Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae)

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Summary. Two to five days before sexual maturation, female sierra dome spiders (*Linyphia litigiosa*: Linyphiidae) undergo a transformation in their behavior toward males that visit their webs. During this latter part of their penultimate instar, females change from consistently positioning themselves far away from males to actively maintaining close proximity, reactions I call "avoidant" and "associative" behavior, respectively. Consistent associative behavior ceases after the female's first mating and thus is limited to soon-to-mature penultimate females. When a mate-seeking male finds an associative female, he attempts to guard her until she matures; this is often a *multi-day* affair. In contrast, males guard immature avoidant and mature mated females for only a *single* day. This dichotomy in male guarding times can be understood by the fact that associative behavior signals that the female will soon develop peak reproductive value. Upon completion of their final molt, 98% of females immediately mate with the current guarding male. Secondary suitors are not as likely to achieve mating. Moreover, first mates father 1.8 times more offspring, on average, than secondary mates. Whenever they meet on any female's web, males fight until one of the contestants withdraws. Fights typically are intensive, occasionally deadly, and often result in usurpation of the web by the newly arriving male. Larger males win more fights, but other qualities (e.g., vigor and persistence) appear to be important when contestants differ by less than 10–20% in body weight. Prolonged (i.e., multi-day) guarding of associative females enhances the intrasexual selection process by ensuring that every male that arrives at the web finds it already guarded. Therefore every male that finds the web becomes a participant in a series of male-male conflicts and web usurpations which span the period between the resident female's commencement of associative behavior and her sexual maturation. Since unforced male departures from the webs of associative females are rare, victors are retained on the web until they themselves lose a fight. This facilitates a steady increase in the fighting ability of sequential guards throughout the associative period, up until female maturation and mating. On my study site, first mates represented the final winners in a combative sorting process based on a minimum average of 2 fights; they were heavier and larger than secondary mates and randomly sampled males. The combination of (1) associative behavior by *nearly* mature females, (2) high mating propensity of *newly* mature females, and (3) first male sperm priority, constitutes a system whereby females enhance male-male competition and boost the expected fighting prowess of the principal sire of their progeny. Since males appear to make no material contribution toward progeny, the female's behavior probably functions to improve the genetic constitution of the offspring. In addition, the timing of associative behavior may limit prolonged guarding by food-stealing males to a period (1) encompassing the female's pre-molt fast and (2) before the heavy yolking of eggs, thereby ameliorating the nutritional costs of intrasexual selection.

Introduction

Male-male competition is a widely accepted mode of sexual selection partly because it appears to be such a straightforward mechanism of mate determination. It does not *assume,* for example, the existence of complex female adaptations designed to influence the qualities of mates. However, females that rely upon intrasexual selection to determine the sires of their offspring are not necessarily "pas-

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sive"; they may have behavioral adaptations that exert a crucial influence upon the mate-sorting power or timing of male-male competition (Halliday 1983).

In some species the likelihood of competitive encounters between mate-seeking males depends on the amount of time individual males are willing to guard a given female before copulation (e.g., in populations where males typically discover females at intervals that are greater than the usual time invested in single bouts of guarding). In such a context, females may have an opportunity to increase male guarding times by advertising an especially high probability of paternity in return for a guarding investment.

Encouraging extended precopulatory guarding via an advertisement of high reproductive value could benefit females by enhancing the stringency of male-male competition. It could accomplish this, without affecting male visitation rates or necessarily the intensity with which males are predisposed to fight, by reducing the frequency of unforced male departures. Any reduction in the probability of spontaneous abandonment before copulation will have two effects: (1) an increase in the proportion of visiting males that find the female still guarded by an earlier arrival, and that therefore must fight for the opportunity of mating, and (2) an increased likelihood that male-male fights and supplantations occur in a continuous series, such that the competitive ability of a male present with the female at any moment represents the maximum level demonstrated by any male during the entire period of female advertisement and prolonged guarding.

An ability to modulate the timing of male-male competition by choosing *when* to broadcast an advertisement of high reproductive value also might empower females to lessen costs connected with this mode of mate determination. For instance, if males and females compete for food, there will be nutritional costs connected with the presence of guarding males. Females may respond by restricting the period during which prolonged guarding correlates with high paternity, thereby limiting continuous male foraging interference to a portion of the life cycle during which the impact of poor foraging success on female fitness is minimal.

There are few studies documenting female behaviors that specifically serve to modulate intrasexual selection (Cox and LeBoeuf 1977; Thornhill and Alcock 1983). I propose that the "avoidant" and "associative" behaviors of female sierra dome spiders (*Linyphia litigiosa:* Linyphiidae) provide an example among arachnids. In this species, females more than 2 to 5 days from sexual maturity spend much of the time at the periphery of their dome-shaped web when a male is present, shunning contact and interaction. However, virtually all females change their behavior several days before maturation; they begin associating closely with any guarding male within the central portion of the web. In this paper I document the functional design of female associative behavior, and its positive influence on the duration of male guarding and fitness-related attributes of first mates. I suggest a twofold adaptive function for associative behavior that simultaneously addresses the female's problems of acquiring fit sires while reducing the detrimental effects of male food-stealing.

Natural history

The sierra dome spider is found in forested valleys throughout the mountains of western North America, especially near water. Most webs are located in the shrub layer, 1–3 m above the forest floor. All the observations reported here were conducted on a large natural population (1980–1986) at the Flathead Lake Biological Station (Polson, Montana), located on the eastern shore of Flathead lake. Along with other behaviorally similar members of the genus *Linyphia,* sierra dome spiders typically are distributed in dense populations (Bristowe 1958; Comstock 1912; Gertsch 1979; Janetos 1984). In the middle of the breeding season (i.e., middle to late July), the average density of inhabited webs on my study site was 1 per 4.2 m^2; certain areas often are 3 times as densely populated.

The web is a durable, three dimensional dome-shaped structure that is repaired and enlarged nightly. It consists of a finely woven sheet (i.e., the dome) supported in the vegetation by a cobweb-like superstructure and substructure. The undisturbed spider hangs dorsal-side-down from the underside of the dome's zenith. Most behaviors (e.g., mating, fighting, and prey capture) are limited to the dome portion of the web.

The sierra dome spider has an annual life cycle (detailed in Watson 1988). Immature individuals of both sexes are solitary, site tenacious, and maintain a web of their own construction. Breeding begins in late June and continues through August. Males mature earlier than most females and more synchronously. As soon as they mature, males become nomadic and cease web-building. Wandering males pause upon the webs of both mature and immature females to feed, avoid predators, and pursue mating opportunities.

Most males have a more heavily built cephalothorax, longer legs, and larger fangs and chelicerae

than females. They also are much more prone to engage in sustained, intensive fights. Except in extreme cases of weight difference favoring females (seen in less than 0.5% of all intersexual pairings, N > 500), males are dominant in conflicts over web occupancy and access to prey (Watson 1988). Mature males are vigorously kleptoparasitic while on a female's web.

