sexual characteristics that may play a role in species recognition, female pacification and mate choice (Krafft 1982). Since premating cannibalism is always detrimental to male fitness, one may expect to see morphological or behavioural characteristics in males that minimize female predatory behaviour (Jackson 1982). Many studies have considered male morphology and courtship behaviour from the perspective of species recognition and/or female mate choice (Stratton & Uetz 1983; McClintock & Uetz 1996; Scheffer et al. 1996; Uetz et al. 1996; Parri et al. 1997) and sexual cannibalism has also been cited as a driving force in the evolution of both diverse courtship displays (Darwin 1871; Matthews & Matthews 1978; Manning 1979; Jackson 1980; Elgar 1992; Forster 1992; Prenter et al. 1994; Andrade 1996; Arnqvist & Henriksson 1997) and various forms of sexual dimorphism (Jackson 1980; Elgar & Nash 1988; Elgar et al. 1990; Newman & Elgar 1991; Elgar 1992; Prenter et al. 1994). However, to date, studies on the influence of sexual cannibalism on male ornamentation are lacking.

Schizocosa ocreata is a ground-dwelling wolf spider (Lycosidae) found in leaf litter of deciduous forests of the eastern United States. The courtship behaviour of males includes a visual and a vibratory component to the display (see Stratton & Uetz 1981, 1983 for a detailed description of courtship). Male *S. ocreata*, like other species of wolf spider (Lycosidae) and some jumping spiders (Salticidae) have tufts of bristles on their first pair of legs, which are waved up and down during courtship. Females and juveniles lack such tufts. Previous studies have implicated tuft size as a factor in both increasing visibility of the courtship signal and eliciting female receptivity (McClintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 2000; Uetz 2000). However, these studies have not examined the potential influence of tuft size along with other morphological traits as factors influencing female predatory behaviour. Furthermore, these studies have tended to focus on female receptivity displays in laboratory arenas with flat sheets of paper as the substratum rather than measuring actual mating in more natural environments (complex leaf litter).

Research indicates that wolf spiders are frequently food limited (Wise 1993) and conspecifics may comprise up to 25% of the diet (Edgar 1969; Hallander 1970). Because female *S. ocreata* use visual cues to a large extent to detect

prey and make foraging decisions (Persons & Uetz 1996), the same conspicuous decorations and displays of males that influence mate choice would also be likely to attract the attention of potentially cannibalistic females. Furthermore, an ornament that conveys information about male quality or body condition can simultaneously be used by females to choose mates and assess the male's ability to escape or resist predation attempts. As female *S. ocreata* usually mate only once, but males are capable of mating multiply (Norton & Uetz, in press), the costs and benefits of sexual cannibalism for males and females are likely to vary with mating status, and to change as the stages of the mating encounter proceed. This study examines the potential for mate choice and sexual cannibalism to act on male size and a conspicuous male ornament (foreleg tufts) in the wolf spider, *Schizocosa ocreata* (Hentz). We address the following questions. (1) How often does cannibalism occur and does it occur before or after mating? (2) Are male characteristics that are important in determining mating success also important in determining cannibalism risk? (3) What is the relationship between premating and postmating cannibalism as selection pressures acting on male traits? (4) If females mate multiply, do the criteria for mate choice and cannibalism change after initial mating? To answer these questions, we studied the series of events preceding and following mating, which may represent separate decision-making processes underlying female behaviour towards a courting male. We also compared traits of males and females associated with mating and/or cannibalism outcomes.

METHODS

Schizocosa ocreata were collected as subadults from the University of Cincinnati Benedict Preserve (Hamilton Co., Ohio, U.S.A.) during late April and early May of 1996. Spiders were housed individually in opaque containers (8 cm high × 11 cm diameter) and maintained under controlled conditions: 13:11 h light:dark cycle, 20–22°C temperature and greater than 50% RH. Each spider was provided water ad libitum and fed five live 1-week-old crickets (*Acheta domesticus*) once a week. Spiders matured in the laboratory, which ensured virginity of the males and females at the time of testing. We selected and paired 135 spiders of each sex at random from a pool of over 600 spiders. Fifteen of 135 males subsequently lost one or more of the first pair of legs during courtship interactions and were excluded from all subsequent analyses except measurements of limb loss frequency. All other calculations are based on a pool of 120 male–female pairs.

We made random pairings in laboratory mesocosms, consisting of containers filled with leaf litter (31.5 × 165 × 9.5 cm high). These mesocosms closely approximate the daily home range size of an adult female *S. ocreata* (A. DeLay, C. Hardesty & G. W. Uetz, unpublished data). We also added 17 g of dry mixed deciduous leaf litter (*Querus* and *Acer* spp.) to each container. This is similar to the leaf litter density found in this species' natural habitat during the breeding season and provides a refuge for both sexes and a natural surface for

vibratory courtship communication of males (Cady 1984; Scheffer et al. 1996). In keeping with the Guidelines for the Treatment of Animals in Research (Section 4c), this container size, with associated litter, allowed sufficient space and hiding places for either sex to avoid the other. The effectiveness of the container size and natural cover was demonstrated by the fact that only males that actively courted or pursued females were cannibalized, whereas males that hid or took cover immediately after female aggressive behaviour were not. To provide a source of water, litter was misted when the females were first introduced into the containers and very lightly again immediately before introducing the male.

Females and males were fed five live crickets (*Acheta domesticus*), and denied food thereafter for 6 days prior to pairing and for the duration of the trial. Therefore, both sexes averaged just below one prey item/day, which represents an approximation of natural hunger level for females and males (Edgar 1969; Nyffeler & Breene 1990). Individual females were introduced into a container 10–12 h before the male. This allowed females to lay down silk (and pheromones), which induces male courtship (Stratton & Uetz 1986).

