Male black widows court well-fed females more than starved females: silken cues indicate sexual cannibalism risk

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Male mate choice is predicted to evolve as male investment in mating increases. Thus, taxa in which males pay a high cost for mating offer researchers an ideal system to test traditional sex roles. Males courting potentially sexually cannibalistic females may be under strong selection to bias their courtship efforts away from hungry females that may be more likely to attack. Here we tested the prediction that web-based chemotactile cues of recent female foraging success influence male courtship in the black widow spider, *Latrodectus hesperus*. In addition, we tested the underlying assumption that previous female foraging success reduces precopulatory sexually cannibalistic attacks. We found that males courted well-fed females significantly more than they did starved females, and that this bias was maintained in the absence of the female when males encountered only (1) cues from female webs and (2) cues from female silk after web architecture had been eliminated. A nonsignificant courtship bias in favour of well-fed females was also evident when these females were transplanted to the webs of starved females. Male courtship biases in favour of well-fed females appear adaptive, as starved females were significantly more likely to attack males before mating. We conclude by noting that sexual cannibalism offers a model system wherein the exploitation of cues of predation risk have unique implications such as the effects on male courtship preferences seen here.

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Mating preferences tend to evolve when organisms pay a high price for mating (Trivers 1972; Thornhill 1976; Emlen & Oring 1977). Thus, typical sex roles involve a limiting sex (often females) that discriminates among suitors, and a nonlimiting sex (often males) whose fitness is often optimized by maximizing the number of partners rather than being selective about those partners. Systems wherein males pay a particularly high cost for mating allow researchers to test our understanding of these typical sex roles. Indeed, the evolution of male mate choice in the face of high mating costs has been a popular focus of work (e.g. Bonduriansky 2001). More recently, Barry & Kokko (2010) reviewed the literature on the evolution of male mate choice and provided a model suggesting several reasons why male mate choice may fail to evolve in spite of high costs of mating to males. Specifically, they suggested that when males encounter females sequentially rather than simultaneously, the prospect of future mate availability for males may often be low, thus selecting against choosy males. As such, to find evidence of mate discrimination by males, researchers may

need to concentrate on systems wherein the costs of courtship and mating are extremely high for males.

Mating systems in which courting males experience a risk of fatal, precopulatory sexually cannibalistic attacks by females (reviewed in Elgar & Schneider 2004) offer an outstanding opportunity to examine the evolution of male courtship and mating behaviour in the face of potentially high costs. Here, selection may favour discriminating males, not only because discrimination could yield a higher-quality (e.g. more fecund) female, but also because some females may be more likely to mate, whereas other females may be more likely to kill a male before copulation. Thus, when courting males are simultaneously potential mates and potential prey items for females, male mating costs include potential death. As such, these males may show preferences for low-risk females.

One way courting males may be able to discriminate among females that vary in the risk of sexual cannibalism they pose is through chemical cues (Gaskett et al. 2004). Indeed, chemical signals appear critical in spider systems (Gaskett 2007), a group well known for sexual cannibalism (Elgar & Schneider 2004). The study of kairomones, or chemical cues produced by one organism that are exploited by another organism (Ruther et al. 2007), has proven a popular focus of study within the broad field of chemical communication (e.g. Dicke & Grostal 2001). Specifically, kairomones have been shown to allow spiders to locate prey (Persons

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& Uetz 1996) and avoid predators (Suter et al. 1989; Persons et al. 2001; Wilder & Rypstra 2004). However, we know little about whether chemotactile cues left by sexually cannibalistic females can be used by conspecific males as kairomones, allowing males to discriminate between high-risk predatory females that are unlikely to mate and low-risk predatory females that are likely to mate.

Cues that indicate female mating status are among the few chemical cues that have been addressed in this respect. To the extent that males preferentially court virgin females, males may (1) reduce sperm competition and/or (2) avoid attacks from mated females with presumably relaxed sperm limitation (Newman & Elgar 1991; Hoefler et al. 2009). For example, male redback spiders, *Latrodectus hasselti*, use silk-based chemical cues to discriminate against recently mated females (Stoltz et al. 2007).

However, mating status is only one potential cue that males could intercept from females, their webs and their silk. Here we examined whether male courtship behaviour in the western black widow spider, *Latrodectus hesperus*, is influenced by the use of chemical and behavioural cues of female foraging success, and by extension, relative risk of sexual cannibalism. Barry et al. (2010) noted that male mate choice for well-fed, high-condition females in species where sexual cannibalism is prevalent offers choosy males both the above-stated survival advantage, as well as benefits in terms of the added offspring potentially produced by high-condition females. Indeed, body condition is correlated with fecundity in several sexually cannibalistic species (Wise 2006; Barry et al. 2008) and males are likely to benefit if they bias their mating effort towards high-condition females. However, to obtain these benefits, males must first successfully navigate the extreme intersexual conflict inherent in sexual cannibalism by females prior to copulation. Thus, our focus in the current study was on documenting male courtship behaviour based on cues from female silk, webs and the female's actual presence. We manipulated the previous foraging history of females to create variation in these cues and to determine whether those cues are reliable predictors of the likelihood of precopulatory attacks from females. In support of the hypothesis that males use cues of female foraging success to modulate their courtship intensity to sexually cannibalistic females, male praying mantids, *Tenodera aridifolia sinensis,* are more attracted to well-fed females (Lelito & Brown 2008) and are more cautious in their courtship of hungry females (Lelito & Brown 2006). In addition, female body condition is negatively correlated with propensity to attack in the false garden mantid, *Pseudomantis albofimbriata* (Barry et al. 2008).