The unequal maturation rates in the male and female populations result in a skew of the operational sex ratio (sensu Emlen 1976) toward males during the first two-thirds of the breeding season. High male mortality, sustained in intrasexual fighting and probably in encounters with arachnid and hymenopteran predators during travels between female webs, gradually shifts the sex ratio to one that is female-biased by the final weeks of the breeding season (Watson 1988). Males do not tolerate the presence of same sex conspecifics on any web that they occupy, and typically guard any female's web at least until the evening subsequent to their arrival (see below). Most movements of males between webs begin at night, but many males still are seeking webs to enter during the daylight hours. The graded and stereotyped components of male-male combat, and the presence of sexually dimorphic traits that make males superior fighters, suggest an important evolutionary history for aggressive male-male competition in the sierra dome (Watson 1988), and other linyphiid spiders (Rovner 1968; Suter and Keiley 1984; Austad 1983).

Methods

Operational definitions – female behavior

I shall refer to the two behavioral states of penultimate female sierra dome spiders analyzed in this paper as "avoidant" and "associative". Avoidant behavior is operationally defined as the female positioning herself, without weather or predatory disturbance, *outside* the central (i.e., upper) half of the dome-portion of the web when a sexually mature male is present. Associative behavior is defined as the female positioning herself *within* the central half of the dome with a visiting male. "Highly associative" females are those recorded as behaving associatively toward a given male in at least 70% of the observations of the pair. In the analyses presented below, estimates of degrees of associative beheavior are based on observations performed during daylight, because females seem never to exhibit *strictly* consistent associative behavior at night (see below). Male-male fights may be so frequent at night that the disturbance causes females otherwise disposed to associative behavior to temporarily move out of the central web area, where fighting takes place.

Data collection – immature females

With the help of two field assistants each year (1983 through 1985), I performed scan observations of the webs of free-living females 1 molt from sexual maturity. Scans were done every day and at predetermined intervals (see below). I began observing individual females 2 to 9 days before their maturation, that is, in the middle to late phase of their penultimate instar. Within this age group, my choices of females to study were based on observability (e.g., their web's position in the vegetation) and web integrity (a predictor of the spider's site fidelity).

These "focal" females were marked for identification in 1984 and 1985 with dabs of enamel paint on the tibia of their posterior legs. Females that failed to resume their web position and other behavior within 3 h of being marked (rare unless paint contacted a leg joint), or whose webs were damaged during capture or replacement, were excluded from the study. I relied on natural marks and continuous web occupancy for identification of immature females in 1983. (The latter procedure was justified during the studies of marked individuals in 1984–85; penultimate females rarely displace one another from webs so quickly that I fail to witness the supplantation during scan observations.) Often it was possible to maintain a constant record of a female's interactions with males through the time of her sexual maturation. The data in this paper represent 1010 days of observation on 175 immature female sierra dome spiders. A daily average of 6.5 (SD = 4.2) scans were performed on each female. Of the 7586 total scans, 46% were performed in 1983, 43% in 1984, and 11% in 1985.

During each scan of an immature focal female's web, her pairing status and position on the web (i.e., her avoidant or associative behavioral state) were determined. Identifying characteristics of any males present were noted (e.g., combinations of missing or deformed legs; all years), or males were captured for color-marking and returned to the web within 20 min (1984–85 only). I also noted male-male interactions, particularly agonistic encounters and supplantations.

For reasons germane to other facets of the study, I performed scan observations on associative females more frequently than on avoidant females. This also helped offset the reduced likelihood of detecting new males on associative female's webs due to their being quickly expelled by a capable guard, already present on the female's web, more frequently than on webs of avoidant females. The average interval between successful scans (i.e., scans in which the female actually was seen) performed on avoidant females were 2.8 h (SD = 1.53), 2.48 (0.49), and 2.05 (0.29) during the 1983, 1984, 1985 field seasons, respectively. After a female was observed to behave associatively for at least 2 consecutive scans, the average time between successful scans was reduced to an average of 2.14 h (SD = 2.42), 2.29 (0.45), and 1.91 (0.82), for the same study years. Scan observations were attempted every day from 0800 through 2000 (bihourly), and occasionally at 2400, 0300, and 0600.

Observation of mature females

Free-living mature females were marked and observed throughout their 3–6 week period of sexual activity. Ready-to-oviposit females were captured and I obtained their offspring for use in electrophoretic paternity analyses (Watson 1988). Scans of their webs were done at the following times every day: 0300, 0600, hourly from 0800 through 2000, and at 2200 and 2400. The 0300 and 0600 scans often were omitted during the later half of the breeding season when intersexual encounters occur less frequently (Watson 1988). A standard protocol was used to record the female's pairing status and, if a male was present, the behavior of both sexes. At the end of the pairing, males were captured for physical measurements and use in paternity analyses. Since the female's final molt and most intersexual pairings last several hours, and all copulations are diurnal and require at least 2 h to complete ($\mu = 3.4$ h, SD = 1.28 h, N = 100), hourly scans capture all the sexual events of a female's life.

Operational definitions – male behavior

An intersexual "pairing" was defined as beginning when a male entered a female's web and ending when the same male departed. The circumstances surrounding male departures from the webs of focal females were categorized as (1) spontaneous, (2) fight-related, or (3) post-copulatory. Departures following female departure, inadvertent web destruction, or predator disturbance were ignored.

"Spontaneous" departures were scored when a male that had been guarding a female was absent at the next scan without replacement by another male (i.e., the immature female was left unguarded for at least 1 scan). "Fight-related" departures were recorded when either of the following 2 conditions were met: (a) 2 males were seen on the female's web during 1 scan, but only 1 remained on the subsequent scan (49% of fight-related departures) or, (b) a new male was detected with a female that had been guarded by a different male during the preceding scan, where the preceding scan was performed no more than 3 h beforehand for the 1984 and 1985 field seasons, and no more than 6 h beforehand for the 1983 field season (51% of fight-related departures). Criterion (b) is justified by the fact that males usually try to remain on *any* female's web at least until the evening following their arrival. Therefore a new male that enters a female's web during daylight, is likely to have fought the male that was present at the time of the previous scan. However, for scans more than 6 h apart, I cannot be confident that the 2 males met. Under these circumstances, in 1983, I did not score a departure as fight-related; the observation was ignored. I could afford to be more conservative in 1984 and 1985, using the 3 h criterion, because during these years interscan intervals were shorter than in 1983.

"Post-copulatory" departures were recorded when males left the female's web after the female matured and copulation was completed. In most cases (80%), the female's final molt and copulation with the male were observed directly. Otherwise, these events were inferred by the presence in the web of all 3 of the following: (a) a freshly molted female exoskeleton (with correct paint marks, when appropriate), (b) a newly molted female (distinguishable from older females by their pale coloration), and (c) a sperm web. (Sperm webs are durable, conspicuous, and always built in the dome portion of the web between the preinsemination and insemination phases of every copulation [*sensu* Austad 1982 and Watson 1988]; they verify that a complete copulation has occurred.)