We maintained paired spiders for 7.5 h, during which time we checked them every 3 min for mating status and noted attempted cannibalism (lunges), leg loss, successful cannibalism events (before or after mating), time of copulation and copulation duration. Because copulation duration is exceptionally long in this species (mean $\pm$ SD = 223.44 $\pm$ 31.60 min; $N = 84$), we were able to accurately record all mating events. Males that were fatally bitten were immediately removed and sacrificed in 80% ethanol. Six days following initial pairings, all mated females were paired with another randomly selected, previously mated male. These males mated with a female from the first pairing, or had been used for other experiments in which they had both mated with a female and survived a 12-h postmating period without cannibalism ($N = 73$ pairs from first pairing, 14 from other experiments). The same male was not paired with the same female. We used the same experimental set-up for spiders paired a second time as those used in the initial pairing.

One week before male–female pairings, we anaesthetized the spiders with CO_2 for 90 s, placed them on graph paper used to scale size, and videotaped them at close range from a dorsal view. We measured morphological traits of spiders using a customized measurement software program (Measurement T.V., Datacrunch, Inc., San Clemente, California, U.S.A.) after digitizing each video image. Two measures of body size, cephalothorax width (CW) and body length (BL), were derived from this method. Body length was measured from the tip of the abdomen just anterior and dorsal to the spinnerets to the anterior portion of the chelicerae (mm). Cephalothorax width has been shown to be a good indicator of body size in spiders (Hagstrum 1971; Marshall & Gittleman 1994; Jakob et al. 1996) and was measured across the carapace at the maximum distance between the second and third pair of legs (mm). A mean of three measurements of each morphological character was used in the statistical analysis to minimize measurement error. All spiders were weighed to the nearest 0.1 mg the evening before the experiment using a Mettler microbalance. Limb loss was also noted where relevant. Data on male and female CW, BL and mass were examined with linear regression and correlation analyses to determine relationships between variables. Because measures of size (CW, BL) and mass were significantly intercorrelated (Table 1), cephalothorax width (CW) was chosen as the best predictor of size for subsequent analyses and for obtaining residual indices of body condition and tuft size. We generated a body condition index by using the residual of the regression of mass on cephalothorax width as in Jakob et al. (1996) and Taylor et al. (2000). Following completion of this study, females were returned to the laboratory population and used in other experiments.

Males were killed by CO_2 anaesthetization at the end of the experiment. The legs were then removed and submerged in 70% ethanol for subsequent tuft measurements. Legs were identified by a unique identification number and tuft area was measured blindly with respect to mating and/or cannibalism outcome. Legs were videotaped at 15 $\times$ power magnification using an Olympus B071 binocular dissecting scope with a video camera attachment. Left and right legs were placed in corresponding positions, videotaped from a lateral view, and strongly backlit to facilitate outlining the bristles of the leg. Bristles surrounding the tibia and patella of each front leg were measured by tracing the tuft outline, and the measurement software package then computed the area of the

Table 1. Pearson correlation coefficients for morphological variables

	Mass		CW		BL		TA	
	r_{118}	P	r_{118}	P	r_{118}	P	r_{118}	P
Males								
CW	0.8759	<0.0001						
BL	0.793	<0.0001	0.784	<0.0001				
TA	0.8136	<0.0001	0.757	<0.0001	0.675	<0.0001		
FA	−0.034	0.722	−0.046	0.626	−0.034	0.769	−0.266	0.0046
Females								
CW	0.587	<0.0001						
BL	0.906	<0.0001	0.476	<0.0001				

CW: cephalothorax width; BL: body length; TA: tuft area; FA: fluctuating asymmetry of tuft area.

irregular polygon. As with other body measurements, a mean of three measures was used for statistical analysis. Average tuft area was measured as the mean of three measures of the total of left and right tuft area (mm^2). We measured fluctuating asymmetry (FA) of male tuft area as the absolute value $|L - R|$, using the average of three measures of area for each tuft (Møller & Swaddle 1997; Palmer & Strobeck 2003). We measured relative tuft area as the residual of the regression of average tuft area on cephalothorax width. All statistical analyses were conducted with JMP (version 4.0.2, SAS Institute 2000).

We used stepwise logistic regression analyses (JMP, version 4.0.2) to test for effects of male and female size (CW), age since sexual maturity, body condition, male tuft size and male tuft FA on the probability of (1) attempted premating cannibalism, (2) successful premating cannibalism, (3) mating and (4) postmating cannibalism for initial pairings of males with virgin females. We conducted additional stepwise regression analyses on the same variables for second pairings of males and previously mated females. Logistic regression is appropriate for determining the relationship between a binary or nominal variable (e.g. cannibalized/not cannibalized) and one or more continuous variables (e.g. male size), and is being used more frequently in analyses of behavioural data (Singer & Riechert 1995; Hardy & Field 1998). In this analysis, we eliminated predictors in a stepwise fashion as in Hardy & Field (1998), and determined the significance level for each predictor variable at the point at which each was eliminated from the regression model. Using this approach, the final model in each analysis only contains significant predictors, which provides the most economical combination of the initial variables (Hardy & Field 1998). In addition, we analysed the lack-of-fit statistics for each model, which test for appropriate model form (a significant result indicates an inappropriate model).

RESULTS

Frequency of Mating and Cannibalism

Of the 120 virgin females paired with males, 87 (72.5%) attempted cannibalism by lunging repeatedly at the male (Fig. 1). Ten of these attempts (11.49%) at premating cannibalism were successful. However, most males were able to avoid cannibalism attempts and continued to court despite lunging responses and being chased by the female. The majority of virgin females (75.63%) mated with a randomly paired male, suggesting a relatively low level of mate choice. Virgin females engaged in both pre- and postmating sexual cannibalism with nearly equal frequency (Fig. 1); there was no significant difference in the proportion of males cannibalized before versus after mating (chi-square test: $\chi_1^2 = 0.630$, $P = 0.572$).