Experimental Design

Below we present a series of experiments that test the idea that males use cues of recent female foraging success to heighten the prevalence of their courtship, as well as the intensity of that courtship as defined by a male's readiness to mount and court on the female's abdomen. First, we predicted that in the absence of the female, males would court on the webs of well-fed females significantly more than on the webs of starved females (experiment 1). Second, we predicted that in the presence of females, males would court well-fed females significantly more than they would starved females (experiment 2). Third, we examined the relative importance of cues from silk/webs and cues from the female's presence by switching well-fed females to the webs of starved females and starved females to the webs of well-fed females (experiment 3). Lastly, we conducted a follow-up experiment with a different set of males and females to examine the effect of recent female foraging success on male courtship behaviour in the presence of silk deconstructed from webs (experiment 4). Throughout each of these experiments we quantified male courtship intensity

as the proportion of time spent courting across a 3 h trial, and in experiments 2 and 3, we also quantified the prevalence of precopulatory sexually cannibalistic attacks by females. Experiments 1–3 also allowed us to examine male courtship behaviour in response to both (1) variation across our manipulation of female feeding regimes and (2) variation among different females/webs.

We first present the male perspective (male as the experimental unit), wherein each male was paired with a well-fed female and a starved female (order randomized), allowing us to test for male courtship preferences based on silk, web and behavioural cues of female feeding status. Second, we present analyses from the female perspective (female as the experimental unit), wherein repeated measures of male courtship response to each female's web allowed us to quantify individual variation in a series of male responses to different females/webs, thus testing the current hypothesis that individual variation is important in animal behaviour (Sih et al. 2010).

MATERIALS AND METHODS

Study System

Latrodectus hesperus males use long-distance, airborne chemical cues to distinguish conspecific female webs from the webs of heterospecific females (Kasumovic & Andrade 2004). Short-range chemotactile cues in the webs of female *L. hesperus* are known to stimulate male courtship behaviour, even in the absence of the female (Ross & Smith 1979). Black widow females are relatively sedentary web-building spiders that typically inhabit a single web throughout adulthood (Kaston 1970). Thus, it seems likely that cues of foraging success could accumulate in females' webs and provide chemical information for males visiting the webs in search of mates. In addition, *L. hesperus* web architecture is condition dependent (Blackledge & Zevenbergen 2007; Zevenbergen et al. 2008): starved spiders increase their investment in sticky silken threads that attach to the ground and improve prey entanglement, whereas sated spiders invest more in structural fibres and spin silk that is twice as wide as that spun by starved spiders. Thus, feeding history in *L. hesperus* leads to structural differences in a female's web architecture that has the potential to affect male courtship behaviour.

General Protocol

Males and females used in the experiment were F1 laboratory-reared offspring of 50 gravid females collected from urban habitats throughout Glendale, Arizona, U.S.A. in the summer of 2007. One hundred and thirty virgin males were used in mating trials within the first 2 weeks following their adult moult and did not feed as adults (experiment 1: $N = 42$; experiment 2: $N = 38$; experiment 3: $N = 30$; experiment 4: $N = 20$). Individual males were used in only one experiment, although experiments 1–3 entailed the paired testing of each male in both treatments (order randomized). Experiment 4 employed a unique set of male and female spiders, and tested the effect of recent female foraging success on male courtship towards female silk in the absence of any web architecture. None of the original 50 families were represented by more than one male in any given experiment and males were never paired with a sister, her web or her silk. Females were identified at the antepenultimate moult, reared individually in transparent plastic boxes ($10 \times 10 \times 12$ cm) and fed weekly two house crickets, *Acheta domesticus*, weighing 50–75% of their body mass until their penultimate moult. At the penultimate moult, females remained on the same diet regime but were moved to individual large, open-air (unlidded) plastic tubs ($55 \times 39 \times 14$ cm). In the centre of each tub a rectangular Styrofoam 'island' ($14.5 \times 10 \times 4$ cm) was glued to the

floor of the tub. Tubs were filled with water to a height of 2 cm to prevent the spider from escaping from the island. Four wooden dowels were inserted into the top of the Styrofoam projecting 11 cm above the island floor. Widow spiders cannot escape from these islands and weave extensive webs using dowels and the Styrofoam floor as substrate (J. C. Johnson, personal observation).