Classes of males

"First mates" were defined as males that achieved a complete copulation with a previously unmated focal female. "Secondary mates" were males that copulated with nonvirgin females. "Randomly sampled males", which serve as a population baseline, were collected from nonfocal females' webs without knowledge of how long they had been on that web, the reproductive state of the female, or whether the pair had copulated. Random males (N = 103) were collected gradually over the course of the 1982 and 1983 breeding seasons by walking transects at the border of the main study site, examining every web seen, and capturing any male discovered. The number of random males collected on a given day (usually 2–4) was predetermined.

Measurement of males

Male weights and cephalothorax widths were determined on the morning after capture. Captive males spent the night isolated in 15 cm petri dishes with moist filter paper substrates. Weights were taken to the nearest 0.1 mg on a Mettler® H33

analytical balance. Cephalothorax width (i.e., the widest distance between lateral edges of the carapace, viewed dorsally) was measured to the nearest 0.5 mm using a Wild® M5A dissecting microscope, fitted with an eyepiece micrometer, at a magnification of 15X.

Male "body condition" was calculated as the quotient of observed over expected weight, where expected weights were determined by entering the male's cephalothorax width into the following "species typical" prediction equation:

$$\text{expected weight} = e^{(-0.23 + 2.74(LN(\text{ceph. width})))}.$$

The constants in this equation are based upon linear estimation using a sample of 103 randomly collected males that had their size and weight directly determined (see above).

Statistics

Statistical computations were done using the SYSTAT® computing package (Wilkinson 1988; v. 4.0) with the LOGIT supplementary module for multinomial logistical regression analyses (Steinberg 1985; v. 1.1).

Results

Avoidant versus associative behavior

Male sierra dome spiders matured during the first 2 weeks of the breeding season and became nomadic. Wandering males often entered the webs of immature females, eliciting 1 of 2 responses. Some females took up a position on the web far away from the visiting male, typically leaving the interior of the dome and settling in the web's superstructure or at the dome's edge. The rapidity of this "avoidant" reaction varied. At one extreme, I often saw it occur immediately, with the female walking out of one side of the dome just as the male entered the opposite side. At the other extreme, some females took over an hour to move into a position away from the male. There was never an indication that male agonism elicited female avoidant behavior.

On the whole avoidant females remained quietly in their peripheral location, did not attempt to capture prey, performed no web maintenance, and seemed to avoid attracting the male's attention. Males remained within the dome, foraging freely, and made no attempts to confine avoidant females to the central portion of the web or to force their return there from peripheral locations. Although some avoidant females permanently abandoned their webs within several hours of male entry (11.9% of such encounters; N = 154), most returned to the web's dome and resumed foraging and web maintenance after the male's departure.

The alternative female response toward a visiting male entailed maintenance of a position close to the male within the central portion of the dome. Such "associative" females were highly tolerant

of physical examination and brief copulation attempts by the male (intromission is impossible). At rest, the legs of the male and the female often were interdigitated or touching. Associative females reestablished their position near the guarding male whenever he moved away (e.g. during prey capture or agonistic interactions with other males). Besides maintaining proximity to the male, associative females were inactive. They neglected web maintenance and often ignored potential prey.

Males accepted the proximity of associative females without signs of agitation, and often contributed to it by their choices of resting positions on the web. However, the spatial proximity of the sexes was not simply the result of males approaching immobile females; associative females moved swiftly in response to threatening disturbances. Moreover, females that were consistently associative during daylight often exhibited predominantly (i.e., $\geq 50\%$) avoidant behavior during hours of darkness. In 368 nocturnal observations (performed between 2200 and 0600) of guarded females that were associative during the day, avoidant behavior was noted in 101 scans (27.4%). Females that were avoidant in the daytime remained avoidant at night (95.7% of 163 scans). Thus throughout the female's penultimate instar, it clearly was she that modulated the proportion of time spent close to any visiting male.

Behavior of mature females

Mature females varied in their behavior toward males. While their behavior sometimes mimicked that of an associative or avoidant penultimate female, it usually was characterized by foraging activity and agonism of intensities far exceeding those seen in penultimate females. For example, in observations of 624 pairings involving mature nonvirgin females, 44% of all prey were captured by females ($N = 198$ prey). Penultimate females seldom even *attempt* to capture prey while being guarded. Mature females frequently exhibited behaviors (e.g., web shaking and strumming; see Watson 1988), often in response to male prey capture or courtship, that *never* were performed by penultimates. The morphological differences between mature and penultimate females probably assure that even the most associative and passive mature females are readily distinguishable from immature individuals. Mature females that behaved associatively usually allowed copulation soon after male arrival at the web (Watson unpublished), a final testament to their mature status.

After sexual maturation females nearly always

Table 1. Influence of the number of complete matings in which a female sierra dome spider previously has engaged upon the likelihood of her accepting or rejecting her current suitor. Data represent the outcome of 801 intersexual encounters involving 183 different females. Every encounter involved a different male. Numbers in parentheses are percentages of the row total accounted for by that cell of the table

Female's number of previous mates	Female's mating decision		Total
	Reject current suitor	Mate w/current suitor	
0	4 (2.45%)	179 (97.55)	183
1	166 (54.43)	139 (45.57)	305
2	126 (70.79)	52 (29.21)	178
3	82 (83.67)	16 (16.33)	98
4	26 (83.87)	5 (16.13)	31
5	5 (83.33)	1 (16.67)	6
Total	409	392	801

accepted a complete copulation with the first male they encountered (97.5%, $N = 183$ females). Afterwards, females exhibited a reduced propensity to mate throughout the 3 to 6 week period before laying their first clutch of eggs (Table 1). During this interval, a female usually was visited by 7 to 14 additional males. From among these secondary suitors females mated with a nonrandom subset of 1 to 4 males. For 104 free-living females on whom I was able to compile exhaustive sexual histories, the average total number of matings before the first oviposition was 2.3 (SD = 0.98). The mating propensity of already-mated females was principally related to their recent foraging success and number of previous matings (both negative relationships). The likelihood of remating was modulated only weakly by a suitor's phenotype, but larger males were significantly favored (Watson 1988; Table 4.3). As determined by electrophoretic paternity analyses, first mates sired an average of 80% more offspring than secondary mates (N = 44 first mates and 69 secondary mates of 44 females; see Watson 1988).