Some males and females mated multiply (Fig. 2), but at a frequency (14%) that was significantly lower than that for individuals that mated only once ($\chi_1^2 = 59.20$, $P < 0.0001$). Cannibalism was slightly lower among virgin females (17% combined premating and postmating cannibalism) than among previously mated females (24% combined), but these differences were not significant ($\chi_1^2 = 1.37$, $P = 0.241$). The proportion of females that engaged in sexual cannibalism before mating was significantly higher ($\chi_1^2 = 8.74$, $P = 0.0031$) for mated females, (23%) and nearly triple that for unmated females (8%). However, the majority of previously mated females neither mated nor cannibalized the second paired male (Fig. 2).

In general, males showed two types of behaviour when encountering aggressive females. Males either persisted in courting females or retreated under leaves. Males that remained hidden after female lunges ($N = 11$) survived in all cases, but never acquired a mating. Males that persisted in courting despite lunges met with mixed success. Among virgin pairs, the majority (72%) successfully mated despite some aggressive behaviour from females (Fig. 1). Among previously mated pairs, far fewer males mated successfully after cannibalism attempts by the female (15.7%; Fig. 2). Some males began courting the female immediately after dismounting ($N = 7$), and in all cases, the males were cannibalized without an immediate second mounting. Attempted cannibalism also inflicted injury on males; leg loss was observed 24 times overall (11% of pairings). The first pair of legs in males was lost significantly more often than any other pair ($\chi_3^2 = 10.02$, $P = 0.018$), similar to observations of leg loss in the field (Uetz et al. 1996). As a result of leg loss during cannibalism attempts, measurements of tufts for 15 males (there were originally 135 virgin pairs) were not available because of female damage or removal of one of the first pair of male leg tufts.

Because mating and sexual cannibalism are not mutually exclusive, we analysed the results of initial pairings with virgin females as three separate dichotomous outcomes: (1) male cannibalized/not cannibalized premating; (2) male mated/not mated; (3) male cannibalized/not cannibalized postmating (Tables 2, 3). We analysed the results of second pairings of previously mated females in the same manner (Tables 4, 5).

Predictors of Premating Cannibalism Attempts and Success among Virgin Pairs

For initial pairings of virgin adults, probability of attempted premating cannibalism varied significantly with male tuft size, tuft fluctuating asymmetry (FA), male size and body condition, as well as female size (Table 2). Larger females were more likely to attack smaller males and males in poor condition, with smaller and more asymmetrical tufts (Table 3). This suggests that females may use male characteristics that signal condition to discriminate between potential mates and prey. Male and female size (CW) and female body condition (residual index) were significant predictors of the probability of cannibalism (Table 2). Because the probability of cannibalism was positively related to female size but negatively related to male size, we examined the relation between female and male size difference and the probability of cannibalism separately with logistic regression. There was a significant positive relationship between the probability
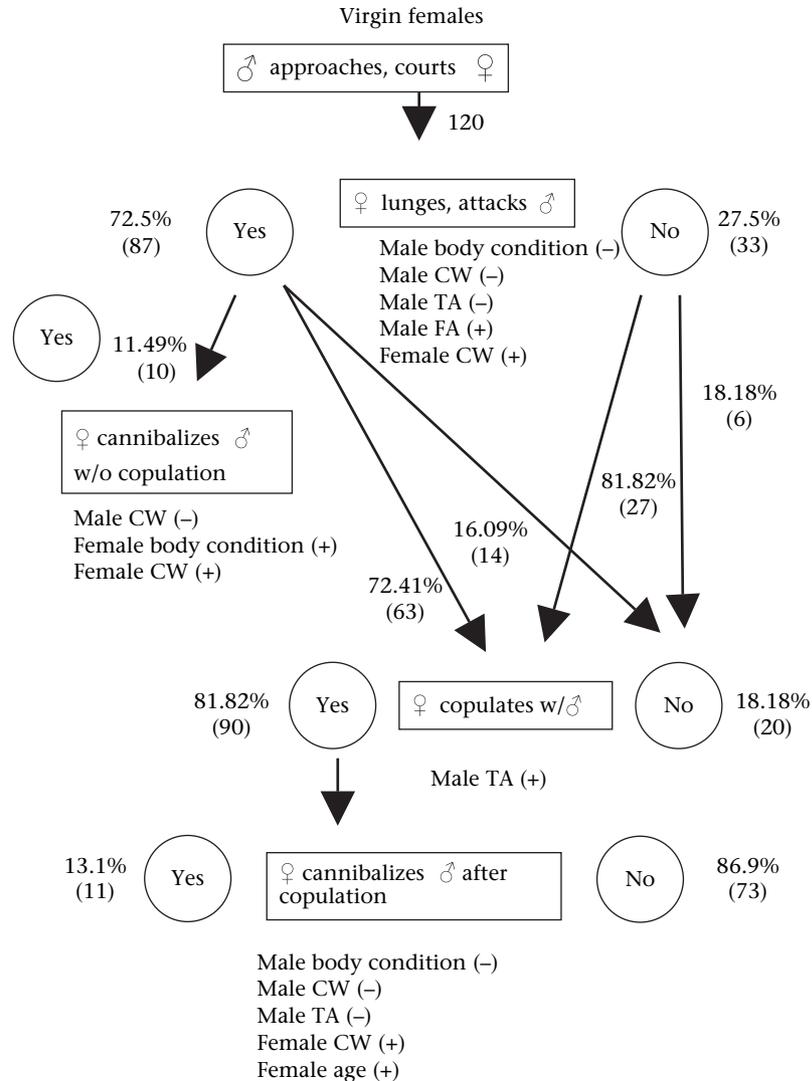
Virgin females