Female Stimuli (Silk and Presence)

One day following their adult moult, 14 females were selected for courtship trials. Experiments 1–3 below used a repeated measures design in which webs/females from each feeding treatment experienced a sequence of different males such that we could simultaneously quantify (1) within-web/female variation, (2) among-web/female variation and (3) variation among our feeding treatments. This repeated measures aspect of our design was necessitated by the number of reasonably sized female webs that we could observe in the laboratory, but also allowed us to quantify the extent to which within-female/web variation was responsible for male courtship. The potential importance of individual variation in animal behaviour is currently receiving renewed interest (Sih et al. 2010). Thus, our design allowed us to examine the magnitude of variation among females and reduce the error variation that stems from individual variation in our attempt to quantify whether our feeding treatments significantly affected male courtship and sexual cannibalism. Finally, individual variation in male courtship behaviour was controlled in experiments 1–3 by employing a paired design in which each individual male encountered a web/female from each feeding treatment (order randomized).

Upon maturity females were fed one adult female house cricket. Experimental food treatments began after this initial adult feeding: fed females ($N = 7$) received one adult female house cricket every third day for 1 month prior to the experiment, and remained on this diet regime through the course of the 2-week experiment. Feedings were never conducted on the same days as a courtship trial (see below). Following their initial adult feeding, starved females ($N = 7$) were provided with no prey as adults for 1 month preceding the onset of courtship trials and were starved throughout the course of the 2-week experiment. Prey carcasses were left in the webs of fed females in experiments 1–3 to enhance the differences between web types; however, at no time during any courtship trial did we observe males feeding upon prey carcasses. Experiment 4 involved male courtship in the presence of silk with no web architecture and no visible prey remains.

Throughout all experiments, we estimated body condition both as body mass corrected for cephalothorax area (Moya-Laraño et al. 2008) and from residuals of a linear regression of spider mass/cephalothorax area (Jakob et al. 1996). As these measures produced similar results, we report only analyses of body mass corrected for cephalothorax area. Following their final (adult) moult, we photographed the area of the cephalothorax for each spider (male and female) used in the study using a digital camera. These images included a reference scale allowing us to later digitally measure the area of the cephalothorax (mm^2) using the program Imagepro. Spider body mass (mg) was obtained for each spider 1 h prior to each trial.

Experiment 1: Web Only (Female Absent)

After the month-long female food regime, courtship trials began. In this initial experiment, all resident females were removed from their webs 1 h prior to introduction of the male ($N = 42$) so that we could measure male behaviour based on cues found in the female's web. On the following day, males were weighed again and introduced into the web of a female whose food treatment they had not encountered the day before. The sequence of webs encountered

by males (i.e. well-fed female webs seen first or second) was randomized. Thus, male spiders were tested in each treatment to control for individual variation in male behaviour. Male courtship behaviour in the female's absence was noted at 15 min intervals for 3 h, a typical duration for courtship in this species prior to insemination (J. C. Johnson, personal observation). We scanned each web at 15 min intervals and scored which males were courting. Males not scored as courting at first glance were observed for 1 min to determine whether they would be scored as courting in that interval. Male courtship intensity was quantified as the proportion of scans that males were observed courting out of a total of 12 possible scans. All proportions were arcsine transformed to meet assumptions of normality.

Experiment 2: Female in Home Web

Male courtship behaviour was also tested in the presence of females in their webs to examine the combined effect of chemotactile cues from the web and cues from actual male–female interactions. Virgin males ($N = 38$) not used in experiment 1 were weighed and photographed prior to being introduced into a female's web. Male courtship intensity was measured as described above. In addition, we measured the proportion of intervals in which the male courted on the female's abdomen. To maintain all females as virgins during the experiment we ended trials when we recorded a male courting on the abdomen of a female for four consecutive 15 min intervals, which is the typical duration of mounting required before males attempt to mate with a female (J. C. Johnson, personal observation). We also recorded precopulatory attacks/kills by females observed during courtship trials. To maintain the integrity of food/web regimes, in all cases of successful sexual cannibalism, females were not allowed to consume the male, and male carcasses were immediately removed from the web.

Experiment 3: Females and Webs Mismatched

We repeated the above protocol with a new set of virgin males ($N = 30$) comparing mating interactions when males were paired with (1) a well-fed female inhabiting the web of a starved female and (2) a starved female inhabiting the web of a well-fed female. Prior to trials, each female was removed from her home web and placed into a web that had been vacated by a female from the opposite feeding treatment. Females were allowed to acclimate to the foreign web for 1 h before males were introduced. We observed these transplanted females during this acclimation hour to determine the extent to which transplanted spiders spun silk in the foreign web before trials started.

