

FORAGING ADVANTAGE OF POLYANDRY FOR FEMALE SIERRA DOME SPIDERS (*LINYPHIA LITIGIOSA*: LINYPHIIDAE) AND ASSESSMENT OF ALTERNATIVE DIRECT BENEFIT HYPOTHESES

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Abstract.—This article evaluates four potential phenotypic benefits of remating for female sierra dome spiders. The finding that foraging success of paired females improves in copula is discussed in light of evidence that multiple paternity also confers genetic benefits. Nonvirgin females face frequent daylong visits to their webs by dominant, kleptoparasitic males. Females reduce prey losses by engaging some males in 2–6 h of aspermic copulatory courtship. During this “preinsemination phase” of copulation, females increase the percentage of prey they consume from 25.1% to 49.0%. Female sexual receptivity depends more on recent foraging success than on phenotypic attributes of males, whereas sperm-use patterns are related to physical and behavioral qualities of mates. The preinsemination phase of copulation is well designed both to improve the foraging success of females and test male quality: (1) it is strenuous and exacting for the male but inactive for the female, (2) genitalia are continuously joined and detached, keeping the male occupied but maintaining freedom for the female to pursue prey, and (3) it is lengthy, which reduces male prey stealing for a substantial portion of his visit. Despite the foraging benefits of remating, females reject 66% of their suitors, probably because remating entails costs and provides diminishing genetic benefits.

As paternity estimates come into wider use in studies of reproductive behavior, the known taxonomic range of multimale mating by females is expanding. Benefits and costs of polyandry are being scrutinized in birds (Birkhead et al. 1987; Westneat et al. 1990), mammals (Dewsbury and Baumgardner 1981; Hanken and Sherman 1981; Schwagmeyer 1984; Xia and Millar 1991), social insects (Page and Metcalf 1982; Starr 1984; Crozier and Page 1985; Sherman et al. 1988), nonsocial insects (Walker 1980; Thornhill and Alcock 1983; Gwynne 1984a; Ridley 1988), arachnids (Austad 1984; Thomas and Zeh 1984; Watson 1991b), and other groups (Smith 1984). Understanding the function of overt or covert polyandry is elemental to the study of female reproductive behavior.

Female reproduction is limited mainly by ability to sequester resources to support the growth of offspring and select sires of high genetic quality (Borgia 1979). When males make no overt investment in offspring it seldom is clear how remating helps females reproduce. Nonadaptive models for the evolution of polyandry

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based on genetically correlated responses in females to selection for frequent remating in males have been proposed (Halliday and Arnold 1987; Arnold and Halliday 1988, 1992) and received support from some laboratory-based selection studies (e.g., Stamenkovic-Radak et al. 1992) but not others (Cheng and Siegel 1990; Gromko 1992). Since males and females of many species probably share genes regulating their mating behavior, single-trait artificial selection studies should often uncover a degree of intersexual genetic correlation. Such results bolster the correlation hypothesis as a valid "null model" but cannot reveal whether it explains remating by naturally selected females. When costs of polyandry likely to be incurred by free-living females are considered (e.g., increased exposure to predators or disease), the compensatory benefits that maintain polyandry in natural populations beg for elucidation (Sherman and Westneat 1988; Watson 1988). Laboratory environments used to culture individuals and test responses to selection lack just those selective forces and sensory inputs that could maintain and modulate sex differences in sexual receptivity despite a degree of genetic correlation. Tests of the importance of the genetic correlation hypothesis should include examination of field populations for sex-specific factors modulating sexual receptivity. The existence of such factors would indicate that the regulation of remating in males and females is sufficiently independent to result in sex-specific adaptations regarding mating frequency.

Numerous nonmutually exclusive hypotheses for the advantages of polyandry have been proposed (Walker 1980; Thornhill and Alcock 1983; Sherman et al. 1988; Westneat et al. 1990). If females control sperm precedence, genetic and phenotypic benefits of remating are particularly compatible, because females can remate as necessary for phenotypic benefits and then use the various ejaculates to fertilize eggs in proportions yielding genetic benefits.

This article details a field study of direct benefits of polyandry in sierra dome spiders (*Linyphia litigiosa* Keyserling: Linyphiidae). In this species females mate immediately after sexual maturation (Watson 1990) and then remate up to five times before their first oviposition, even though males make no obvious material investment in offspring.

I evaluate four hypotheses via multivariate analyses of the impact of 12 factors on female sexual receptivity, data on the fertility and fecundity effects of remating, and observations of antipredator behavior and foraging ecology. I discuss the finding that remating increases female foraging success via reduction of male kleptoparasitism in copula vis-à-vis previously reported evidence that nonrandom multiple paternity yields genetic benefits (Watson 1990, 1991a, 1991b).

Hypotheses and Predictions

Fertility insurance.—If one mating does not ensure that all of a female's eggs will be fertilized, remating may function to augment or revitalize sperm stores. The hypothesis may seem dubious on theoretical grounds, as there should be tremendous selection on males to fertilize all of a female's eggs with a single ejaculate and on females to store sperm effectively. However, Ridley (1988) tentatively concluded that insectan females may seldom attain full fertility without repeated mating. The hypothesis predicts that (1) female fertility will be positively

associated with mate number, if sperm numbers must be augmented (Pyle and Gromko 1978; Petersson 1991), (2) female sexual receptivity will be positively associated with the time since the previous copulation, if viability of stored sperm gradually decreases (Khalifa 1950; Petersson 1991), (3) sexual receptivity will increase after oviposition, if sperm stores can be depleted (Nakatsuru and Kramer 1982), and (4) variance in fertility will be less within groups of multiply versus singly mated females, if risks of infertility are due to impotent matings. Furthermore, if remating functions to ensure fertility, nearly all females should accept at least two or three matings.

Nuptial gifts.—If males pass valuable substances during mating, females may remate to increase the total amount of male investment they receive (Gwynne 1984*b*, 1988; Thornhill and Gwynne 1986; Simmons and Parker 1989). The hypothesis predicts that (1) mate number, copulation durations, and mate sizes should be positively related to fecundity, (2) females should not sacrifice opportunities to remate in order to feed independently of the male, especially on small food items, and (3) females should remate regularly throughout their lives, especially when nutritional status is low (Thornhill and Alcock 1983).

Male protection.—If a sexually attracted male reduces the probability that the female will be killed by predators (Hamilton 1971; Sivinski 1980; McCawley and Lawson 1986) or harassed by competitors (McLain 1981) or other males (Rubenstein 1984; Wilcox 1984), prolonged sexual receptivity might function to extend such protection. Since successful attacks by predators often happen quickly, they often are indistinguishable from departures of females from the study area, making the efficacy of male protection hard to assess. So, to test this hypothesis I appraise whether (1) either sex exhibits specific adaptations to reduce female predation risk during intersexual contacts and (2) intersexual behavior is likely to enhance or weaken predator-evasion tactics used by solitary individuals. Assuming constant pressure from competitors or predators, this hypothesis also predicts that females should remate throughout life or “lead males on” sexually even when they are unwilling to remate.

Convenience.—Females may accept superfluous copulations to avoid the time and energy costs of rejecting males (Parker 1970). Such costs arise when courtship interferes with female resting or foraging or if females must expend energy to avoid forced copulation (Thornhill 1980). Mating could cut costs of male attendance during copulation itself or afterward if males depart sooner or behave more favorably toward a female they have mated (Alcock et al. 1977). The hypothesis predicts that an important cost of associating with sexually active males should be reduced by mating. If remating itself entails costs, then female sexual receptivity should be sensitive to factors affecting expected benefits of remating, such as the density of wasp competitors in soldier beetles (McLain 1981) or prey availability in water striders (Wilcox 1984; Sih et al. 1990).