$\boxed{\text{♂ approaches, courts ♀}}$

120

$\boxed{\text{♀ lunges, attacks ♂}}$

Male body condition (–)
Male CW (–)
Male TA (–)
Male FA (+)
Female CW (+)

72.5%
(87)   Yes

No   27.5%
(33)

Yes   11.49%
(10)

18.18%
(6)

$\boxed{\begin{array}{l}\text{♀ cannibalizes ♂}\\ \text{w/o copulation}\end{array}}$

Male CW (–)
Female body condition (+)
Female CW (+)

81.82%
(27)

16.09%
(14)

72.41%
(63)

81.82%
(90)   Yes

$\boxed{\text{♀ copulates w/♂}}$

No   18.18%
(20)

Male TA (+)

13.1%
(11)   Yes

$\boxed{\begin{array}{l}\text{♀ cannibalizes ♂ after}\\ \text{copulation}\end{array}}$

No   86.9%
(73)

Male body condition (–)
Male CW (–)
Male TA (–)
Female CW (+)
Female age (+)

Figure 1. Flow chart of events in male and female pairings with virgin adult wolf spiders. Numbers indicate the percentage (N) of male spiders for the outcome of female decisions. Below each decision outcome are factors determined significant by logistic regression (see Table 2) and the positive or negative direction of the relationship. CW: cephalothorax width; TA: tuft area; FA: fluctuating asymmetry of tuft area.

of cannibalism and the difference between female and male size (logistic regression: $\chi^2_1 = 19.604$, $P < 0.0001$); when larger females were paired with smaller males, cannibalism was more likely (Fig. 3). This result might suggest that cannibalism of courting males is primarily a foraging decision, because there was also a significant relationship between the probability of cannibalism and female body condition ($\chi^2_1 = 3.443$, $P = 0.049$). However, this relationship only explained a small proportion of the variance ($R^2 = 0.062$).

Predictors of Mating Success among Virgin Pairs

Probability of mating was best predicted by male tuft size (Table 2). Although mating success was positively related to tuft size (residualized) and males with relatively larger tufts (residualized) were more likely to mate, the

high percentage of mating success (70%) suggests that this result more likely reflects discrimination against males with smaller tufts (Fig. 4a). Residualized male tuft size was positively correlated with the male body condition index (Fig. 4b), supporting a previous finding that tufts may be a condition-indicating trait (Uetz et al. 2002).

Predictors of Postmating Cannibalism among Previously Virgin Pairs

Among virgin females, postmating cannibalism was significantly related to several variables, including female size (CW) and female age postmoult, as well as male size (CW), tuft size (residualized) and male body condition (residual index) (Table 2). Larger and older females were more likely to cannibalize males after mating when males were small or in poorer condition with relatively small tufts (Figs 2, 5, Table 3).
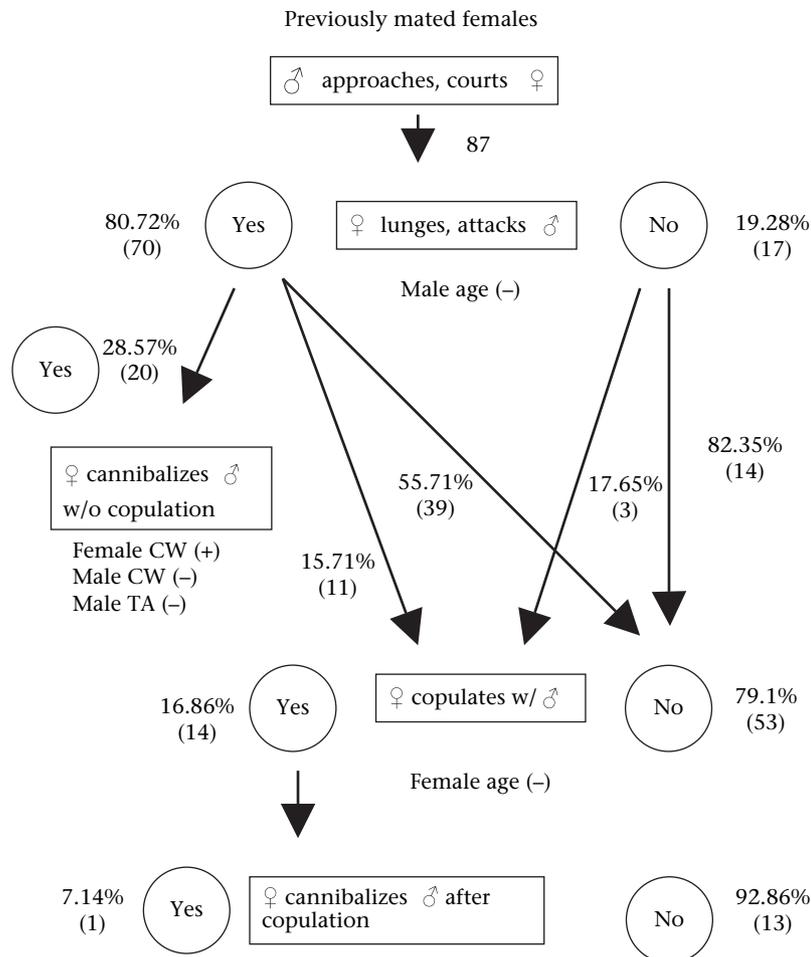
Previously mated females

Figure 2. Flow chart of events in male and female pairings with previously mated adult wolf spiders. Numbers indicate the percentage (*N*) of male spiders for the outcome of female decisions. Below each decision outcome are factors determined significant by logistic regression (see Table 4) and the positive or negative direction of the relationship. CW: cephalothorax width; TA: tuft area.