Experiment 4: Silk Cues Only (Female Absent, Web Deconstructed)

Because past research has shown that the three-dimensional web architecture of *Latrodectus* webs is condition dependent (Blackledge & Zevenbergen 2007; Zevenbergen et al. 2008), we conducted a final experiment to isolate silken cues from web structure and prey remnants in webs. Modelled after the work of Prenter et al. (1994), we introduced a unique set of males ($N = 20$) into transparent plastic boxes ($4 \times 4 \times 5$ cm) each containing two toothpicks wrapped tightly with 1.75–2.00 mg of silk taken from the web of a female that had been either starved for 4 weeks or fed weekly for the 4 weeks prior to the experiment. Males used in this experiment were drawn from 10 laboratory-reared families. Two males from each sibship, each no older than 5 days post maturity, were randomly selected and split between our two treatments. Thus, 10 males representing 10 different families encountered the silk of well-fed females and an additional 10 males representing the

same 10 families encountered the silk of a starved female. Males were never paired with the silk of a sister. Male courtship intensity was measured as described in experiment 1 above.

Statistical Analysis

We used independent samples *t* tests to test for an effect of the order in which males encountered the two treatments (well-fed then starved versus starved then well-fed). Given that we found no effect of order on courtship, we performed paired *t* tests to test whether males courted significantly more on webs of well-fed females than on webs of starved females, as predicted. Linear regressions were used to test for an effect of (1) silk accumulated in prior courtship trials on courtship activity in a focal trial and (2) male body condition on courtship intensity. We used repeated measures ANOVA to assess the relative magnitude of (1) variation in courtship elicited across feeding treatments, (2) variation in courtship elicited by individual webs/females across repeated measures with different males (i.e. within-female/web variation) and (3) variation in courtship elicited among females (between-female/web variation). The sample size of males available to court females in this repeated measures design varied across experiments from six repeated measures (males) per female in experiment 1 to four repeated measures (males) per female in experiments 2 and 3. No such paired or repeated measures design was used for experiment 4. Instead, we used an independent samples *t* test to examine differences between silk treatments. All analyses were conducted in SPSS v.16 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Potential Confounds

We found no significant effect of the order in which males experienced web treatments (i.e. well-fed female seen first or second) on courtship response (experiment 1: $t_{82} = -0.16$, $P = 0.87$; experiment 2: $t_{73} = 1.19$, $P = 0.24$; experiment 3: $t_{47} = 0.96$, $P = 0.34$). While our repeated measures design had the advantage of quantifying within-female (web) variation in courtship response, this design also entailed some unique potential confounds. For example, the repeated use of female webs within and among the series of experiments below necessarily involved the accumulation

of male silk as trials progressed. As such, courtship in later trials and/or experiments may have been influenced by courtship silk left by previous males. Nevertheless, we found no evidence that male courtship was influenced by the accumulation of silk across trials and/or experiments. Figure 1 shows that no relationship existed within experiment 1 between the accumulated time of previous courtship before a focal trial and the amount of time a male courted in that focal trial. Furthermore, we found no evidence that male courtship behaviour changed among trials within and across experiments 1 and 2 (see Fig. 2). While males consistently courted more on the webs of well-fed females in both experiments (see below), and both treatments experienced an increase in male courtship when females were present in their webs for experiment 2, no discernible trends were apparent as a function of the simple progression of trials and presumed accumulation of male silk. This result is further substantiated by the nonsignificant effect of within-subject (web) variation in the repeated measures analyses reported below. Thus, the repeated use of female webs in these experiments should not confound our ability to draw conclusions about the hypothesized role of female feeding history on male courtship.

Using a Bonferroni correction for the eight tests performed (four experiments, each analysed separately for two food treatments), male body condition had no significant effect on courtship intensity towards well-fed webs/females (experiment 1: $r = 0.16$, $F_{1,40} = 1.10$, $P = 0.30$; experiment 2: $r = 0.22$, $F_{1,36} = 1.81$, $P = 0.19$; experiment 3: $r = 0.005$, $F_{1,24} = 0.001$, $P = 0.98$; experiment 4: $r = 0.004$, $F_{1,8} = 0.001$, $P = 0.99$) or starved females (experiment 1: $r = 0.19$, $F_{1,40} = 1.51$, $P = 0.23$; experiment 2: $r = 0.35$, $F_{1,37} = 4.38$, $P = 0.04$; experiment 3: $r = 0.03$, $F_{1,24} = 0.02$, $P = 0.88$; experiment 4: $r = 0.13$, $F_{1,8} = 0.14$, $P = 0.72$).