METHODS

Natural History

At the Flathead Lake Biological Station (Polson, Montana), sierra dome spiders mate from late June through August. Female densities during the middle of the

breeding season average $4.1/\text{m}^2$ (range = $0.6\text{--}10.3/\text{m}^2$). Ninety percent of all males mature in the first 2 wk of the breeding season, but female maturation extends through mid-August. Males spend their adult lives wandering between female webs and provide no offspring care. The operational sex ratio is skewed toward males early in the season (50% of males are mature when the first fractions of a percent of females mature; Watson 1988) but shifts constantly toward female bias as males suffer higher mortality during trips between webs and intrasexual fighting. By late August, when females begin ovipositing, most males are dead.

Averaged over the breeding season, individual females receive a male visit of at least 1 h every 3 d. Visitation rates are three to five times greater early in July when male population densities are highest. Most intersexual pairings begin before 0900 hours ($N = 404$ pairings). Sometimes males depart quickly, but those that stay at least 1 h usually do not depart until evening (median departure time is 2002 hours, $N = 153$ pairings). No male spends more than 18 h with a mature, nonvirgin female (Watson 1990).

Although gravid females may weigh two to four times as much as a male, males are better built for fighting. Sexual dimorphism in body length or prosoma width is seldom more than 15%, but for their overall size males have longer legs and larger and more heavily armored prosoma, chelicerae, and fangs. Adult males never build webs and feed only on prey taken on female webs. Males never relinquish prey to females (cf. Eberhard and Briceño 1983). Females cannot aggressively deter males from entering the web, capturing prey or occupying the preferred position in the central dome portion of the web.

Precopulatory courtship and secondary matings are diurnal. Mating begins with 2–6 h of aspermic preinsemination-phase copulation ($\bar{X} = 3.7$ h, $SD = 1.26$, $N = 100$ matings), during which the male performs hundreds of rapid intromissions (P. J. Watson, personal observation; Austad 1982; Helsdingen 1983). Each 1–3-s intromission is punctuated by 2–6 s of grooming the intromittent organ in the mouth. Males seemingly try to perform cycles of intromit-groom-intromit as fast as possible. Preinsemination-phase copulation is followed by a several-minute period in which the male performs sperm induction. Then follows the 0.7–1.5-h insemination phase of copulation when intromission rates decline to 1–3 per minute.

In spite of male dominance, females dictate whether mating occurs. Males do not attempt to intromit nonreceptive females, and the design of the genitalia seemingly renders forced copulation impossible. Male genitalia consist of many moving parts connected by flexible membranes (Merrett 1962), whereas female genitalia are solid. Males risk damage to their genitalia with no possibility of insemination if they try to intromit into an uncooperative female during the preinsemination phase of copulation. Females easily avoid precopulatory courtship by moving out of the dome, where they are not pursued.

Most newly mature, virgin females (98%, $N > 250$) mate with the first male they contact. After their first mating, females become far more agonistic toward males and, on the average, reject 66% of their opportunities to remate ($N = 617$ pairings). Many nonvirgin females display a web-strumming behavior signaling sexual nonreceptivity; some males respond by leaving the web within a few minutes after arrival (see below). Females usually mate 2–4 times (range = 1–6, \bar{X}

= 2.3, SD = 0.98, N = 104 females continuously observed from maturation to first oviposition in 1982, 1984, and 1985). In 1989 and 1991, 25 of 101 continuously observed females (24.8%) refused to remate; I did not detect monogamous females in earlier years.

Field Observations

Females maintained the same web for days or weeks, where they consistently were in view during sexual interactions and feeding. I marked all females during the middle to late penultimate instar and again immediately after their final molt. During daily scans of each female's web I recorded her feeding and pairing status. If a male was present, I made extended behavioral observations.

Data on 12 factors influencing female mating propensity were collected during the 1982–1985 breeding seasons:

- I. Female sexual history
 - A. Number of previous suitors—number of males that previously courted the female, regardless of whether mating took place
 - B. Number of previous mates—number of previous matings by the female that included at least 20 min of insemination-phase copulation
- II. Temporal factors
 - A. Number of days since the female's last prior mating
 - B. Date—number of days since the first-observed copulation by any female on the study site
 - C. Male arrival time—time male was first detected on the female's web; most males leave by nightfall, so arrival time is associated with the expected length of a male's visit
- III. Female foraging history—foraging success during the 4-d period prior to the arrival of the prospective mate
- IV. Male physical attributes
 - A. Weight—live body weight measured to the nearest 0.1 mg
 - B. Length—anesthetized spider measured from the anterior surface of the chelicerae to the posterior tip of the abdomen measured to the nearest 0.1 mm
 - C. Condition—quotient of observed weight versus weight predicted by a species-typical equation based on male prosoma width, where predicted weight = $\exp^{-0.230 + 2.744 \ln(\text{prosoma width})}$; constants are based on measurement of 111 males collected from webs of randomly selected females over the course of the 1983 and 1984 breeding seasons; values > 1 denote a male that is heavier than average for his body size
 - D. Number of bad legs—total number of legs missing or deformed
- V. Male precopulatory courtship—intersexual behavior occurring before any genitalic contact
 - A. Intensity—number of precopulatory courtship behaviors performed during one or more 30-s observations taken during scans of the female's web, divided by the number of observations
 - B. Attentiveness—proportion of scans prior to copulation in which the male was facing the female; the male was considered to be facing the

female if, at the moment the scan begin, any part of the female's body (not legs) fell within a 30-degree angle originating at the male's face

Data on female web-strumming and its effect on the duration of male visits date from 1991, and data on the foraging cost of cohabitation with males come from 1989 and 1991. In 1982–1985 I observed 801 intersexual pairings, each involving a different male. I performed scans at 0300 hours, 0600 hours, hourly from 0800 to 2000 hours, and at 2200 hours and 2400 hours on every day of the breeding season (I omitted the 0300 hours and 0600 hours scans in 1985 and during the second half of the 1982–1984 seasons). In 1989 and 1991, I performed general scans every 1–3 h between 0900 and 2200 hours and visited paired females, on the average, every 1.48 h ($SD = 0.903$).

Captive Spiders

I brought females into the laboratory when they became fully gravid or, to isolate them from males, after they had engaged in a predetermined number of matings. Captive females were fed on *Drosophila melanogaster* and wild-caught mayflies (Ephemeroptera). Captive spiders regularly received sprinklings of de-ionized water. I kept egg sacs produced by captive females individually in large petri dishes or test tubes at high humidity.

Regression Analyses

I used univariate logistical regression to examine the influence of 12 factors on the probability of remating by females (see above). I used measures of male physical attributes and courtship intensity to help weigh the relative importance of sexually selected characters versus other factors in determining female sexual receptivity. All models employed a dichotomous dependent variable coding whether a female rejected or accepted an opportunity to remate and were analyzed with the Logit package (version 1.12) of the SYSTAT statistical computing system (Steinberg 1985; Wilkinson 1988). Tests of significance were based on likelihood ratio tests (Hosmer and Lemeshow 1989).

Estimates of multivariate models used a subsample of the data (344 pairings of 140 females; $\bar{X} = 2.46$ pairings per female, $SD = 1.53$) for which there were no data missing for any variables; this facilitated comparison of models. In selecting the final multivariate model, factors with the highest T ratio (β/SE) in each of five categories were added according to their order of presentation to females in nature (ordered as listed in Methods). Factors remaining in the model met three criteria: (1) level of significance of not more than .01, (2) independent variable derivative of not less than .10, and (3) correlation with an already chosen variable of less than .5.