Predictors of Remating among Previously Mated Pairs

Females that have previously mated may have different mate choice criteria than virgin females. A small number of females mated with a second male 6 days following their first mating (*N* = 13 of 87; Fig. 2), indicating that females were either more selective when choosing second mates, or less receptive overall (Norton & Uetz, in press). We examined the same male and female traits for second pairings that we examined for first pairings to determine whether the factors that were significantly associated with the outcome of first pairings were also significantly associated with the outcome of second pairings. Although based on a smaller sample size, we found that the probability of remating was primarily related to female age postmoult (Fig. 6, Table 4). Although a much smaller proportion of females mated a second time (14%), those that did were more likely to be within 1–2 weeks postadult moult. Relative male tuft size, which was significantly related to the probability of mating among virgin pairs, was not significantly related to mating success among nonvirgin pairs (Table 4).

Predictors of Cannibalism Attempts and Success among Previously Mated Pairs

For males paired with previously mated females, none of the measured male morphological characteristics influenced the probability of cannibalism attempts; the probability of attempted premating cannibalism was influenced only by male age (Table 4). However, among previously mated adults, probability of successful premating cannibalism was significantly associated with female size (Fig. 7), male size and male tuft size (Table 4); larger females were more likely to cannibalize smaller males with relatively smaller tufts, similar to virgin females (Table 5). The lack-of-fit analyses for the final logistic regression models did not reveal significance, indicating that the models were appropriate in all cases.

DISCUSSION

Data from this study indicate that selection pressures acting on male traits are dynamic and may be dependent on the mating status of the female. Overall, our results

Table 2. Stepwise multiple logistic regression analysis of male and female size/morphology variables associated with sexual cannibalism and mating for virgin females

	χ^2	df	P
Premating cannibalism attempted/not attempted			
Source			
Eliminated predictors			
Female age	0.087	1	0.768
Male age	0.234	1	0.628
Female body condition	0.933	1	0.324
Final model	45.368	5	<0.0001
Male body condition	11.539	1	0.0007
Male CW	6.913	1	0.0086
Male FA	6.397	1	0.011
Female CW	6.321	1	0.012
Male TA	5.227	1	0.022
Lack of fit	40.458	108	0.947
Male cannibalized/not cannibalized			
Source			
Eliminated predictors			
Male FA	0.0004	1	0.985
Male body condition	0.022	1	0.883
Male age	0.482	1	0.511
Male TA	2.084	1	0.149
Female age	2.63	1	0.104
Final model	26.277	3	<0.0001
Male CW	9.834	1	0.0017
Female CW	14.085	1	0.0002
Female body condition	6.182	1	0.013
Lack of fit	36.846	116	>0.999
Male mated/not mated			
Source			
Eliminated predictors			
Male FA	0.001	1	0.965
Female age	0.062	1	0.804
Male CW	0.186	1	0.667
Female CW	0.783	1	0.376
Male body condition	1.396	1	0.237
Female body condition	1.162	1	0.203
Male age	3.291	1	0.069
Final model (male TA)	5.42	1	0.019
Lack of fit	110.422	106	0.365
Male cannibalized postmating/not cannibalized			
Source			
Eliminated predictors			
Male age	0.0002	1	0.987
Female body condition	2.102	1	0.147
Male FA	2.511	1	0.113
Final model	51.283	5	<0.0001
Male body condition	20.616	1	<0.0001
Female age	14.537	1	0.0001
Male TA	13.415	1	0.0002
Female CW	10.568	1	0.0012
Male CW	9.203	1	0.0024
Lack of fit	9.786	77	>0.999

CW: cephalothorax width; FA: fluctuating asymmetry of male tuft area; TA: tuft area.

support the conclusion that larger male body size and larger tuft size are potentially subject to selection from both sexual cannibalism and female mate choice, but to varying degrees and at different times in the female's decision process.

Because the latency to cannibalism was generally shorter than that for acquiescence to mate, it is probable that the first female decision regarding a courting male is whether to attack and eat him. Whether this is a foraging decision, or a case of 'mate choice with extreme prejudice' is hard to discern, but the decision appears to be made on the basis of male signals associated with suitability as a mate (e.g. body condition, secondary sexual traits, fluctuating asymmetry of tuft area) as well as the relative size of the male and female. The 'rule of thumb' appears to be if the male is not suitable as a mate, attack and eat him. Thus, the risk of attempted cannibalism appears to be greater for smaller males and males in poorer condition with relatively smaller tufts, resulting in selection for larger male body size and larger tuft size. The second female decision, whether or not to mate, suggests potential sexual selection for relative tuft size, because males that were accepted as mates had relatively larger tufts. A third female decision is whether to engage in cannibalism postmating, and this decision appears to be related to a set of variables that include female size and age, as well as male size, body condition and tuft size. The majority of males that do mate escape unharmed (or at worst lose a leg). Because males can and do mate multiply, there is clearly an advantage for males to avoid postmating cannibalism (Norton & Uetz, in press). Even without the possibility of a second mating for either sex, sexual cannibalism and sexual selection could impose directional selection for larger male size and tuft size.

Variables influencing mating decisions of previously mated females were somewhat different from those of virgin females. Female body size and age and male body size, tuft size and age all influenced whether previously mated females attacked and/or cannibalized a courting male (Tables 3, 5). Although mating decisions of previously mated females appear to be based primarily on female age postmoult, and not on tuft size, tufts of second mates were significantly larger than those of first mates (paired t test: $t_{13} = 2.26$, $P = 0.047$). Thus, reinforcing selection pressure for male size and males with relatively larger tufts may increase in intensity as males encounter previously mated females and older females, whereas the selection pressure on tuft size via female mate choice decreases when males encounter previously mated females.