Experiment 1: Web Only (Female Absent)

First, our manipulation of female feeding regime successfully rendered well-fed females (474.1 ± 41 mg) in significantly better condition (body mass corrected for body size) than starved females (132.1 ± 10 mg; unequal variances *t* test: $t_{9.39} = 9.60$, $P < 0.0001$). In the absence of the female, males courted significantly more on webs of well-fed females than on webs of starved females ($t_{41} = 5.63$, $P < 0.0001$; Fig. 3; see also separation of lines in Figs 1 and 2). Repeated measures ANOVA showed no significant within-subject (web/female) effect on male courtship across trials ($F_{5,60} = 0.41$,
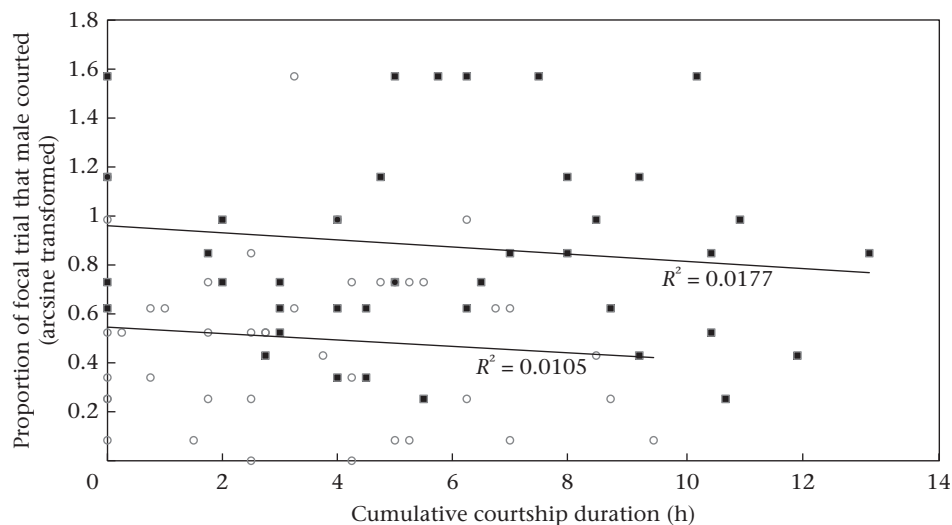

Figure 1. Relation between cumulative courtship duration of male black widows on females' webs in previous trials (total silk deposited by all males) and the proportion of courtship that each female's web received in the focal trial in experiment 1. Solid square: web of well-fed female; open circle: web of starved female.
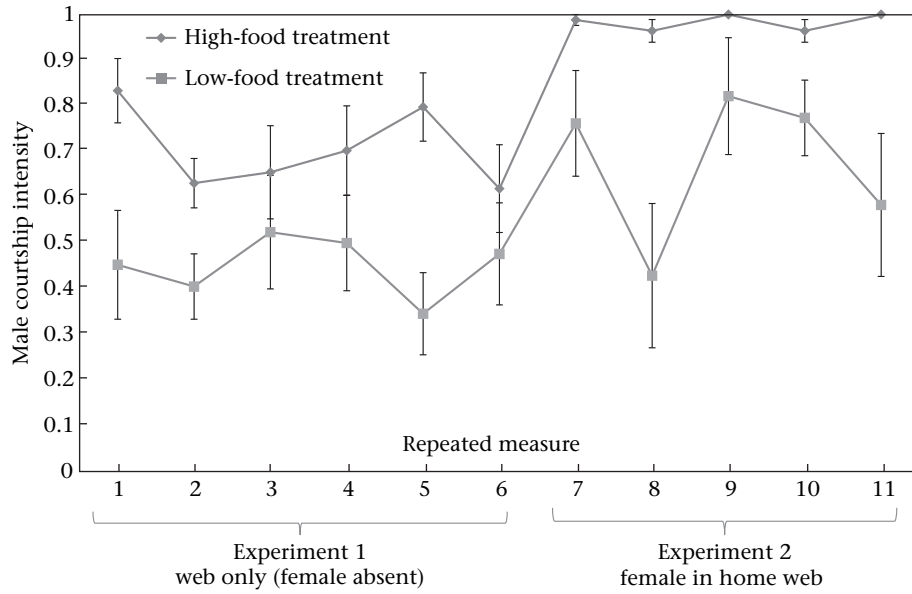
Figure 2. Relation between courtship intensity of male black widows and repeated measuring of female webs across experiments 1 and 2.

$P = 0.84$). This repeated measures analysis from the female perspective also confirmed the above effect of feeding treatment ($F_{1,12} = 14.74$, $P = 0.002$).

Experiment 2: Female in Home Web

In the presence of both the female and the chemotactile cues from the female's web, males courted significantly more towards well-fed females ($t_{37} = 5.45$, $P < 0.0001$; Fig. 3). Repeated measures ANOVA showed no significant within-subject (web/female) effect

($F_{3,36} = 0.76$, $P = 0.52$), but there was a significant effect of feeding treatment, confirming the male analysis above ($F_{1,12} = 11.97$, $P = 0.005$). Males also spent significantly more time courting directly on the abdomen of well-fed females than on the abdomen of starved females ($t_{37} = 3.57$, $P = 0.001$; Fig. 4). We found no effect of individual female variation on this male courtship response ($F_{3,36} = 0.42$, $P = 0.84$), but again, there was a significant treatment effect ($F_{1,12} = 5.59$, $P = 0.04$), confirming the male analysis.