Female Fertility and Fecundity

I used percent-hatch data to test the fertility insurance hypothesis and measures of fecundity (egg mass weight and egg number) to help test the nuptial gift hypothesis. I weighed cocoons produced by females of known mate number within 36–72 h of oviposition and stored them at room temperature and high humidity for over 4 wk to allow ample time for hatching. I then opened the cocoons and counted

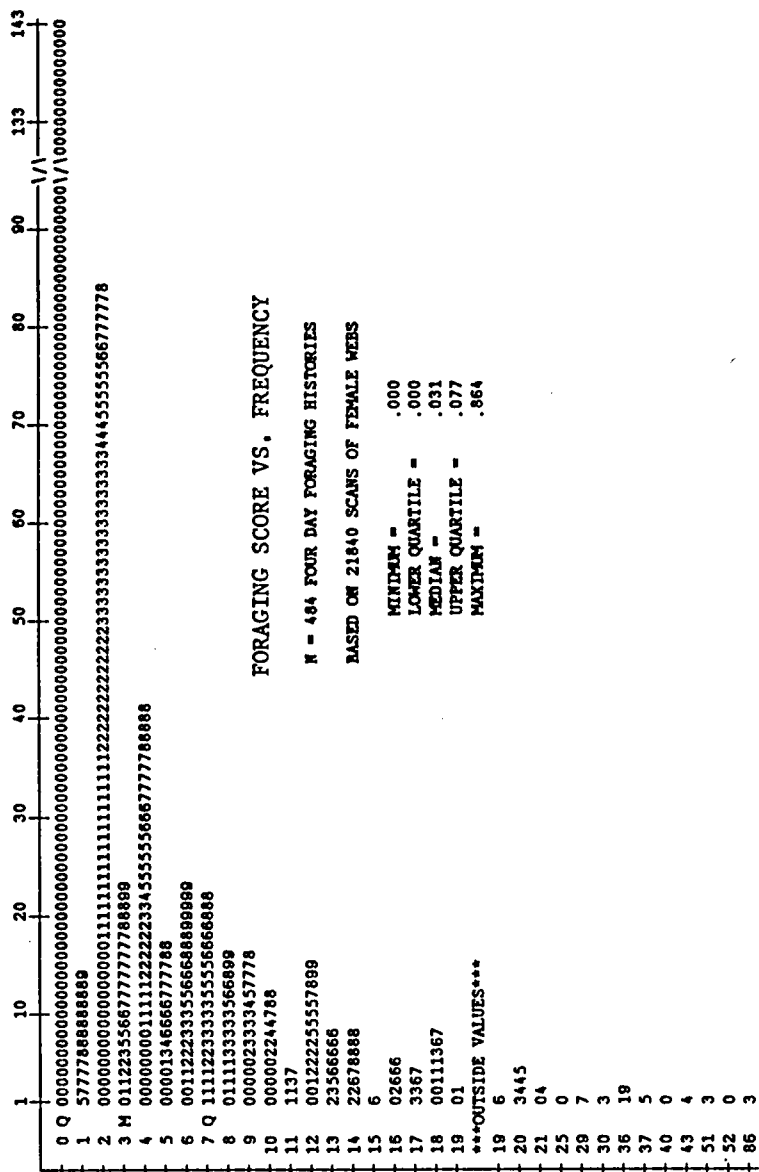


Fig. 1.—Frequency distribution of 484 foraging scores of 146 females. Scores are given on the vertical axis and frequencies on the horizontal. For statistical purposes, I split females into three groups based on the upper and lower quartiles of this distribution. Females within the upper or lower quartile were classed as having high or low foraging success, respectively; medium success females were between quartile boundaries. Each score is based on an average of 45.35 scans (SD = 6.71) of the female during the 4-d period prior to the arrival of a prospective mate. Scores account for the number and size of prey items captured and the number of observations performed on the female during the period. Adjustments for prey size are based on the time typically spent feeding on small, medium, or large prey (1 h, 4 h, and 8 h, respectively). Thus each score equals [(no. of small prey) + (no. of medium prey) × 4 + (no. of large prey) × 8]/(no. of observations).

unhatched eggs, egg shells, and first- and second-instar hatchlings under a dissecting microscope.

Hatchlings of 1989 stayed in their natal cocoons at 2°–6°C and high humidity until April 12 (batch 1) or May 15, 1990 (batch 2). I determined percent hatch at this time. I weighed living spiderlings in groups of 10 and raised them within 2.5-L boxes with *Drosophila* as prey. I tracked spiderling mortality and kept feedings equal between sib groups on a per-spiderling basis. I reweighed surviving spiderlings on May 1 (batch 1) and June 4, 1990 (batch 2).

Female Foraging Success and Copulation

Drosophila trials.—To test for differences in the prey capture success of copulating versus paired noncopulating females, I dropped wild-type *Drosophila melanogaster* into webs of such pairs and recorded whether the male or female took possession of the fly. No individual of either sex was involved in more than one of the 96 trials. I used only pairs in which both male and female were in the central 50% of the dome portion of the web and attempted to drop the flies onto a point above the dome equidistant from the male and female. All copulating pairs were in the preinsemination phase.

Natural variation in foraging success.—In 1982–1985 I compiled sexual and foraging histories on 183 females ranging in duration from several days to the entire breeding season. Consumption of small prey takes 40–60 min, so foraging activity is well estimated with hourly scans. I used records of prey consumption to estimate female foraging success and examine its relationship to sexual receptivity. For every day covered by an estimate of foraging success for a particular female, she was either in view or not on a web and so not feeding. I based my determination that a female was not on a web on intensive daily searches and the female's position relative to the search area at the time of her eventual relocation. Females that might have eaten unobserved had their foraging records reset to begin at the time of relocation. I used the foraging data to generate 484 foraging scores (fig. 1). Each score represents the female's foraging success during the 4-d period prior to a given male's arrival on her web. The scores are based on a total of 21,840 scans of the webs of 146 females (\bar{X} = 3.24 scores per female, SD = 2.41).

Manipulation of female foraging success.—I manipulated female foraging success to further examine the effect on sexual receptivity. During 1983 and 1984 I monitored the mating activity of 31 free-living, marked females that consumed at least one large hand-fed mayfly subsequent to their first mating. Each mayfly weighed two to three times as much as an average female and took 6–10 h to consume. Some females that received three or four mayflies (ca. 20%) showed signs of satiation (i.e., reduced web maintenance and refusal of additional mayflies). I fed females at night so that feeding itself would not inhibit matings. Concurrently, I monitored 56 free-living control females that consumed only prey they captured themselves. I assigned females randomly to these groups and observed both sets four times daily at 0900, 1300, 1700, and 2100 hours, recording interactions with 226 secondary suitors. At each observation I noted the female's

TABLE 1

THE INFLUENCE OF 12 FACTORS ON THE LIKELIHOOD OF REMATING WITH SIMPLE LOGISTICAL REGRESSION

Factor	β	SE	D	χ^2	P	N
Number of previous suitors (♀)	-.476	.055	-.099	111.339	10^{-6}	617
Number of previous mates (♀)	-.622	.108	-.138	38.482	10^{-6}	617
Days since mating (♀)	-.242	.028	-.047	128.393	10^{-6}	617
Date	-.057	.009	-.013	39.113	10^{-6}	617
Arrival time (♂)	-.103	.036	-.023	9.007	.003	404
Foraging score (♀)	-5.770	1.792	-1.275	13.447	.0002	473
Weight (♂)	-.006	.025	-.001	.048	.827	457
Body length (♂)	-.041	.129	-.010	.106	.745	445
Body condition (♂)	-.770	.542	-.190	2.042	.153	446
Number of bad legs (♂)	-.207	.150	-.049	1.976	.160	545
Courtship intensity (♂)	-.036	.142	-.008	.066	.797	404
Attentiveness (♂)	-.527	.246	-.121	4.985	.026	361

NOTE.—Negative derivatives (D) denote an inverse relationship between the factor and the odds of remating and larger absolute values suggest stronger effects. The standard errors of each coefficient (SE), the results of likelihood-ratio tests of $H_0: \beta_i = 0$, and the number of pairings (N) are given.