Timing of associative behavior

The switch from a voidant to highly associative behavior occurred at a point in time close to the female's sexual maturation (Fig. 1). The mean time
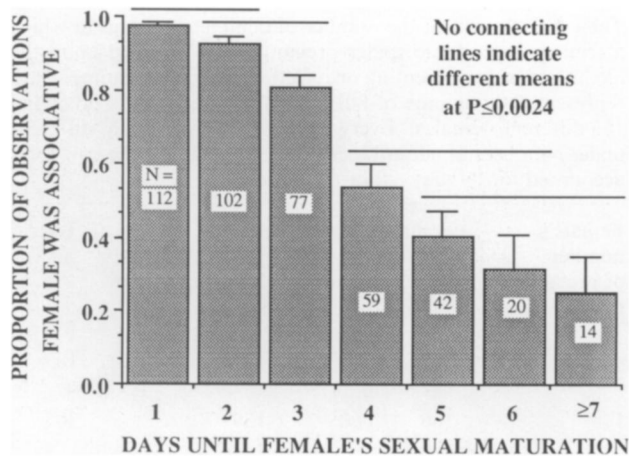
Fig. 1. The mean proportion of daily observations in which guarded, immature females were scored as associative, versus the number of days these females were from sexual maturation. The sample consists of 416 sets of daily scan observations; each set consists of an average of 6.4 observations per female (total scans = 2665). The number of sets of daily observations for each female age class are given within each bar. A total of 322 pairings (some lasting more than 1 day) of 175 females are represented. Error bars represent 1 SE. Horizontal lines above the bars extend across age classes that do *not* differ in the mean proportion of observations associative at $P = 0.0024$; this pairwise level of significance provides an overall level of protection of 0.05. The multiple comparisons were done by a least squares procedure (Wilkinson 1988)

before maturation at which highly associative behavior began was 65.2 h (SD = 37.7, range = 193, $N = 63$ females). Only about 20% of pairings involving females more than 5 days from maturation were marked by highly associative behavior ($N = 34$). I found no evidence of highly associative females more than 8.5 days from maturation. Especially in the early part of the breeding season, any given avoidant female may be up to 4 weeks from maturation.

Each bar in Fig. 1 represents the mean of a strongly skewed or bimodal distribution of behavior among females within a given age category. For instance, among the 59 females 4 days from maturing, 29 were associative in 67–100% of observations and 27 were associative in 0–33% of observations, while only 3 females were associative in 34–66% of observations. Figure 1 may foster the illusion that transformations from avoidant to associative behavior were gradual when, in fact, most females switched in less than 1 day. Most transformations were so quick that within any single male's tenure on a penultimate female's web, she exhibited either strongly avoidant or highly associative behavior (Fig. 2). Males seldom met female's showing ambiguous, transitional behavior.

Females were consistently avoidant until their
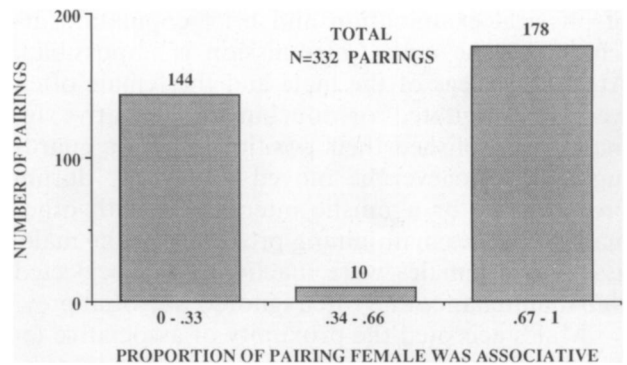
Fig. 2. Frequencies of pairings between penultimate females and mature males in which the female was recorded as associative in 0–33%, 34–66%, and 67–100% of the scan observations on the pair. All the age classes of Fig. 1 are combined in this histogram. Each pairing involved a different male. Note that in the majority of pairings females were either largely avoidant or associative

first day of highly associative behavior, and consistently associative thereafter, even when new males arrived at the web and supplanted earlier guards. In other words, individual females switched from avoidant to highly associative behavior only once. Highly associative behavior was exhibited in 67 of 84 pairings (79.8%) recorded after the first day in which the female spent at least 50% of the time behaving associatively toward a guarding male; In 6 of the pairings (7.1%) females showed reduced, but still predominantly associative behavior compared with the level exhibited on their first day of predominantly associative behavior. Females reverted (always for ≤ 24 h) to avoidant behavior in only 11 of these pairings (13.1%).

Overall, the onset of associative behavior occurred suddenly, usually within 5 days of sexual maturation, and once in place the behavior was shown consistently within and between intersexual pairings. Thus for any male that guarded a female for at least several hours, consistent associative behavior provided a clear signal that the female was approaching sexual maturation.

Male responses: short versus long-term guarding

Males usually attempted to remain on any web they occupied on a given day at least until nightfall, regardless of sexual circumstances. However, males seldom continued guarding past this time unless the resident female was highly associative (Table 2).

In most cases where males stayed with a female for more than 24 h, the female was scored as behaving associatively in at least 70% of the observa-

Table 2. Frequencies of males that guarded females for 1 day or more than 1 day versus the proportion of scan observations in which the females were associative. Each pairing involved a different male. Expectations based on a log-linear model are given in parentheses. Pearson's Chi-square = 66.11, $P < 0.001$; a constant of 0.35 was added to every cell to avoid expected frequencies less than 0.5
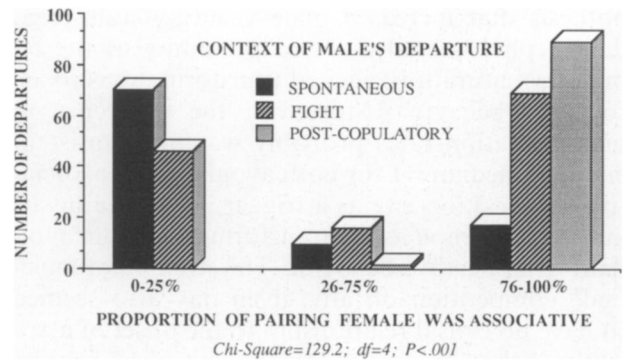
Time male spent guarding female	Estimated proportion of male's visit during which female was associative				Total
	0–25%	26–50%	51–75%	76–100%	
One day	132 (102.3)	15 (13.5)	14 (13.5)	88 (120.6)	249
Two or more days	7 (37.2)	3 (4.9)	4 (4.9)	76 (43.9)	90
Total	139	18	18	164	339

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 9 ┼ 9
10 ┼ 2346                Minimum = 9.98 (i.e. 9:59 am)
11 ┼ 126677              Lower Quartile = 16.87 (4:52 pm)
12 ┼ 3777788             Median = 20.03 (8:02 pm)
13 ┼ 0001135             Upper Quartile = 22.00 (10:00 pm)
14 ┼ 223445              Maximum = 24.30 (12:18 am)
15 ┼ 58
16 Q 457788899
17 ┼ 01113588999
18 ┼ 01114599
19 ┼ 00111122356699
20 M 0011222233444566677778888888889999
21 ┼ 0044689
22 Q 00122224566667789
23 ┼ 00112222234455677788
24 ┼ 3
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Fig. 3. Departure times of 153 sierra dome spider males from the webs of mature, nonvirgin females. Data are given for males that were in attendance at a mature female's web after 0600. All departures occurred within 18 h of the male's arrival. The histogram times are given in decimal hours of the day (e.g., a value of 14.5 denotes that the time was 2:30 pm). These data were collected during hourly web scans in 1981, when male's departed from webs completely of their own accord (i.e., we did not attempt to capture them when we thought they were preparing for departure). The symbols "M" and "Q" show the lines of the histogram that contain the median and quartiles, respectively

Fig. 4. Context specific frequencies of male departures from the webs of avoidant and associative females. There was a significant association between male departure context and the proportion of scan observations in which the female was showing associative behvior. Males seldom departed spontaneously from a web that harbored a highly associative female (Pearson Chi-square = 129.2; $N = 319$ pairings; $P < 0.001$)

tions on the pair. In contrast, most males that departed within 24 h of their arrival were seen in close association with the female in fewer than 30% of the scans done on the pair. Multi-day guarding was restricted to highly associative penultimate females, because males also never guarded mature females for more than a single day (Fig. 3).