If decision criteria for mate rejection and cannibalism are similar with respect to an ornament or other trait, then male ornaments may also confer both a mating and a survival advantage. As demonstrated here, smaller male body size and relative size of male ornaments may affect cannibalism risk, and larger ornament size may serve as a visual signal in female mate choice. Many male ornaments confer information about male condition (Andersson 1994); consequently, signals used to assess mate quality could simultaneously reflect males' ability to escape or resist female predation attempts and the subjugation costs of preying on a particular male. Males with greater expression of the trait are less likely to be cannibalized and more likely to be chosen as mates, so mate choice and sexual cannibalism reinforce selection for trait magnitude and probably provide directional selection for larger male body size and tuft size. Since male body condition, body size, tuft size and fluctuating asymmetry

Table 3. Characteristics (mean ± SE) of males and (virgin) females across cannibalism/mating categories (N = 120)

| Characteristic | Premating | | | Male mated | Male not cannibalized/ not mated | Male cannibalized postmating |
	Cannibalism attempted	Male cannibalized	Cannibalism not attempted			
Male TA (mm^2)	3.622±0.074	3.037±0.199	4.162±0.106	3.927±0.067	3.764±0.179	3.295±0.231
Relative TA (residual)	−0.083±0.127	−0.237±0.127	0.231±0.054	0.047±0.041	−0.159±0.080	−0.021±0.143
Male FA	0.252±0.036	0.342±0.221	0.124±0.016	0.202±0.025	0.236±0.056	0.261±0.142
Male CW (mm)	2.748±0.029	2.505±0.099	2.827±0.044	2.816±0.028	2.812±0.055	2.594±0.061
Female CW (mm)	2.907±0.068	3.18±0.068	2.944±0.046	2.859±0.029	2.87±0.194	3.16±0.226
Relative female–male weight difference (%)	32.831±2.20	57.118±5.01	27.469±2.234	27.462±2.306	35.961±5.572	49.013±2.753
Male body condition (residual)	−0.001±0.0004	−0.002±0.0014	0.003±0.0007	0.0011±0.0005	−0.0013±0.001	−0.004±0.001
Female body condition (residual)	0.0002±0.0009	0.006±0.003	−0.0005±0.010	−0.0006±0.001	−0.0006±0.001	−0.001±0.002
Female age (days postmaturity)	24.302±1.140	23.875±4.994	22.937±1.980	22.128±1.127	22.128±1.127	32.454±2.379

TA: tuft area; FA: fluctuating asymmetry of tuft area; CW: cephalothorax width.

were all related to the probability of female cannibalism attempts among virgins, we suggest that females may be using one or more of these traits to evaluate males as potential prey. Among previously mated females, these characteristics were not significantly related to the probability of cannibalism attempts, but tuft size was a significant predictor of cannibalism success. This finding suggests that males with relatively larger tufts may indeed be better able to avoid female predation attempts.

Previous studies that have examined *S. ocreata* tuft size as a trait involved in female mate choice have provided mixed evidence. Studies with live males have found that experimental removal of tufts reduces female receptivity responses when vibratory cues are absent, but not when they are present (Scheffer et al. 1996). However, Scheffer et al. (1996) found no difference in actual mating success between males with legs experimentally shaved and males that had intact tufts. Similar studies in visual-only arenas found that mating success was not independent of natural variation in tuft size; males from the smallest tuft size category (lowest third of the tuft size distribution) had reduced success eliciting female receptivity, but there was no difference between the middle and largest tuft size categories (McClintock & Uetz 1996). Studies using video playback of courting male *S. ocreata* (without audio cues) found that females show reduced receptivity to images of males with either the tufts removed or reduced, but they show no appreciable increase in receptivity response to enlargement of male tufts compared to a control video (McClintock & Uetz 1996; Uetz 2000; Uetz & Roberts 2002). These studies raise the question of why males would develop large tufts in the apparent absence of female preference. None of these studies, however, measured the relation between natural variation in tuft area and actual male mating success on natural substrates. Results of the present study suggest that large-tufted males may accrue substantial fitness benefits via both increased mating success and increased survival during the breeding season.

Table 4. Stepwise multiple logistic regression analysis of male and female size/morphology variables associated with sexual cannibalism and mating for nonvirgin females paired with a second male

	χ^2	df	P
Premating cannibalism attempted/not attempted			
Source			
Eliminated predictors			
Male TA	0.005	1	0.942
Female CW	0.068	1	0.794
Female body condition	0.020	1	0.652
Male body condition	0.715	1	0.398
Male CW	1.803	1	0.179
Male FA	2.694	1	0.100
Female age	2.312	1	0.128
Final model	6.567	1	0.010
Male age	6.657	1	0.010
Lack of fit	36.748	13	0.908
Male cannibalized/not cannibalized			
Source			
Eliminated predictors			
Female age	0.036	1	0.850
Male FA	0.441	1	0.506
Male body condition	0.882	1	0.348
Male age	1.037	1	0.309
Female body condition	2.731	1	0.098
Final model	28.051	3	<0.0001
Male CW	15.033	1	0.0001
Female CW	14.542	1	0.0001
Male TA	6.578	1	0.010
Lack of fit	53.739	74	0.963
Male mated/not mated			
Source			
Eliminated predictors			
Female body condition	0.002	1	0.964
Male body condition	0.277	1	0.599
Male FA	0.386	1	0.534
Female CW	0.613	1	0.434
Male age	0.898	1	0.343
Male CW	1.774	1	0.183
Male TA	2.506	1	0.113
Final model (female age)	9.309	1	0.0023

TA: tuft area; CW: cephalothorax width; FA: fluctuating asymmetry of tuft area.