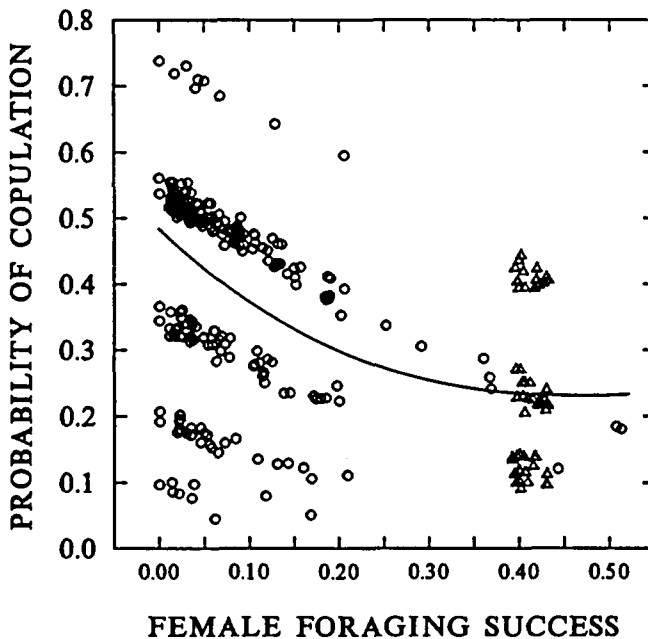


FIG. 2.—Predicted probabilities of remating vs. female foraging success. Data are pooled for unmanipulated females (circles, $N = 342$) and those given supplementary feeding (triangles, $N = 55$) in the years 1983, 1984, and 1985. Probabilities are based on logistical regression with the previous number of mates of each female included as a covariate (this causes banding of points). The curve was fitted by distance-weighted least squares.

pairing status and clear evidence of mating (i.e., either seeing the pair in copula or a new sperm web, which typically lasts well into the night after mating).

In 1985 I gave supplementary feeding of at least two mayflies to 13 free-living females. Again, some females became satiated. In addition, I created a group of 18 females with very poor foraging success that lived inside a $4 \times 4 \times 3$ -m prey enclosure built on the study site. A third group of 18 control females lived just outside the enclosure and had unmanipulated foraging success. All females inhabited their own webs within the same general area of the study site and were randomly assigned to treatments. I monitored the females every 2 h during daylight and observed 144 intersexual pairings.

The prey enclosure consisted of nylon "no-see-um" netting affixed to a wooden frame. Females built webs at normal densities on the undisturbed vegetation inside. I occasionally sprinkled females in the enclosure with rainwater to prevent dehydration. During a 3-d evaluation of the efficacy of the enclosure, I observed females inside feeding in two of 73 scans (2.7%), compared with 35 of 318 scans (11%) for females just outside the enclosure ($\chi^2 = 4.74$, $df = 1$, $P = .03$), a reduction in prey capture within the enclosure of 75.5%. Females spent 15 d in the enclosure prior to my introducing one freshly captured male to each of their webs to assay sexual receptivity.

Mating and Male Departure Time

In 1981 I recorded departure times of 137 males from webs of nonvirgin females. All these males were on the female's web for at least 2 h between 1100 and 1700 hours; this restricted the analysis to pairings in which there was a reasonable chance of copulation. None of the departures were forced by rival males or predators.

RESULTS

Factors Influencing the Probability of Remating

Univariate models.—Female foraging success during the 4 d prior to a new mating opportunity was the strongest single predictor of the probability of remating (table 1). Females with greater foraging success were less likely to remate (fig. 2). The number of previous courtships or matings, date, number of days since the female was last inseminated, and suitor arrival time all were inversely related to the likelihood of remating. The finding that a female's number of previous mates was a stronger predictor than either date or number of previous suitors suggests that receipt of ejaculates per se is important in reducing female sexual receptivity (Watson 1990). Physical characteristics of males had no detectable effect on female sexual receptivity; neither did the frequency of male precopulatory courtship behaviors. Male attentiveness toward the female was inversely related to the probability of remating (table 1).

Multivariate models.—I constructed multivariate models of female remating propensity including, at most, one factor from each of five categories (see above). The best model included these predictors: (1) female foraging success, (2) male

TABLE 2
BEST MULTIVARIATE MODEL PREDICTING THE LIKELIHOOD OF REMATING

Factor	β_i	SE	D	χ^2	P
Foraging score (♀)	4.312	1.801	-1.041	153.87	10^{-6}
Condition (♂)	1.623	.670	-.392	81.18	10^{-6}
Previous mates (♀)	.696	.151	-.168	25.08	10^{-6}
Number of bad legs (♂)	.572	.195	-.138	9.26	.0023

NOTE.—The overall model was highly significant ($\chi^2 = 42.504$, $df = 4$, $P < 10^{-6}$, $N = 344$ [146 copulations + 198 rejections]). The results of single df tests of the significance of individual factors are shown; factors are listed in descending order of influence. Interaction terms were insignificant ($P > .20$) or highly correlated with main effects and were not included in the final model. Negative derivatives (D) indicate that a suitor was less likely to be accepted as a mate for each unitary increase in the factor.

body condition, (3) the female's number of previous mates, and (4) the male's number of missing or deformed legs. All these factors had inverse relationships with the female's likelihood of remating (table 2). Independent-variable derivatives from the final model indicated that female foraging success exerted a greater influence on the probability of remating than male attributes or the female's number of previous mates. For example, a unitary increase in the foraging score (equivalent to one additional mosquito consumed during the 4 d prior to a suitor's arrival) was associated with a change in her probability of remating approximately 2.5 times greater than the change expected from a unitary increase in male body condition.

Monogamous females.—I observed females that refused all opportunities to remate only in 1989 and 1991 (10 of 62 and 15 of 39 individuals, respectively). On the average, monogamous females matured earlier than polyandrous females ($\bar{X} = 8.2$ d into breeding season, $SD = 6.7$, vs. $\bar{X} = 13.5$ d, $SD = 6.4$, respectively; $T = 3.52$, $P = .001$) and were heavier at maturity than polyandrous females ($\bar{X} = 18.7$ mg, $SD = 3.6$, vs. $\bar{X} = 16.0$, $SD = 3.4$, respectively; $T = 3.31$, $P = .001$). These observations suggest that female condition, not sperm supply, controls sexual receptivity.

Females Signal Nonreceptivity

Nonvirgin females were commonly agonistic toward males. Such behavior never forced a male to depart but often sped voluntary departure, probably because it signals low sexual receptivity. In addition to general agonistic behaviors, nonvirgin females possess a specific web-strumming behavior that they use exclusively to signal sexual nonreceptivity to males (front legs alternating rhythmically at 4–6 strums/s). Often, female strumming began during the first minutes a male was on her web. It never occurred after mating. In 85% of 78 pairings during which strumming was observed in 1991, it began within 2 h of male arrival. Females that strummed had a probability of remating of 0.096 compared with 0.372 for nonstrummers (logistic regression, $\chi^2 = 20.85$, $df = 1$, $P = .000005$, $N = 196$ pairings of 51 different females). The median duration of male visits was 2.6 h shorter in pairings in which I observed female strumming (fig. 3; Mann-