Many males left the webs of highly associative females within 1 day of arrival (88/164; 53.7%; Table 2), but it is essential to note the *contexts* of male departures from webs of avoidant versus associative females. Male departures were placed into 1 of 3 categories: (1) spontaneous (i.e., un-

prompted), (2) fight-related, or (3) post-copulatory. The majority of males that departed from webs of highly associative females did do after losing a fight with a rival male (39.4%), or after the female matured and the pair copulated (50.9%) (Fig. 4). Few males spontaneously abandoned highly associative females (9.7%).

In pairings where the female was avoidant, spontaneous departures by males were far more common (55.6%). Many males departed from webs of avoidant females after the loss of a fight (43.1%), but most of these supplantations occurred on the *same day* as the supplanted male's arrival on the web (83.0% of fight-related departures). Few males that departed from the webs of avoidant females did so after copulating (1.3%), because females were almost always seen to be highly associative before maturing (97.9% of females that were guarded on the scan preceding commencement of their final molt; $N = 94$).

Female associative behavior causes the prolonged male guarding, not *vice versa*. Only 3 of 53 females (5.7%) that I monitored for ≥48 h prior to their transformation to associative behavior had experienced multi-day guarding by a single male during their avoidant phase. On the other hand, of 90 males that performed prolonged guarding, 76 (84.4%) did so in the presence of highly associative females (Table 2). Could other aspects of male behavior trigger associative behavior? Estimates of daily male visitation rates were higher on webs harboring avoidant versus associative females (Mann-Whitney U = 30967.5, $N = 523$ male visits detected over 614 female/days of observation, $P < 0.001$). The direction of this difference is opposite to that predicted under a hy-

pothesis that increased male visitation rate (e.g., due to pheromonally sensed proximity of the female to maturation) elicited transformations to associative behavior. Moreover, the difference in male visitation rates probably was not consistent enough (median = 1 for both avoidant and associative females) to serve as a trigger for such a invariant phenomenon as the transformation from avoidant to associative behavior. The strength of male-male competition on any given day also seemed to have no causal relationship to the onset of associative behavior. In the same group of 53 females mentioned above, 26 (49.1%) had at least 1 male-male fight occur on their web during the 48 h period before transformation. The other 27 females transformed without any fights occurring. These observed frequencies are indistinguishable from those expected given the probability of having two or more males arrive at the web of an avoidant female on a single day, summed over a two day period ($X^2 = 1.21$, $df = 1$, $P = 0.27$). (Single day probability = 0.208; N = 275 males detected during 249 female/days of observation at $\mu = 6.7$ scans/female/day (SD = 3.7)).

Is associative behavior the cue?

Associative behavior is easily noted by humans and is a strong predictor of long-term guarding attempts by males. However, males might have been adjusting their guarding times in response to a less obvious indicator of female age that merely was correlated with the degree of her associative behavior.

If prolonged guarding was stimulated by an age-related cue from the female that I failed to detect, then for a given intersexual pairing, the actual time until a female's sexual maturation (a quantity I can know retrospectively for any given pairing) should be at least as strong a predictor

of the (1) duration of male visits and, (2) likelihood of spontaneous male departures, as the female's degree of associative behavior. This prediction assumes that males respond most strongly to the best available indicator of female age.

Linear regression analysis indicated that the proportion of observations on a given pair in which the female was associative was a better predictor of the duration of male guarding than the actual time to female sexual maturation or a model containing both predictors (Table 3). I used logistic regression to determine the relative strengths of the same 2 factors as predictors of a dichotomous dependent variable coding male departure context (i.e. either (a) spontaneous or (b) after losing a fight or copulating). The number of hours until maturation was a statistically significant, but relatively weak predictor of spontaneous male departures compared with the degree of associative behavior shown by the female (Table 4).

Thus if males detect an unobserved cue linked to the female's proximity to maturation (e.g., web condition or a pheromone), it does not influence guarding time as heavily as the female's level of associative behavior. While undetected signals that are very highly correlated with associative behavior still may be present, it is not necessary to invoke them to explain prolonged male guarding.

Enhanced intrasexual selection: the mechanism

There is no evidence that associative behavior influences male visitation rates or fighting intensities. The female's advertisement that her reproductive value is about to reach its apogee leads to an enhancement of the fight-winning capacities of first mates via a twofold mechanism linked only to the *prolonged* guarding that it elicits. First, associative behavior increases the proportion of new male visits where the incoming male is *met* by an earlier

Table 3. The influence of the degree of associative behavior (POA) and the time until a female's sexual maturation (HTM) on the duration of male visits (D). The results of estimating 3 linear regression models are given. Based on the regression coefficients (βi) and degrees-of-freedom adjusted coefficients of determination ($R^2 a$), the consistency of associative behavior within an intersexual pairing is a stronger predictor of male guarding time than the number of hours until the female's maturation, although both predictors have coefficients different from zero. Significance levels (P) are based on t-tests

Model	Factor	βi	SE	P	$R^2 a$	N
$D = \beta 0 + \beta 1$ (HTM)	HTM	−0.06	0.03	0.025	0.061	251
$D = \beta 0 + \beta 1$ (POA)	POA	24.29	3.06	<0.001	0.171	302
$D = \beta 0 + \beta 1$ (HTM)	HTM	0.05	0.03	<0.001	0.144	248
$\quad + \beta 2$ (POA)	POA	28.59	4.63	<0.001		

Key: D = Duration of male's visit; POA = Proportion of observations female was associative; HTM = Hours until female maturation at midpoint of pairing

Table 4. The influence of the degree of associative behvior (POA) and the number of hours until a female's sexual maturation (HTM) on the probability of spontaneous male departure. The table gives the results of estimating 3 logit models predicting the odds of a male departing either spontaneously or in 1 of 2 other contexts: (1) after losing a fight, or (2) after female maturation and completion of copulation. Two univariate and 1 bivariate logit models were estimated. Based on the magnitudes of regression coefficients (βi) and independent variable derivatives (D), the degree of female associative behavior is a much stronger predictor of spontaneous male departure than the time until maturation, although both predictors have coefficients significantly different from zero. Significance levels (P) are based on likelihood ratio tests

Model	Factor	βi	SE	P	D	N
$S = \beta 0 + \beta 1$ (HTM)	HTM	0.025	0.004	<0.001	0.0054	251
$S = \beta 0 + \beta 1$ (POA)	POA	−3.177	0.340	<0.001	−0.7043	302
$S = \beta 0 + \beta 1$ (HTM)	HTM	0.013	0.004	<0.001	0.0025	248
$+ \beta 2$ (POA)	POA	−2.593	0.429	<0.001	−0.5004	

Key: S = Odds of spontaneous departure by male; POA = Proportion of observations female was associative; HTM = Hours until female maturation at midpoint of pairing

arriving male and therefore *required* to fight, because once found by any male a highly associative female is rarely abandoned spontaneously. Considering 190 records of males arriving at webs of avoidant females, 112 (58.9%) found the resident female unguarded, while of 163 males entered webs of associative females only 43 (26.4%) found the female alone on her web (Pearson $X^2 = 37.8$, $df = 1$, $N = 353$, $P < 0.001$).