Well-fed, high-condition females never attacked a courting male (0/7). In contrast, 71% (5/7) of starved, poor-condition females
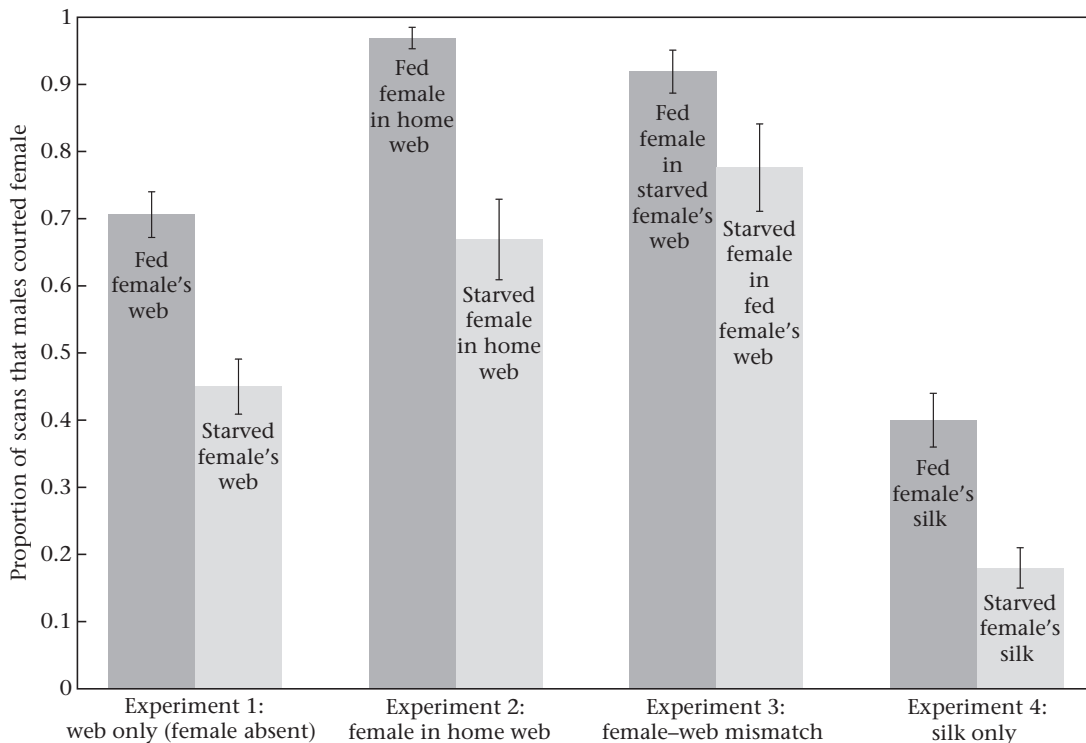

Figure 3. Relation between male courtship and female foraging success in black widows (experiments 1–4).
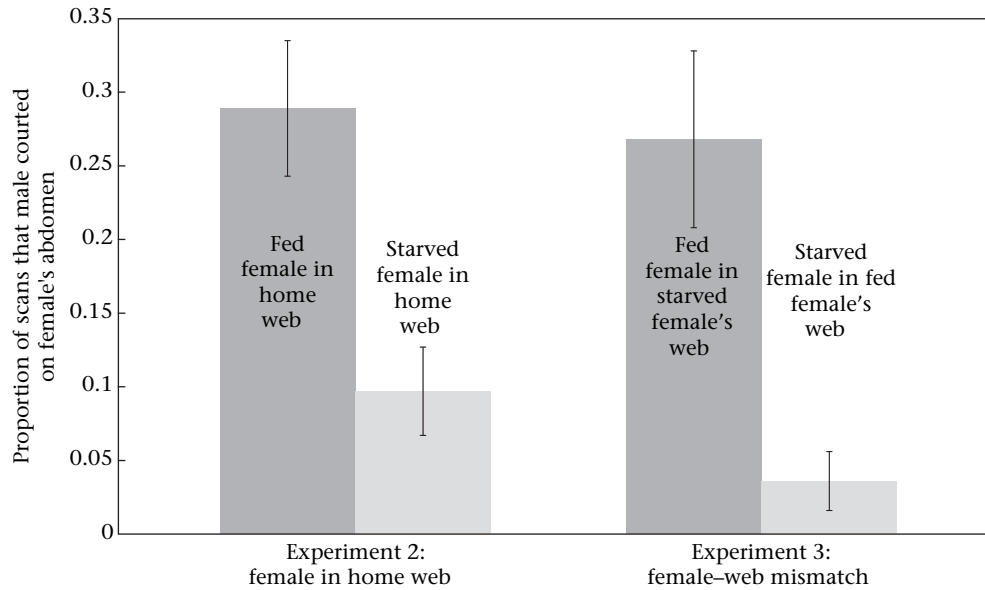
Figure 4. Relation between male courtship on the female's abdomen and female foraging success in black widows.

attacked at least one male, and two of these females were successful in killing the male. Thus, the likelihood of attacks was significantly greater from starved females ($\chi^2_{12} = 7.78$, $P = 0.005$).