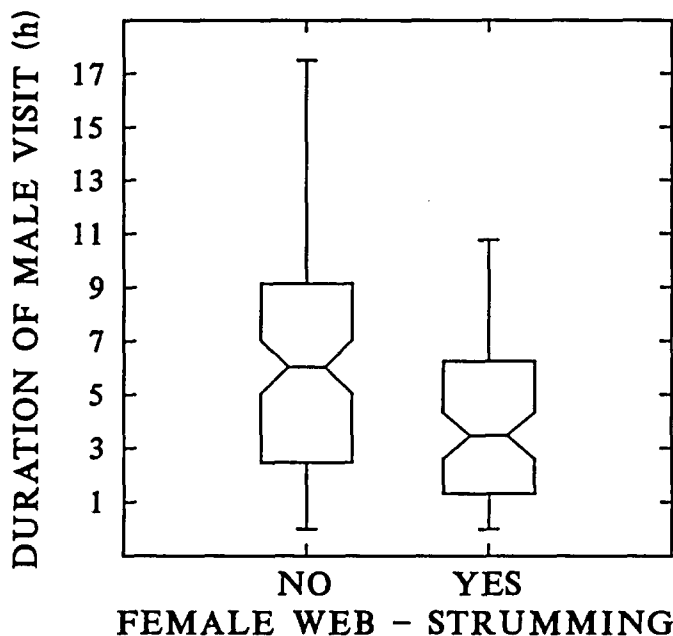


FIG. 3.—Duration of male cohabitation in pairings in which females either were ($N = 83$) or were not ($N = 112$) observed to perform web-strumming behavior. *Box notches* delimit 95% confidence intervals around the medians; *box edges* denote upper and lower quartiles; *whiskers* mark values adjacent to the quartiles (the most extreme values in these data).

Whitney, $\chi^2 = 12.35$, $df = 1$, $P = .0004$). Clearly, males perceive and respond nonrandomly to information concerning female reproductive value (see also Watson 1990; cf. Suter and Walberer 1989; Suter and Sanchez 1991). The fact that females possess a display to encourage male departure before mating suggests that male presence is costly and that mating only provides a semieffective way to recoup costs.

Foraging Cost of Cohabitation

Averaged over the breeding season females spent 18.7% of their time cohabiting with a kleptoparasitic male. This declined from more than 40% early in the season to near zero as the relative density of males fell (fig. 4; $r = -0.59$, $P < .0001$). A female's ability to capture prey was reduced by a factor of 2.8 when she cohabited with a male, relative to the solitary state (fig. 5; Tukey-Kramer, $P < .0001$). As in other linyphiid spiders (see below), food limits female fecundity. Average clutch size in nature is 48.6 (SD = 15.2, $N = 128$ first broods), whereas females given supplementary feeding during their mature instar produce up to 120 eggs.

Male Kleptoparasitism Is Reduced in Copula

Introductions of *Drosophila* onto webs harboring copulating and noncopulating pairs revealed that the percentage of prey captured by paired females increases

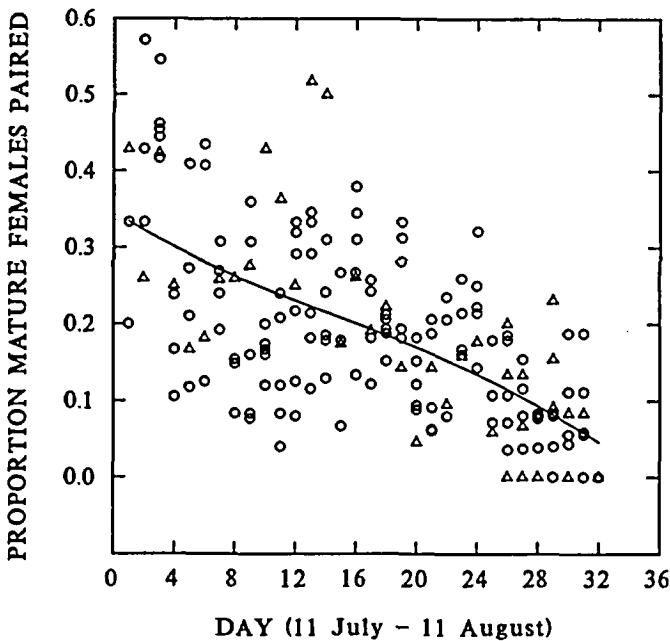


FIG. 4.—Proportion of sexually mature females cohabiting with a male during each of 199 web scans evenly spanning the middle 80% (July 11–August 11) of the 1989 and 1991 breeding seasons (triangles, $N = 42$ scans; and circles, $N = 157$). Each scan covered an average of 24.2 females ($SD = 6.8$, range = 5–35). The curve was fitted by distance-weighted least squares.

from 31.4% when not copulating to 80.8% while copulating (table 3). These results are conservative, because I only collected data from pairs in which both sexes were in the dome portion of the web (foraging from other locations, such as the superstructure, is nearly impossible). This inflates the estimate of prey captured by paired noncopulating females by a factor of approximately 1.25, because they spend more than 20% of their time outside the dome. Thus a better estimate of the percentage of prey captured by noncopulating females is $31.4\% / 1.25 = 25.1\%$.

Genital couplings during the preinsemination phase necessarily increase the lag in response to prey for both sexes by at least 2–3 s. I estimated the effect on prey capture efficiency using natural feeding data. In 624 pairings, I detected 198 prey captures by noncopulating pairs and 12 by copulating pairs. Pairs were in copula in 10.3% of these observations. If copulation did not impair foraging efficiency, copulating pairs should have captured 10.3% of 198 (= 20 prey). Thus, a copulating pair's overall prey capture efficiency seems to be reduced by a factor of 0.60 (12/20). Adjusting the result of the *Drosophila* trials accordingly, a female still raises the proportion of prey she consumes from the noncopulating level of 25.1% to 49.0% ($0.60 \times 80.8\%$) in copula.

Since females experiencing natural levels of foraging success stop mating even to consume small *Drosophila*, it seems likely that any nutrients transferred by

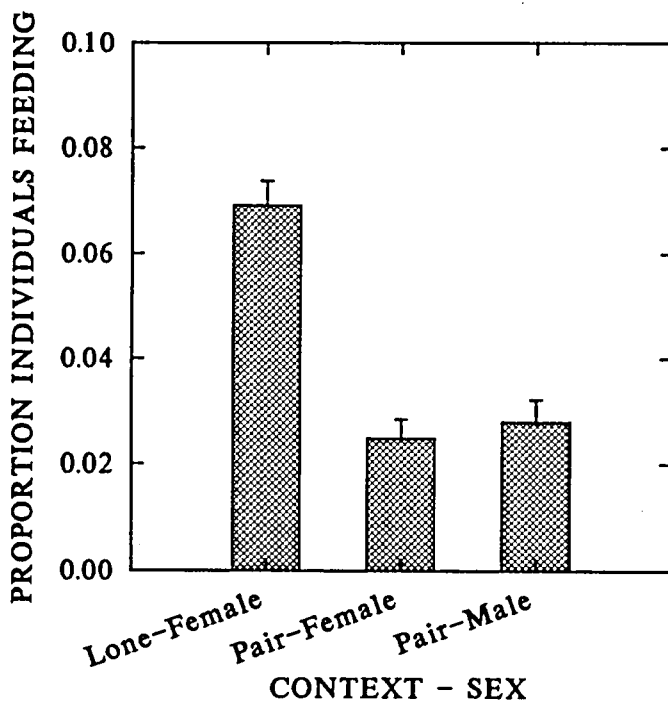


FIG. 5.—Mean proportion of solitary females, paired females, and paired males feeding in 363 scans. *Error bars* = 1 SE; *N* = 5,849 observations of solitary females and 2,514 scans of noncopulating pairs; pooled 1989 and 1991 data.

TABLE 3
SEX-SPECIFIC *DROSOPHILA* CAPTURE FREQUENCIES FOR
COPULATING AND NONCOPULATING PAIRS

CONTEXT	CAPTURING INDIVIDUAL		TOTAL
	Male	Female	
Not copulating	48 (38.65)	22 (31.35)	70
Copulating	5 (14.35)	21 (11.65)	26
Total	53	43	96

NOTE.—Numbers in parentheses are expected values; $\chi^2 = 18.66$, *df* = 1, *P* = .00002.