Perhaps the key mechanism whereby associative behavior enhances intrasexual competition is by ensuring a *continuous* increase in the fighting ability of guarding males throughout the final days of the female's penultimate instar. Prolonged male guarding conduces to this, because supplantations are seldom punctuated by unforced male departures. Thus the fighting ability of the male present on the web of a newly mature female will be at a level determined by the outcome of all the contests on that web since the female started showing associative behavior. The newly mature female will be left to mate with the best fighter to arrive during her entire associative phase. In contrast, no matter how many fights occur on the web of an avoidant (or a mature nonvirgin) female on a given day, the fighting ability of guarding males varies haphazardly *between* days, because these females are abandoned each evening.
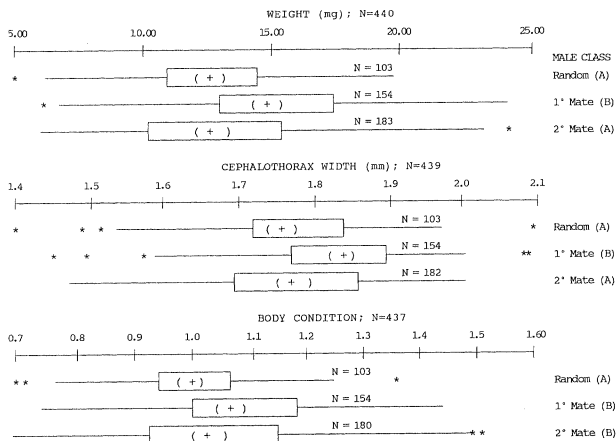
Levels of male-male competition

During daylight, it seemed that males rarely bypassed *any* female's web without attempting to take up a position within the central portion of the dome ($N > 150$ focal observations of newly arriving males and $N > 250$ introductions of males to web edges). At night, when there is a reduction in the activity of predators that webs are effective in deterring (e.g., wasps and foliage-gleaning birds), and foraging opportunities are diminished (Watson 1988), it may be more common for roving males to bypass webs indifferently. Whenever a female was already guarded (as associative females usually were), entry of a new male quickly led to a fight, usually without prior direct contact with the resident female (see Watson (1988) for descriptions).

In my observations of highly associative females, 248 visiting males were detected during 365 female/days of data collection ($\mu = 9.7$ scans per female per day, SD = 4.1). The mean male visitation rate was 0.68 per day (SD = 0.83). Thus during a typical 3 day period of highly associative behavior (Fig. 1), an average of 2.04 (3(0.68)) fights are expected by the time the female molts and is ready to mate. Since I did not witness all fights leading to male-male supplantations and males were not always marked, I undoubtedly (1) mistook some new males for their predecessors, and (2) missed some fights where the new male was quickly chased off. Therefore the above figure is a *minimum* estimate of the number of contests expected per 72 h on the web of an associative female. This number is expected to be greater early in the season and to fall as the male population density declines. Based on data from sets of 10 randomly selected *mature* females monitored continuously for 3 day periods, average male visitation rates ranged from 0.77 per day in mid-July to 0.17 per day by mid-August (season-long $\mu = 1$ male every 3 days, SD = 1.0).

Mature females were never guarded by a single male for more than 18 h (Fig. 3). Males usually departed from webs of mature females around dusk, regardless of their arrival time or whether mating occurred. Since serial fight opportunities accrued over a maximum period of only 18 h on webs of mature females, the average proportion

WEIGHT (mg); N=440

```
5.00        10.00        15.00        20.00        25.00
                                                              MALE CLASS
                                   N = 103
  *    ------------( + )--------                              Random (A)
                                   N = 154
    *   -------------( + )-----                               1° Mate (B)
                                   N = 183
        -----------( + )-----------------  *                 2° Mate (A)
```

CEPHALOTHORAX WIDTH (mm); N=439

```
1.4    1.5    1.6    1.7    1.8    1.9    2.0    2.1
                              N = 103
  *     *  *  ------( + )----       *          Random (A)
                              N = 154
  *    *      *  --------( + )-----       **   1° Mate (B)
                              N = 182
             -----( + )-------                 2° Mate (A)
```

BODY CONDITION; N=437

```
0.7   0.8   0.9   1.0   1.1   1.2   1.3   1.4   1.5   1.60
                              N = 103
 **   --------( + )--------         *          Random (A)
                              N = 154
      ------( + )---------                      1° Mate (B)
                              N = 180
      -----( + )--------------  * *             2° Mate (B)
```

Fig. 5. Comparisons of 3 physical attributes amongst 3 classes of male sierra dome spiders. The classes represented in each set of plots are (top to bottom) randomly collected males, first mates, and secondary mates. The 3 sets of plots compare body weight (mg), cephalothorax width (mm), and body condition (a measure of weight that controls for body size). The plots give the following information: the *median* of each distribution is marked with a plus (+) sign; 95% confidence intervals around each median are delimited by parentheses; the upper and lower quartiles are at the left and right edges of each box, respectively, and the end of the whiskers denote the adjacent values; extreme values are marked with an asterisk; sample size (N) for each plot is given above the right whisker. Distributions with differing *means* have different capital letters beside the male class name (far right of each plot). The overall error rate for each set of multiple comparisons was kept at 0.05 by using a pairwise error rate of 0.05/3 = 0.017

of secondary mates that fought off one rival was somewhat less than 0.59 (0.77^2), even in mid-July when males were plentiful.

Resultant qualities of first mates

The series of contests that occurred on webs of associative females had a significant impact upon the physical stature of first mates (Fig. 5). First mates were significantly greater in weight and cephalothorax width than (1) secondary mates and (2) males collected randomly from webs of nonfocal females (all $P \leq 0.001$). First mates also had higher body condition than randomly collected males ($P = 0.003$), but not secondary mates ($P = 0.405$).