Experiment 3: Females and Webs Mismatched

Transplanted spiders showed no web building during the hour of acclimation prior to courtship trials. Instead, when well-fed females were switched to the webs of starved females they waited 118 ± 21 min before building web in the foreign web (i.e. 58 min into the courtship trial). When starved females were switched to the webs of well-fed females they waited 95.3 ± 17.8 min before building web in the foreign web (i.e. 35.3 min into the courtship trial).

Males courted well-fed females transplanted to the webs of starved females more than they did starved females transplanted to the webs of well-fed females, although this difference was marginally nonsignificant ($t_{25} = 1.84$, $P = 0.078$; Fig. 3). Repeated measures ANOVA showed no significant within-subject (female) effect ($F_{2,20} = 2.67$, $P = 0.10$), but it did show a significant food treatment effect ($F_{1,12} = 8.53$, $P = 0.015$). Males spent significantly more time courting on the abdomen of well-fed females that had been switched to webs of starved females ($t_{25} = 3.57$, $P = 0.001$; Fig. 4). Male courtship on the female's abdomen in experiment 3 showed no within-subject (female) effect ($F_{5,60} = 2.39$, $P = 0.08$), but there was a significant treatment effect ($F_{1,12} = 5.27$, $P = 0.04$).

Well-fed, high-condition females never attacked a courting male while residing in the web of a starved female (0/7). In contrast, when switched to the webs of well-fed females, 71% (5/7) of starved females attacked at least one male and three of these females were successful in killing the male. Thus, attacks were again significantly more common from starved females ($\chi^2_{12} = 7.78$, $P = 0.005$).

Experiment 4: Silk Cues Only (Female Absent, Web Deconstructed)

In the absence of any complex web architecture and visible prey remains, males courted significantly more in the presence of toothpicks wrapped with silk from well-fed females than in the presence of toothpicks wrapped with silk from starved females ($t_{18} = 4.20$, $P = 0.001$; Fig. 3).

DISCUSSION

In the absence of females, males courted significantly more in webs containing cues of recent foraging success. A similar result was found when males were presented only with silk deconstructed from female webs, suggesting that males use silk-based chemical cues to make this discrimination and that our results cannot be attributed simply to architectural differences in webs, including the presence of prey carcasses in the webs of well-fed females. However, courtship was more strongly influenced by cues from the female's presence than by cues of foraging success in the web. These differences in male behaviour appear adaptive, as males were more likely to be attacked by starved females. Below we discuss the implications of these findings.

Male Courtship

Our results show that, in the female's absence, cues of recent foraging success are used by males to influence the intensity of their courtship, even in the absence of any web architecture. Thus, while the presence of web architecture clearly increases male courtship levels (compare experiments 1 and 4 in Fig. 3), cues associated with silk in the absence of any web architecture are sufficient to heighten male courtship towards well-fed females. In extreme cases, males that previously had displayed a high incidence of courtship behaviour on the web of a well-fed female remained motionless for the entire 3 h trial when placed in the web of a starved female. While males of the congener *L. hasselti* have been shown to use cues associated with silk to discriminate virgin females from recently mated females (Stoltz et al. 2007), here we demonstrate that male *L. hesperus* courtship is influenced by silken, web-based cues of recent foraging success.

Most simply, this effect could be explained if the web/silk of a starved female lacks chemical signals that would otherwise be used by males to determine that a web is occupied. However, on average, males courted almost 40% of the time in the webs of starved females, suggesting that the female's recent presence was sufficient to motivate male courtship behaviour, albeit at lowered levels. Alternatively, our repeated use of females and their webs could have artificially enhanced this courtship preference for well-fed females if an initial accumulation of male courtship silk in the

webs of well-fed females resulted in increased courtship by subsequent males. This does not, however, appear to be the case, as we found no relationship between past courtship on a web and courtship intensity in the focal trial (Fig. 1), and no trends were observed to suggest that courtship levels changed in either direction across repeated measures (Fig. 2).

Our experimental mismatch of females and their webs demonstrates that male courtship behaviour is perhaps more heavily influenced by the female's presence than by the cues emanating from her web. However, the strong preference for well-fed females/webs/silk documented in this study was marginalized when we transplanted well-fed females into the webs of starved females. Thus, while well-fed females tend to receive intense courtship from males, artificially transplanting well-fed females into the webs of starved females was successful at weakening male preferences.