TABLE 4

THE FREQUENCIES AT WHICH FEMALES WITH DIFFERENT LEVELS OF NATURAL FORAGING SUCCESS
ACCEPTED AND REJECTED MATING

FEMALE'S MATING DECISION	FEMALE FORAGING SUCCESS			TOTAL
	Low	Medium	High	
Mate	79 (55.24)	71 (32.13)	32 (26.67)	302
Reject	64 (44.76)	150 (67.87)	88 (73.33)	182
Total	143	221	120	484

NOTE.—Numbers in parentheses are column percentages. Females in the low and high categories had foraging scores within the lower and upper quartiles of the distribution of scores for all females, respectively; others were classed as having medium success (fig. 1). In 2×2 analyses, females with low vs. high success and low vs. medium success differed in the proportion of remating opportunities accepted ($\chi^2 = 21.85$, $df = 1$, $P < .0005$, and $\chi^2 = 19.15$, $df = 1$, $P < .0005$, respectively). Females with medium vs. high success differed in the predicted direction but not significantly ($\chi^2 = 1.10$, $df = 1$, $P = .294$). The overall 3×2 analysis is significant ($\chi^2 = 27.91$, $df = 2$, $P < .0005$).

the male while mating are insufficient to outweigh minimal prey losses; this is evidence against the nuptial gift hypothesis. Discovery that the foraging cost of male cohabitation is reduced in copula is supportive of the convenience hypothesis.

Foraging Success and Sexual Receptivity

Natural variation in foraging success.—Females with low foraging success accepted a higher percentage of remating opportunities than those in the medium or high categories (table 4). Females with high foraging success tended to mate less than those with medium success, but not significantly so. One might expect such a relationship epiphenomenally if the desirability of males as mates were correlated with their location at foraging sites of differing quality. However, I found no significant differences in the body weights of males found in webs of females with high, medium, and low foraging success ($F = 2.441$, $N = 355$, $P = .089$). Furthermore, female foraging success was negatively correlated with the total duration of copulation ($r_s = -0.199$, $P = .05$, $N = 103$ matings of 69 females in 1982–1984; durations of zero are not included).

Experimental variation in foraging success.—Females given supplementary feeding in 1983 and 1984 accepted 17 of 107 suitors as mates (15.9%), while unfed controls accepted 50 of 119 (42.0%) ($\chi^2 = 18.44$, $df = 1$, $P = .00002$). In 1985, results of supplementing female foraging success again indicated that receptivity to remating is negatively related to nutritional state, but the direction of the influence on food-deprived females was contrary to prediction and opposite that exhibited by females at the low end of natural variation in foraging success. Both fed and starved females mated with a smaller percentage of their suitors (25.5%, $N = 55$, and 32.6%, $N = 43$, respectively) than control females (58.7%, $N = 46$) (fig. 6).

The observation that foraging history modulates sexual receptivity could be

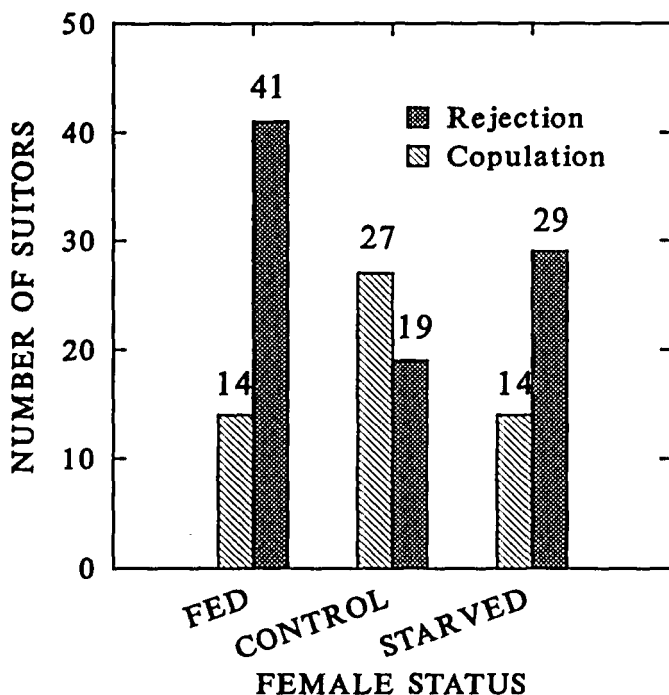


FIG. 6.—Numbers of suitors accepted and rejected as mates by three groups of nonvirgin females differing greatly in their levels of foraging success. In separate 2×2 analyses, both the artificially fed and starved groups mated at a lower frequency than the unmanipulated controls ($\chi^2 = 11.48$, $P = .001$, and $\chi^2 = 6.11$, $P = .013$, respectively). The fed and starved groups did not differ between themselves ($\chi^2 = 0.60$, $P = .440$).

taken as evidence either for the convenience or the nuptial gift hypothesis. However, since females (1) prefer consumption of small prey to mating, (2) try to send males away before resorting to mating, and (3) mate less if prey availability has been chronically low, I pick the convenience hypothesis as the better explanation.

Mated Males Do Not Depart Sooner

A female's most productive foraging time is between 1900 and 2300 hours (Watson 1988). This encompasses the period in which most male visits of 1 h or more are spontaneously terminated. If remating increases the probability that a male departs early in this period, this too could improve female foraging success. However, median departure time for males that mated was 2044 hours ($N = 39$), versus 1917 hours for rejected males ($N = 98$) (Mann-Whitney, $df = 1$, $P = .058$); mating may even have delayed departure. Considering that females were less likely to mate with late-arriving males (table 1) together with the likelihood of male departure at dusk suggests that the benefits of remating are associated with how long a male's visit and consequent kleptoparasitism is likely to last; this is consistent with the convenience hypothesis.

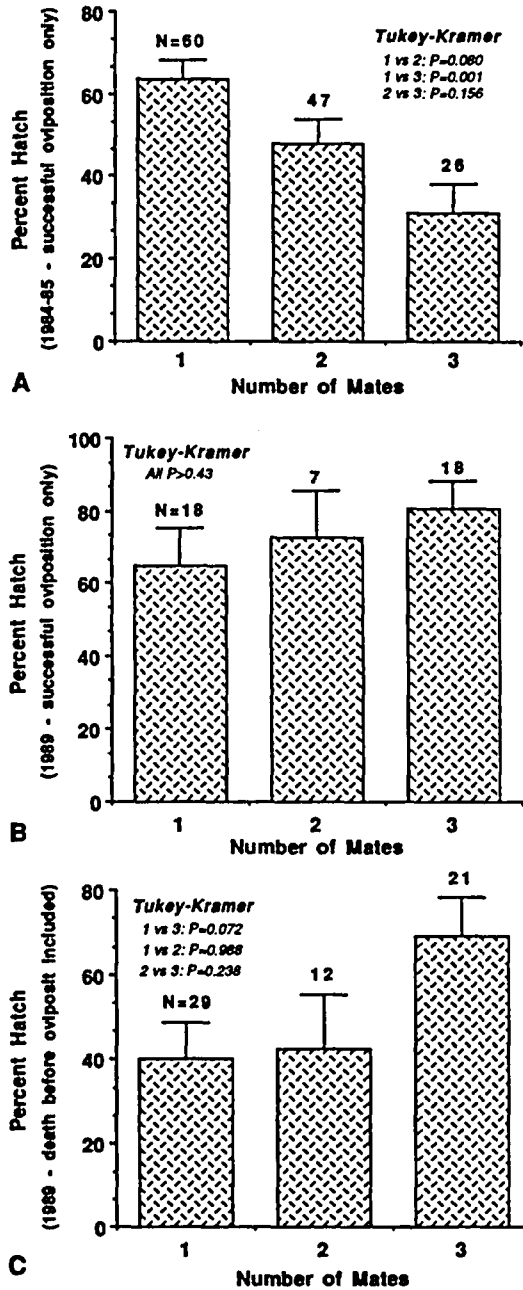


FIG. 7.—Percent hatch vs. final mate number for females studied in (A) 1984 and 1985 and (B, C) 1989. Only data on females that survived through oviposition are available for 1984–1985 ($N = 133$). Separate histograms for the 1989 data (B) exclude ($N = 43$) and (C) include ($N = 62$) gravid females that died before oviposition with percent hatch as zero.