Body size is known to be associated with fighting ability in a variety of invertebrates, including spiders (Austad 1983; Wells 1988). In the sierra dome spider, the probability of winning a fight also is influenced by size-related attributes of the contestants. Thirteen staged fights on female webs involving 26 randomly chosen sierra dome males, resulted in the heavier male winning 11 (85%) of the contests (the lighter male always was intro-

duced onto the web 10 min before his rival). The average percent difference in weight for these encounters was high, 38.3% (SD = 23.8). In 39 natural fights on the webs of focal females on my study site, the heavier contestants won 30 encounters (76.9%). The average difference in the weights of these contestants was 23.8% (SD = 26.4), but in the 9 unstaged fights won by the lighter contestant, the weight difference was smaller: 11.4% (SD = 7.1) (unequal variance $t = 2.79$, $P = 0.009$, $N = 39$). Based on these data, it seems that the magnitude of weight difference needed to reliably predict which contestant wins a fight is between 10% and 25%. My subjective impression, based on observation of many fights where the relative weights of the males were estimated by eye, is that the minimum weight difference likely to determine the outcome of a fight is near 15%. Percent weight differences calculated for first mates versus secondary mates and randomly collected males (Fig. 5) were 11.9% and 20.1%, respectively. I conclude that the statistical size differences between first mates, secondary mates, and randomly collected males are of sufficient magnitude that one should expect first mates, on average, to exceed secondary mates and random males in fighting-ability.

First mates were not always the largest male a female encountered before laying her first clutch of eggs. Considering all the secondary suitors of 128 free-living, ad-libitum mating females, 32.1% exceeded the female's first mate in weight ($N = 374$ suitors), 28.8% exceeded the first mate in cephalothorax width ($N = 371$), and 23.7% were greater than the first mate in both measures ($N = 371$). The percentage of females that encountered a secondary suitor at least 15% heavier than their first mate was 32.0%.

Modulation of the onset time of associative behavior

Factors that modulate how far in advance of sexual maturation a female becomes highly associative are unclear. Maturation date seemed a logical candidate, because the operational sex ratio and male visitation rates fall as the breeding season progresses. Consequently, the average time required for a given number of males to meet and fight on the female's web increases. I tested the possibility that late-maturing females make up for the reduced efficiency of male-male competition by commencing associative behavior at an earlier age; this idea was not supported. Linear regression analysis indicated that the week of the breeding season in which a female matured was unrelated to the number of days before maturation that she became

Table 5. The influence of male body weight (MWHT) and the number of hours until a female's sexual maturation (HTM) on the probability of a female switching to highly associative behavior during a male's visit. The table gives the results of estimating 2 univariate and 1 bivariate logit models. There was no evidence that male body weight modulated the odds of a female commencing associative behavior, whether or not the time until female maturation at the beginning of the male's visit was controlled. Time until female maturation was a strong predictor. Significance levels (*P*) are based on likelihood ratio tests. The sample consists of 79 pairings involving females that had shown predominantly avoidant behavior toward all earlier males. In 39 of the pairings included in this analysis the female remained avoidant, and in the remaining 40 the female transformed to associative behavior

Model	Factor	βi	SE	P	D	N
$T = \beta 0 + \beta 1$ (MWHT)	MWHT	0.05	0.06	0.390	0.012	79
$T = \beta 0 + \beta 1$ (HTM)	HTM	−0.07	0.02	<0.001	−0.016	79
$T = \beta 0 + \beta 1$ (HTM)	HTM	−0.07	0.02	<0.001	−0.016	79
$+ \beta 2$ (MWHT)	MWHT	0.03	0.07	0.907	0.008	

Key: T = Odds female transforms to highly associative behavior; MWHT = Male body weight; HTM = Hours until female maturation at beginning of pairing

highly associative ($r = 0.10$, $P = 0.427$, $N = 67$ females).

I also investigated whether penultimate females initiate associative behavior further in advance of their maturation if they receive an early visit by a male of exceptional stature. Females might benefit by preventing such a male's departure, since he probably would not be replaced by an equivalent individual during a later and shorter period of prolonged guarding. This hypothesis also was not supported. Logistical regression analysis indicated that the likelihood of a female switching to associative behavior during a given male's visit was independent of male weight (Table 5). The result was the same if the time until female maturation (clocked from the beginning of the male's visit) was incorporated as a covariate in the regression model. As expected, the number of hours until female maturation was negatively related to the odds of switching from avoidant to associative behavior during a given intersexual pairing.

Discussion

Information content of associative behavior

Precopulatory guarding is an often mentioned male behavior in spiders and probably is based on behavioral or pheromonal cues that advertise the female's reproductive value (Austad 1984). The data presented above indicate that associative behavior of female sierra dome spiders is an example of such an advertisement. Highly associative behavior constitutes an unambiguous signal indicating that a female is late in her penultimate instar (Figs. 1, 2). A male's certainty of being accepted as a mate by a newly mature female (Table 1), coupled with the fact that first mates typically sire more offspring than secondary mates (Watson 1988) means that, indeed, associative behavior amounts to an announcement of high reproductive value.

Male sierra dome spiders respond to the about-to-mature female's advertisement by attempting to guard her until she matures. Since associative behavior typically begins 2–5 days before the female matures, this guarding effort must span several days or, if the male arrives late in the female's associative phase, he usually will have to supplant a rival that has won other fights on that web. Most male departures from the webs of highly associative females are attributable to forceful supplantation by a rival male or follow female maturation and completion of copulation (Fig. 4). Unforced male departures from the webs of avoidant females occur more often (Fig. 4), and after shorter guarding times (Table 2), than from the webs of highly associative females. Males also register the status and diminished reproductive value of mature females; in this context they again limit their guarding to less than a single day (Fig. 3).

Associative behavior increases the effectiveness of male-male competition as a mate-sorting mechanism by (1) increasing the proportion of visiting males that find the female guarded and so must fight to become a prospective first mate, and (2) assuring that any male successful in claiming the web remains either until he is forced out by a rival or the female matures and he copulates with her. Males must fight more often to enter a highly associative female's web, and the most capable fighter to arrive during the female's entire associative phase is retained for mating. On webs of immature avoidant and mature mated females, the sample of males from which intrasexual selection may draw a first mate is reset to zero each time a spontaneous male departure occurs.

Primary and secondary sires determined differently

Perhaps because male kleptoparasitism renders continued dependence on male-male competition too costly, females discontinue elicitation of prolonged guarding after their first mating. Nevertheless, secondary mates sometimes are required to repel other males in order to complete precopulatory courtship and copulation. Given the season-long average male visitation rate for mature females of 0.33 per day, it follows that in about 11% $((0.33^2)100)$ of all day-long pairings the attending male will be required to fight off 1 rival. This probably accounts for the larger size of secondary mates versus randomly collected males (Fig. 5); randomly collected males include individuals that had been present on the web from which they were captured for just a few hours, whereas most secondary mates successfully defended a female all day before capture (Watson 1988).