Table 5. Characteristics (mean $\pm$ SE) of males and (previously mated) females showing significant differences (by logistic regression) across cannibalism/mating categories ($N = 87$)

| Characteristic | Premating | | | Male mated/ not cannibalized | Male not mated/ not cannibalized |
	Cannibalism attempted	Male cannibalized	Cannibalism not attempted		
Male TA (mm^2)	3.914$\pm$0.085	3.412$\pm$0.178	3.804$\pm$0.153	4.144$\pm$0.127	3.845$\pm$0.084
Relative TA (residual)	$-$0.022$\pm$0.059	$-$0.170$\pm$0.135	0.086$\pm$0.102	0.169$\pm$0.117	$-$0.031$\pm$0.057
Male CW (mm)	2.849$\pm$0.031	2.653$\pm$0.051	2.731$\pm$0.059	2.854$\pm$0.067	2.821$\pm$0.031
Female CW (mm)	2.891$\pm$0.033	3.033$\pm$0.054	2.855$\pm$0.061	2.883$\pm$0.068	2.885$\pm$0.033
Relative female–male weight difference (%)	34.547$\pm$2.171	48.142$\pm$1.953	31.705$\pm$2.088	30.269$\pm$5.169	35.269$\pm$1.843
Female age postmoult (days)	28.000$\pm$1.28	26.500$\pm$2.567	24.75$\pm$2.413	19.787$\pm$2.56	28.913$\pm$1.187
Male age postmoult (days)	32.328$\pm$0.426	32.000$\pm$1.02	34.937$\pm$1.018	31.920$\pm$0.645	33.319$\pm$0.515

TA: tuft area; CW: cephalothorax width.

In the current study, males and females were paired in mesocosms with natural leaf litter, rather than in the smaller open arenas used in some of the aforementioned studies. A natural leaf litter substratum may reduce the effectiveness of vibratory signals considerably (Scheffer et al. 1996) and increase the relative importance of visual signals in mate choice and sexual cannibalism. There is evidence that tufts may serve as attention signals or as amplifiers (Hasson 1989, 1991, 1997) of the courtship display of males, since leg waving is a large visual component of the display. Hebets & Uetz (2000) found a positive significant correlation between leg waving and the presence of leg tufts for several species of *Schizocosa* and other species of wolf spider with active leg-waving displays. Wolf spiders are highly biased towards movement cues in their ability to detect prey (Persons & Uetz 1997) and conspecifics (Rovner 1993), and leg tufts may have evolved to increase the efficacy of courtship signals (Hebets & Uetz 2000). Visual cues from leg tufts may
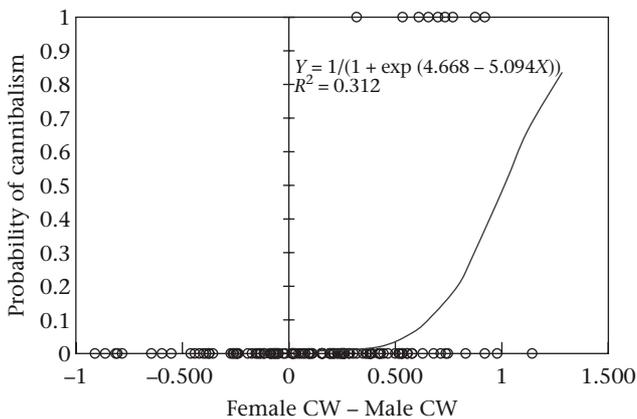

Figure 3. Logistic regression and probability of premating cannibalism as a function of female and male size difference in virgin females. The line represents the predicted probability of cannibalism derived from a logistic regression. Circles above the line indicate premating cannibalism events. Circles below the line indicate that no premating cannibalism occurred. CW: cephalothorax width.
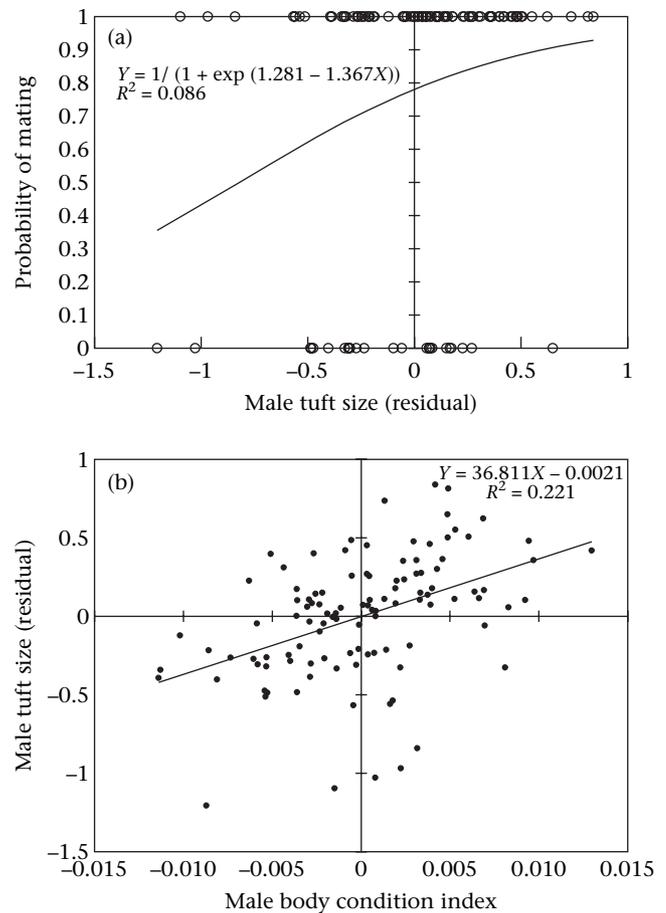