Fertility and Mate Number

I found no difference in the variance in fertility (i.e., percent hatch) between multiply versus once-mated females (Levene's test, $F = 0.041$, $df = 193$, $P > .90$; pooled 1984, 1985, 1989 data). In data pooled from 1984 through 1985 I found a negative relationship between the number of matings accepted by a female and fertility (fig. 7A; $r_s = -0.290$, $N = 133$, $P < .001$); this may be due to venereal disease (see below). I detected no relation between mate number and fertility in 1989 (fig. 7B; $r_s = 0.189$, $N = 43$, $P > .20$), except when I added females that died prior to oviposition to the analysis with fertility as zero (fig. 7C; $r_s = 0.280$, $N = 62$, $P = .03$). (I kept no records of preoviposition death in 1984–1985.) The positive correlation in 1989 was solely due to higher fertility of thrice-mated females. Overall egg viability was lower in 1984–1985 (i.e., disease virulence higher), when the negative relationship with mate number was detected (1984–1985: average percent hatch = 51.76%, $SD = 38.99$, $N = 6,226$ eggs from 133 broods; 1989: $\bar{X} = 72.56\%$, $SD = 38.30$, $N = 1,568$ eggs from 43 broods; $T = 3.05$, $df = 174$, $P = .003$).

In 1982 I released 23 females into the field after collecting their first batch of eggs in the laboratory. Only three (13%) of these females remated although all had at least one opportunity. This represents proportionally the same remating propensity as shown by 135 preoviposition females that previously had mated three or more times ($\chi^2 = 0.16$, $P = .693$, $df = 1$, $N = 158$). Combined with the observation that sexual receptivity does not increase with the time passed since a female's last mating (table 1), these data refute all specified versions of the fertility insurance hypothesis.

Fecundity versus Mate Number and Copulation Duration

Once- and twice-mated females that spent approximately 70% of their adult instars in the lab did not differ in the average number of eggs laid ($T = 0.129$, $N = 92$, $P = .897$; 1984 and 1985 data), nor did twice- and thrice-mated females that were captive for less than 25% of their adult instar ($T = 1.642$, $N = 36$, $P = .110$). In 1989 all females spent equal time in the lab. Mate number was unrelated to egg number ($F = 1.811$, $N = 62$, $P = .173$), total egg-mass weight ($F = 0.749$, $N = 42$, $P = .480$), and the average weight of 10 second-instar spiderlings ($F = 1.589$, $N = 34$, $P = .220$). These results were not altered by controlling for female postoviposition weight, an index of egg capacity and predictor of egg number ($F = 25.95$, $N = 89$, $P < .00001$, $R_a^2 = 0.221$) and egg-mass weight ($F = 23.22$, $N = 87$, $P = .00001$, $R_a^2 = 0.205$) but not hatchling weight ($P = .678$).

I examined four measures of fecundity in relation to females' (1) cumulative duration of preinsemination-phase copulation (all matings), (2) cumulative duration of insemination-phase copulation, and (3) cumulative duration of both phases. I included combinations of up to three covariates in these models. Covariates were (1) average weight of all the female's mates, (2) female postoviposition weight, and (3) the interaction between summed cumulative copulation time and the percentage of summed copulation in which the male used two pedipalps.

Egg-mass weight was negatively related to all three measures of copulation

duration (e.g., $T = 2.31$, $P = .029$, $N = 31$, $R_a^2 = 0.354$ with summed copulation duration as dependent variable and covariates 2 and 3 in the model; the covariate-free model gave $P = .038$). Neither copulation duration nor covariates were associated with hatchling weight (all $P \geq .099$) or the average weight of single eggs (all $P \geq .326$). Egg number was unrelated to all measures of copulation duration ($P \geq .158$). No measure of fecundity was related to the average weight of mates.

Male sierra dome spiders do not give obvious nuptial gifts such as prey or large spermatophores. Ejaculates are about 1 μL in volume, and no more than two are transferred per mating (P. J. Watson, unpublished data). However, fluids produced within the male's copulatory organs (pedipalps) or imbibed into the intro-mittent organ from the mouth could be transferred cryptically during copulation. If so, copulation durations and male body size could be important in determining the amount or quality of investment females receive. The nuptial gift hypothesis would be supported if such factors were positively associated with female fecundity, but they are not.

Predators and Competitors of Solitary and Paired Females

Antipredator behaviors in the sierra dome spider involve (1) sudden free-fall to the ground, usually when ambushed by visual predators such as birds or wasps, or (2) use of vibro-crypticity (i.e., running onto web-supporting vegetation) when attacked by spiders that use web-borne signals to track prey. When faced by small predators such as male theridiid spiders, male sierra dome spiders sometimes fight.

Males flee immediately from avian and hymenopteran predators and larger spiders. However, even when males fight small predators they do not take into account the female's presence or movements; male behavior is purely self-defensive. Also, females show no behaviors to take advantage of a male's presence when a predator arrives, failing even to keep the male between themselves and the source of danger.

On theoretical grounds, one expects a passive benefit for females by having a male on the web as a second target for predators. However, such benefits would be partly canceled by intersexual behaviors that reduce the efficiency of basic defensive tactics; here are three examples. First, I witnessed many instances in which an ambushed pair confused or bumped into one another while running toward web-supporting vegetation, thereby delaying attainment of vibro-crypticity. Second, during the day, solitary females spent all of their time within the central dome portion of their web. In contrast, while being attended by a male with whom they eventually mated, nonvirgin females spent only 80.8% (SD = 30.8, $N = 338$ pairings) of their time within the dome. Since predators enter the web via its periphery, females outside the dome center risk shorter warning times. Females at the periphery also lose the physical protection of the finely woven dome that envelops them more fully if they are within it. It also is harder for spiders to flee rapidly in the tangle-web areas outside the dome, and spiders that try free-fall escapes often "hang-up" atop the dome for several seconds,

struggling to cut through and complete their descent. Third, vulnerability to predation must increase during mating, when the male and female are intermittently joined by their genitalia. Pairs locked in copula cannot run from predators or free-fall. Uncoupling requires 0.5–4 s of tugging by the male and up to 20–30 s if either member of the pair has shifted slightly out of the copulatory posture, as sometimes happens when the spiders are startled. I have seen one pair, still locked in copula, wrapped and killed by a theridiid spider (*Enoplognatha* sp.) The sierra dome spider's abstinence from nocturnal copulation may be related to the abundance of this predator at night.

The main competitors of female sierra dome spiders are conspecifics. Males did nothing to deter nonresident females from entering a web or supplanting its original owner. Male fighting usually keeps males from accumulating on a female's web, but since even one male is strongly kleptoparasitic this poses little advantage for the female. Finally, the observation that females actively discourage male presence on the web is inconsistent with the protection hypothesis, as considerable predation risk is always present.