However, for secondary mates, tests of fighting ability cannot be as stringent as for most males that attain first mate status. Just as when they meet an avoidant penultimate female, males abandon any mated female less than a day after their arrival on the female's webs. Since guarding bouts by individual males are short, males that acheive a mating with a nonvirgin female usually enter her web unchallenged, and rarely are required to battle a rival that already has won fights with other males on that web. Furthermore, secondary mates do not guard long enough to ensure that a challenge from a later arriving male occurs during their tenure on the web. Thus, although male-male competition influences the outcome of some secondary pairings, variation in the fertilization success of secondary mates must depend mainly upon direct sensory discriminations by females or sperm competition (Watson 1988). A substantial percentage of females eventually mate with a secondary suitor that probably would have stood a good chance of winning a fight with the female' first mate, or that, by virtue of his size, may have an advantage over her first mate in sperm competition. However, if direct male-male combat provides a more reliable test of male quality than other mechanisms of sexual selection, first male sperm priority might be explicable as a female adaptation to bias fertilizations toward males that pass this more rigorous test.

It is worth noting that the evolution and maintenance of female behaviors specifically designed to enhance any process of intrasexual selection cannot be based on female preferences for mates exhibiting arbitrary traits. Neither the female's behavior nor the male traits germane to the selection process could have evolved solely via a process of Fisherian runaway selection (Fiher 1958; O'Donald 1980; Lande 1981; Kirkpatrick 1987), because the functional significance of the favored traits are judged in the context of deadly male-male conflict, not according to arbitrary, "aesthetic" conventions of females. In species such as the sierra dome spider, where males contribute only genes to offspring, female behaviors designed to promote the efficiency of intrasexual selection probably are best explained by "good genes" models of sexual selection.

"Honesty" of the female's signal

Selection has settled upon a loose connection between a female's proximity to maturation and the onset of associative behavior. A male has considerable assurance that any highly associative female is within 5 days of maturation, but associative behavior does not answer the question, "How close is close?". This imprecision may be an important aspect of the functional design of associative behavior, that is, specific forces may counter the selection of fully "honest" female behavior.

Any tightening of the correlation between female age and behavior would promote further tuning of male guarding time strategies. It might seem, on the one hand, that males would be less likely to abandon an associative female if they could determine, for example, that she was only 2 days from maturation as opposed to 4 or 5. Any reduction in the probability of spontaneous male departures during the female's associative phase would be beneficial to her, because the efficacy of intrasexual selection hinges upon *every* male maintaining his guarding effort until he is forceably displaced. On the other hand, males might be less likely to engage in prolonged guarding of a female that they could tell was more than 2 days from maturation (e.g., during parts of the breeding season when females closer to maturation are easy to locate). This refinement in male behavior would degrade the efficacy of intrasexual selection. Overall, it seems that younger females would benefit by indicating that they are closer to maturation than they actually are, while older females should be selected to indicate their age accurately. Thus the female's advertisement should be designed, within limits, to indicate close proximity to maturation regardless of her true age. Females probably are selected to commence associative behavior as far in advance of maturation as they can afford to begin incurring the nutritional costs of constant

male guarding (see below). The sudden, nongraded transformation from avoidant to associative behavior helps obfuscate the precise time that must pass before a female matures, forcing males to invest more time guarding her than they might if it were possible to assess her age more exactly.

Material benefits of associative behavior

Associative behavior enhances male-male competition in a way that minimizes the foraging cost connected with this mode of sexual selection. The fecundity of sierra dome spider and other linyphiids is food-limited (Watson unpublished; Wise 1975). The timing of associative behavior results in concentration of prolonged male guarding, and the uninterrupted food-stealing that goes along, into a period of the female's development that is nutritionally least costly for her, namely, her pre-molt fast (Miyashita 1968; Humpherys 1977; Gertsch 1979). Thus a portion of the prey taken by males guarding her during this period would have been ignored by the female anyway. The impact of being continuously guarded during their penultimate instar may be further reduced since females do not begin the heavy yolking of eggs until after maturation (Foelix 1980, Watson unpublished).

Austad (1984) hypothesized that a benefit of first male sperm priority for female spiders might be a reduction in the expected payoff to males for investing time in guarding nonvirgin females; this could limit the duration of male visits and thereby reduce foraging interference. This benefit probably is important for mature female sierra dome spiders. First mates always depart within several hours of completing copulation, and secondary suitors spend no more than a single day guarding nonvirgins, affording egg-yolking females periodic relaxation of male food-stealing. Austad also predicted that in systems where first male sperm precedence functions to reduce foraging interference, females should advertise their reproductive state; this also has been borne out in sierra dome spiders. As I have illustrated above, advertisements of reproductive value also may result in females acquiring superior sires for their offspring, and the timing of the advertisements may ease material costs of intrasexual selection.

A simpler explanation for associative behavior?

Should associative behavior be interpreted more parsimoniously as a means of ensuring mating? By signalling that she is close to maturation the female might ensure that a visiting male remains with her until she matures, a voiding the loss of what could be her sole mating opportunity.

Several observations make this explanation unlikely. Sierra dome spiders generally occur in dense populations. Females should have little trouble being discovered by mature males. On my study site 74.2% of all females, including those that mature late in the season when male population densities are low, already are guarded by a male at the time they mature ($N = 128$). Moreover, females sustain a 1–2 month period of sexual receptivity between the time of their maturation and first oviposition, but I have never detected a free-living female to go unmated for more than 2 days after maturing. The fact that female maturation is not compressed toward the beginning of the breeding season, when male densities are highest, also suggests that females can afford to spend much of the breeding season as subadults without risking infertility. Of course, female sierra dome spiders must occasionally occur in populations sparse enough to render infertility a risk. Indeed, females possess a specific adaptation that probably functions to ensure mating in such circumstances; they produce an airborne male attractant pheromone if they remain unmated 7 to 10 days after maturation (this condition was experimentally induced; Watson 1986). However, the fact that the pheromone is deployed *only* after a week of virginity suggests again that going unmated is not a chronic problem for females, and probably an inappropriate explanation for such an invariant phenomenon as associative behavior.

Onset time of associative behavior

There is considerable variation in how far in advance of maturation females begin highly associative behavior. Female maturation date failed to explain a significant proportion of this variation. Thus females that mature later in the season do not compensate for the inevitably lower male visitation rates by beginning highly associative behavior earlier. Size-related attributes of guarding males also have no effect on the likelihood of a female switching to highly associative behavior during a given pairing. One other factor that might influence how early a female becomes associative is her foraging history.

Female foraging success is the factor that most strongly modulates the sexual receptivity of nonvirgin females (Watson 1988), and it also may influence the duration of associative behavior. For example, a female that had high foraging success

early in her penultimate instar might be able to afford commencement of constant male guarding and kleptoparasitism further in advance of her pre-molt fast, or her fasting period itself might be longer. The duration of pre-molt fasting is known to be positively associated with body weight in some spiders (Humphreys 1977). Beginning elicitation of prolonged male guarding as early as possible would benefit females by enlarging the expected number of males that participate in the fights leading to determination of the first mate, making it more likely that an exceptionally fit male will be among their numbers.

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