Chemicals from female webs may provide information regarding female quality (Gaskett et al. 2004). Volatile, silk-based cues are used by male *L. hesperus* to locate conspecific females as well as discriminate against conspecific females from other geographical subpopulations (Kasumovic & Andrade 2004). Thus, we argue that web-borne chemotactile signals are important to male courtship behaviour. In nature, males are likely to rely heavily on chemotactile cues in early phases of courtship. For example, female *L. hesperus* are known to favour web sites that allow them to extend their web from a secure retreat (e.g. rodent burrows, rock crevices; D'Amour et al. 1936). To the extent that females are commonly found in refuges off the main portion of the web, males visiting the web will encounter web-based chemotactile cues from a female before they receive vibratory feedback from a female. Thus, chemotactile cues of recent female foraging success will influence early stages of courtship, and thus can provide males with critical information as to the relative cannibalistic risk that a female presents.

Our results suggest that males use variation in chemical and behavioural cues to adjust their courtship behaviour such that well-fed, high-condition, low-risk females receive intense courtship, whereas starved, poor-condition, high-risk females receive significantly reduced courtship. While such a courtship bias by males has immediately obvious survival benefits via reduced sexual cannibalism (see below), choosy males may also benefit by preferentially courting the most fecund, high-condition females (e.g. Barry et al. 2010). Indeed, previous foraging success has long been implicated as a key factor underlying fecundity in female spiders (Wise 1975; Foelix 1996). Thus, male courtship behaviour in widow spiders appears likely to be shaped by both the risk that a female poses and the fecundity benefits she offers. Future studies that wish to disentangle these benefits will need to compare the fitness outcome of male mating strategies that vary in choosiness. For example, while the costs of courting poor-condition females and the benefits of courting high-condition females are apparent, we need to better understand the threshold at which males may become choosy. Ultimately, we would need to know the average fitness difference between choosy males that experience low risk of sexual cannibalism but therein pass up mating opportunities and less choosy males that are willing to risk courting poor-condition females and, if successful, compromise in terms of potential reproductive output. Note that male as well as female variables will be important in determining this threshold of male choosiness. For example, Johnson (2005) showed that precopulatory sexual cannibalism by female fishing spiders is heightened when females have a prereproductive experience of high male availability. Conversely, male assessments (possibly even chemical assessments) of high web/female density may contribute to male courtship strategies in sexually cannibalistic species.

Sexual Cannibalism

Despite the reputation for female aggression towards mates that has earned them the common name of 'widow spiders', sexual cannibalism has been quantified in remarkably few *Latrodectus* species (for exceptions see Forster 1992; Andrade 1996; Segoli et al. 2008). In particular, no study has quantified precopulatory sexual cannibalism in widow spiders. Previous work suggested that *L. hesperus* only rarely shows postcopulatory sexual cannibalism and never attempts precopulatory sexual cannibalism (Ross & Smith 1979). Our results suggest that precopulatory attacks are, in fact, used relatively frequently by poor-condition females, but are never displayed by high-condition females. While this result is intuitive and consistent with the hypothesis that precopulatory sexual cannibalism is used by females as an adaptive foraging strategy in response to food limitation (Newman & Elgar 1991), surprisingly few studies have found support for this contention in spider taxa (reviewed in Johnson & Sih 2005). While studies of mantids (Barry et al. 2008) and tarantulas (Rabaneda-Bueno et al. 2008) do provide support for this adaptive foraging hypothesis, most studies of spiders fail to support the prediction that precopulatory attacks are most common from poor-condition females (Elgar & Nash 1988; Arnqvist & Henriksson 1997; Johnson 2005). One thing mantids and tarantulas have in common is that males represent a relatively large prey item for females in these taxa. In contrast, here we present data that support this adaptive foraging prediction in *L. hesperus*, a species that, like many spider taxa, shows strong sexual size dimorphism, where males are minute compared to females (e.g. 2% and 7% of the body mass of well-fed and starved females from this experiment, respectively) and are minute compared to females' typical prey, and therefore, where males represent relatively little in terms of quantitative foraging gain for females.

One reason precopulatory sexual cannibalism may fail to conform to the predictions of the adaptive foraging hypothesis for many species is that chemical cues left by poor-condition females tip courting males off to the presence of risk. Thus, poor-condition female spiders may routinely be more motivated to cannibalize males before copulation than are high-condition females, but studies that ignore male traits that minimize such risk will miss this fact.

In conclusion, because sexually cannibalistic organisms (1) epitomize the current emphasis in behavioural ecology on intersexual conflict and (2) blur the lines between foraging, antipredator and mating behaviour, they allow us to address the integrative complexity of chemical communication and remind us that animal behaviour is best studied as a multivariate phenomenon. Our finding that male black widows use chemotactile cues to make risk-sensitive mating decisions provides evidence that an integration of chemical communication, predator/prey dynamics and intersexual conflict will yield exciting answers to questions of great interest to integrative behavioural ecologists.

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