DISCUSSION

Benefits and Costs of Multiple Mating and Paternity

Two payoffs seem to underlie polyandry in the sierra dome spider: receipt of multiple ejaculates permits genetic bet hedging (Watson 1991*b*) and female foraging efficiency is improved in copula. Lorr (1978) found that paired noncopulating females had nearly a threefold greater disadvantage capturing medium-size prey (i.e., houseflies; 8.6% captured by females, $N = 63$) than the females in my experiments involving *Drosophila*. Some pairs in Lorr's study may have involved subadult females (N. A. Lorr, personal communication), which compete less vigorously for food than mature females (P. J. Watson, unpublished data), but the results still suggest that the improvement in foraging success associated with remating may be accentuated when more valuable prey are involved.

There also is evidence that polyandry entails several costs. First, remating increases vulnerability to predators by immobilizing pairs during genitalic couplings. This cost is managed by rejecting many mating opportunities and by restricting accepted matings to daylight hours, when arachnid predators that can quickly penetrate the web are less active. Second, in some years females that mate more often exhibit low egg viability. This cost, apparently due to venereal disease (see below), is minimized by rejecting matings and perhaps by hygienically isolating ejaculates not to be used in fertilizing eggs (Watson 1991*b*). The risk of venereal infection may increase when multiple paternity requires females to draw more ejaculates deeply into soft tissues of the body instead of restricting them to relatively impervious cuticular portions of the sperm ducts. Thus, ostensible genetic benefits of polyandry, which depend on multiple paternity, may require acceptance of disease-related costs over and above that of multiple mating per se. The observation that nonvirgin females actively discourage males from

being on the web by signaling sexual nonreceptivity is strong evidence that frequent cohabitation with males is costly and that the use of sex to reduce costs due to male foraging interference is only an imperfect solution.

Disease-related female infertility is present in all years, as indicated by the poor physical condition of most inviable eggs and bimodal distributions of fertility. Venereal transmission may occur in years of high virulence such as 1984 and 1985; considering females grouped according to mate number, the major skew of the bimodal fertility distributions shifted dramatically toward low fertility with each increase in mate number (Watson 1988). It is unlikely that this pattern is caused by already sick females having low mating resistance, because females so easily avoid male courtship. In support of this view, females in the starvation experiment mated less often than females with average diets, even though the food-deprived females must have had relatively low energy reserves. Moreover, I have found large numbers of rickettsia- and virus-like organisms within developing oocytes removed from females by dissection (P. J. Watson, unpublished data). The observed organisms are similar to types known to inhabit arthropod ejaculates, including those of arachnids (Afzelius et al. 1989), and the rickettsia have morphologies (thin sections viewed through transmission electron microscopy) dissimilar to types known as commensals in many arthropod eggs (e.g., *Wolbachia* sp.).

Female Foraging History and Sexual Receptivity

Female receptivity to secondary suitors is modulated by recent female foraging success, as predicted by the convenience hypothesis. However, under this hypothesis I did not originally predict that female receptivity would drop under prolonged low food conditions. I suggest that the low mating response of experimentally food-stressed females represented an adaptive response to low expected foraging benefits of remating. Females experiencing chronically low prey availability should avoid costs of remating, because expected foraging benefits would not compensate. Other aspects of foraging behavior are known to be affected by foraging success in the sierra dome spider (P. J. Watson, personal observation; Lorr 1978) and other spiders (Janetos 1986; Riechert and Gillespie 1986).

Wilcox (1984) found that female water striders (*Gerris remigis*) forage more efficiently in copula. However, Clark (1988) found no correlation and Sih et al. (1990), a negative correlation between female hunger and mating duration. These results also might be explained by females' opting not to mate if expected foraging benefits are low.

In the linyphiid spider *Frontinella pyramitela*, males also cohabit with females and capture about 32% of prey (Suter 1985). Male kleptoparasitism is less harsh in *F. pyramitela* than in the sierra dome spider but still reduces female fecundity by 6.1%–7.0%. Suter and Parkhill (1990) rejected reductions in male kleptoparasitism as an explanation for prolonged insemination-phase copulation in *F. pyramitela*, observing that, "when prey contact the web, . . . the formerly copulating spiders often immediately become competitors for the same meal [and] prolonged copulation may result in more, rather than less, intraspecific competition" (p. 372). However, it was seemingly not known whether the relative competitive

abilities of the sexes were affected by copulation. Preinsemination- and insemination-phase copulation are relatively short in *F. pyramitela*, however, and females of this species may not use copulation to improve foraging success.

Remating and Fecundity

Female sierra dome spiders are food limited in their fecundity, as are other linyphiid spiders (Wise 1975; Suter 1990). One might suppose that, if remating increases female foraging success, then a positive relationship should exist between mate number or mating duration and fecundity. But this view ignores costs of remating. Well-fed females with high expected fecundity have more to lose and less to gain by remating. Increased risks of predation and disease associated with remating threaten all or most of a female's eggs, whereas expected nutritional gains attributable to any one remating probably translate to just a few eggs, a payoff that means little to females that can already produce many eggs. This explains why females that mature early and are high in weight, or that experience high foraging success as adults, show more resistance to remating as well as higher fecundity. On the other hand, female linyphiids with below-average diets apparently can drastically improve fecundity via minor increases in foraging success (Austad 1989), making use of a risky foraging tactic worthwhile. Accordingly, food-restricted females in my study that ultimately produced egg masses of low weight tended to engage in longer copulations.

Mechanisms Linking Copulation with Female Foraging Success

Males may reduce their foraging efforts while mating, because the cost of a pause in copulation outweighs nutritional benefits. While eating, the male might be supplanted by another male, the female may capture a prey item herself, or female receptivity might decline as evening approaches. However, I occasionally have seen copulating males capture and immediately discard prey; this would seem to be the best action for males to take, if they were actually able to do so. Copulating males may also desensitize themselves to various sensory inputs not associated with copulating to help maintain necessary stability in the copulatory posture. Stable alignment and precise coordination in the use of the pedipalps is important because males that perform rapid preinsemination-phase copulation are favored as sires (Watson 1991b). On the other hand, females are inactive during copulation. Since the web detains prey passively for several seconds, prey entering at the start of a typical 1–3-s intromission will often be retained until the male unlocks the genitalia, permitting timely female pursuit.

Interaction of Mechanisms to Gain Phenotypic and Genetic Benefits

In the sierra dome spider, secondary mates that are larger and more ferocious fighters are favored as sires (Watson 1990, 1991a, 1991b), suggesting that polyandry has been selected to yield genetic benefits. The observation that even well-fed females accept a few secondary matings (fig. 2) bolsters this view. A third indicator of genetic benefits is the decline of female sexual receptivity with increasing mate number. This pattern suggests diminishing benefits or rising costs as mate number increases. Unlike risks of predation and disease associated with remating

and the efficacy of remating as a foraging tactic, expected genetic benefits should change (i.e., decline) as the number of previously accepted matings increases (Williams 1975).

The male traits associated with fertilization success are only weakly related to mating success (tables 1, 2). On the level of mate choice, factors modulating foraging benefits of remating evidently take precedence over the efficiency of sexual selection. However, since females apparently control sperm precedence (Watson 1991a, 1991b), the absence of mate choice from the list of mechanisms underlying sexual selection may not be a major liability (see also Rubenstein 1989). Pressure to cope with both phenotypic and genetic barriers to reproduction probably contributes importantly to the evolution of mechanisms for uncoupling mate and sire selection.

The mechanisms that generate information on male quality and thwart male kleptoparasitism are elegantly fused in the preinsemination phase of copulation. Male intromission rates are positively associated with paternity (Watson 1991b) and should reflect fitness-related traits such as physiological vigor, physical coordination, morphogenetic competence (imperfectly formed pedipalps would not fit easily into the female's genitalia), and fighting ability (see Watson 1991b). The same rapid, exacting intromission cycles that constitute a test of male quality can also account for the efficacy of preinsemination-phase copulation in reducing male kleptoparasitism.

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