Figure 4. (a) Logistic regression and probability of mating (virgin females) as a function of male tuft size (scaled for body size as a residual of tuft area*cephalothorax width regression). The line represents the predicted probability of mating derived from a logistic regression. Circles above the line indicate mating events. Circles below the line indicate that no mating occurred. (b) Regression of male tuft size on male body condition (residual of mass*cephalothorax width regression).
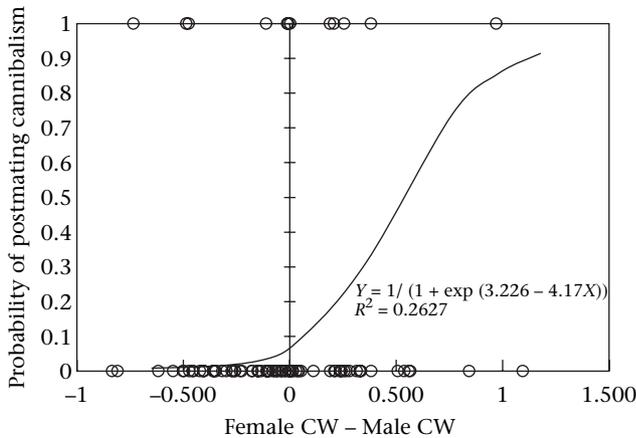
Figure 5. Logistic regression and probability of postmating cannibalism as a function of female and male size difference. The line represents the predicted probability of postmating cannibalism derived from a logistic regression. Circles above the line indicate postmating cannibalism events. Circles below the line indicate that no postmating cannibalism occurred. CW: cephalothorax width.

$Y = 1/ (1 + \exp (3.226 - 4.17X))$
$R^2 = 0.2627$

Figure 7. Logistic regression and probability of premating cannibalism as a function of female size in previously mated females. The line represents the predicted probability of premating cannibalism derived from a logistic regression. Circles above the line indicate premating cannibalism events. Circles below the line indicate that no cannibalism occurred. CW: cephalothorax width.

$Y = 1/ (1 + \exp (10.922 - 3.273X))$
$R^2 = 0.092$

therefore be more important in environments where vibratory/seismic communication is constrained.

Tufts may also serve as an honest indicator of male quality to a female, as relative (residualized) tuft size was significantly correlated with body condition indices in this and several other studies (see Uetz 2000; Uetz et al. 2002). In one study (Uetz et al. 2002), experimental manipulation of feeding regime of juveniles affected adult male tuft size; well-fed males had relatively larger tufts (scaled for body size). Thus, males with relatively larger tufts may be in better condition and more likely to be successful foragers. Two other studies have shown that asymmetry in male tufts (both regenerative asymmetry from leg loss and fluctuating asymmetry from developmental instability) reduces female receptivity and male mating success (Uetz et al. 1996; Uetz & Smith 1999). In
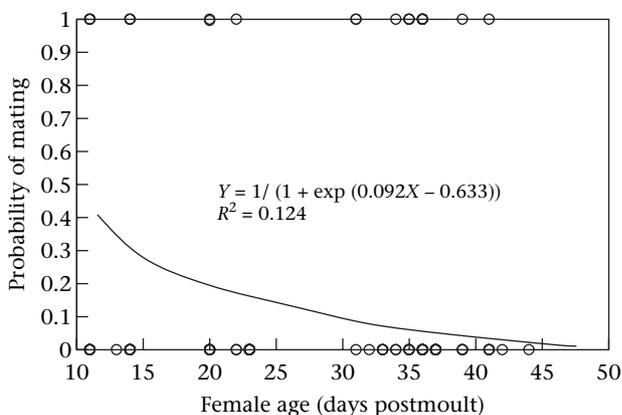

Figure 6. Logistic regression and probability of a second mating (among previously mated females) as a function of female age. The line represents the predicted probability of a second mating derived from a logistic regression. Circles above the line indicate mating events. Circles below the line indicate that no mating occurred.
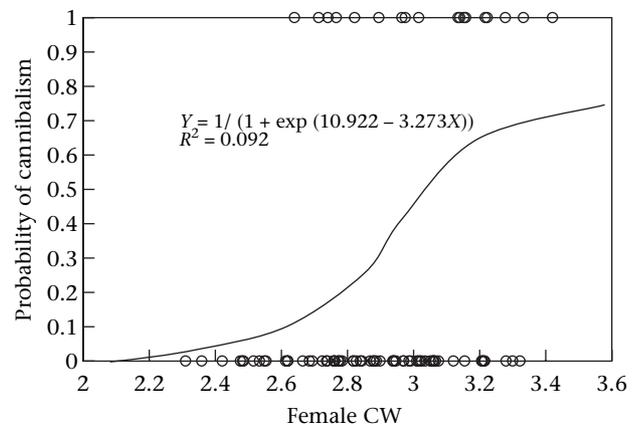
$Y = 1/ (1 + \exp (0.092X - 0.633))$
$R^2 = 0.124$

a sample of males collected from the field during the breeding season, tuft symmetry was positively correlated with male body condition (Uetz & Smith 1999). Video playback studies manipulating asymmetry while holding body size and behaviour constant suggest that asymmetry in the visual signal provided by the tufts is a cue that females use to discriminate between males (Uetz & Smith 1999). Even so, asymmetry of male tufts was not significantly correlated with any of the other variables in this study, and was significantly related to attack probability but not actual cannibalism risk or mating success.

Determining causal relationships between male body size, tuft size, cannibalism and mating success is difficult because many of these variables were intercorrelated in our study and other (unmeasured) variables also may be equally important. For example, females might be selecting males as mates based on some other trait(s) such as the intensity or duration of courtship (K. Delaney, A. Roberts & G. W. Uetz, unpublished data), which in turn may be related to tuft size and body condition. Likewise, the hypothesis that tufts also may function in some other way to minimize cannibalism cannot be rejected. Tufts might increase the apparent size of males and/or serve as a deterrent to female cannibalism attempts. Even so, our results show that males that were attacked and cannibalized were significantly smaller, and that male body size was not significantly related to mating success. Moreover, because we used a residual of tuft size scaled for body size, mating success of males paired with unmated females appears to be influenced by the relative size of this ornamental trait independent of male size.

We believe that a closer examination of complex courtship displays and male morphology among other spiders may find that male traits previously thought to function solely in the context of mate recognition may also influence the potential for sexual cannibalism, and should be considered in that context as well as mate choice.

Acknowledgments

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