

Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae)

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Abstract. Observations of the reproductive behaviour of 44 free-living, polyandrous female sierra dome spiders combined with electrophoretic paternity studies were used to evaluate three hypotheses about genetic benefits of polyandry: (1) best male, (2) genetic diversity, and (3) genetic bet-hedging. Females nearing maturation rely upon intrasexual fighting to determine their first mate (Watson: *Behav. Ecol. Sociobiol.*, 1990, **26**, 77–90). Phenotypic attributes of first mates did not predict their fertilization success. In contrast, copulatory vigour and weight (uncorrelated traits) were among nine factors (out of 23 tested) that predicted the fertilization success of later, secondary mates. Secondary mates were seldom required to fight other males; variation in their reproductive success was apparently due to female choice. The value of copulatory vigour and weight in predicting the outcome of fights between males suggested that intrasexual and intersexual selection are in accord. First mate sperm precedence may have evolved because intersexual selection of secondary mates is a weaker test of male quality than the purely combative process that determines first mates. However, when by chance only inferior males discover a virgin female, her first mate will merely be the best of a bad lot. Such ‘errors’ in the selection of primary sires may underlie the adoption of a bet-hedging strategy, whereby genetically based correlations in viability among offspring are reduced, especially when selection fails to prevent fertilizations by a low quality male. Further, examination of linyphiid genitalia suggested a female mechanism to sequester male ejaculates, allowing control of sperm precedence and possibly reduced risks of venereal infection.

Multiple mating by females and mixed paternity within broods has been documented in a variety of taxa (Thornhill & Alcock 1983; Brown & Brown 1988; Sherman & Westneat 1988). However, particularly in systems lacking material investments by mating males, the functions of this fundamental female behaviour are still debated (e.g. see Crozier & Page 1985; Sherman et al. 1988). In this paper I present the results of a 3-year study of correlates of male fertilization success in the sierra dome spider. These data are used to evaluate three hypotheses concerning genetic benefits of polyandry. I present additional observational and experimental data on the roles of intrasexual competition and female choice in the female spider’s overall strategy of sire selection. Finally, I present observations on the structure of female and male genitalia and propose a mechanism whereby females might control the fate of male ejaculates.

Sierra dome spiders occur in dense local populations, usually near water, in mountainous regions of western North America. They have an annual life-cycle, breeding from late June through to late August. Females are sedentary, easily marked, and usually continuously observable.

Ninety-eight per cent of all females mate with the first male they encounter after sexual maturation ($N=183$ females; Watson 1990). Although females reject many opportunities to remate, they typically do mate more than once ($\bar{X} \pm SD = 2.3 \pm 0.98$ total matings, $N=104$ females) during the 1–2 month adult instar prior to oviposition. Males must normally fight other males to become a female’s first mate, but such combat is less important in determining secondary mates (Watson 1990). Multiple paternity is common (16% of broods based on direct inspection of electrophoretic data, 34–49% and 96% based on the Empat and Bipat paternity algorithms (see below), respectively; Watson 1991). Several lines of evidence indicate that females exert

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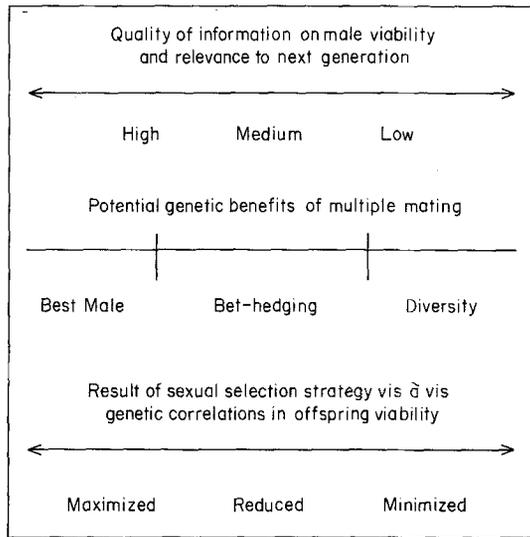


Figure 1. Potential genetic benefits of polyandry (centre) and the selective circumstance (top) and genetic result (bottom) associated with each strategy. The strategy chosen depends on the quality of information females can obtain about the genetic constitution of their mates that can be expected to be relevant to the viability of their offspring. If all else is equal, pressure on females strictly to diversify their broods is transformed into pressure to bet-hedge as the predictability of the value of male genes for the next generation increases from nil to a biologically significant level. Females should not play at a 'sweepstakes' when they can place a bet based on real, albeit imperfect information. Compared with diversification, bet-hedging increases expected offspring viability while still controlling variance that would arise from an overly strict reliance on fallible assessments of mates. Bet-hedging provides a contingent safety mechanism; genetically based correlations in offspring viability are reduced most when a genetically odd male (relative to those normally 'passed' by processes of quality assessment) slips through the sexual selection screening process. Females should attempt to raise expected viability even further by abandoning bet-hedging for a best male strategy whenever highly reliable quality assessments are possible.

substantial control over sperm precedence (Watson 1991).

Polyandry has nutritional benefits for females. These stem from improved foraging efficiency of females during copulation compared with pre-copulatory phases of pairings when males, always the dominant sex, steal most prey (Watson 1988). However, enhancement of foraging efficiency cannot explain (1) the non-random manner in which females use sperm obtained in multiple mating (see Watson 1991 and below) or (2) the observation that both satiated females and those that have experienced very low prey availability (i.e. individuals with nothing nutritional to gain from remating) still mate multiply, albeit at a lower level, than females with a history of moderate foraging success. This latter tendency exists in spite of the risks of disease and predation associated with remating (Watson 1988; unpublished data). It thus makes sense to consider additional genetic benefits of polyandry in this spider.

HYPOTHESES

All the hypotheses about the genetic benefits of polyandry assume that female choice can result in either increased mean or reduced variance in female fitness via genetic effects on the viability of offspring. As an aid in distinguishing the hypotheses I find it helpful to consider two related factors: (1) the quality of information available to females about the heritable viability of mates and (2) desirable levels of genetically based correlation in viability among a female's offspring (Fig. 1). Whether there is selection on females to adopt a best male, pure genetic diversity, or genetic bet-hedging strategy hinges on the information they can obtain about the genetic constitution of their mates relevant to the viability of offspring.

Best Male

Under this hypothesis females mate multiply in order to replace the sperm of earlier mates with

those of a later, superior mate. The hypothesis implies that females promote correlations in viability among offspring, because they can select a single sire whose genes will reliably benefit their offspring. If females control sperm precedence, then multiple paternity should be minimal. Further predictions include (1) a strong bias in fertilization success towards later mates and (2) an association between male fertilization success and specific values of favoured male traits, that is, stabilizing or unidirectional sexual selection.

Genetic Diversity

This hypothesis states that females mix sperm from different males in order to increase the genetic diversity of their offspring (Williams 1975; Parker 1984). This formulation is difficult to evaluate empirically, because any system of multiple paternity increases diversity within a brood. It is even impossible to specify a null hypothesis with distinct predictions, such as random mating or sperm use, as for example might occur if polyandry arose purely through genetic correlations with males (Halliday & Arnold 1987; Arnold & Halliday 1988; Sherman & Westneat 1988). Therefore, for the purposes of this study, I take the diversity hypothesis as pertaining only to situations in which females cannot predict which males carry genes that will increase offspring viability. In other words, under this hypothesis females do not possess sire selection criteria capable of modulating the probability that favourable genes are passed into the next generation. The sexual behaviour of such females evolves in a classic 'sweepstakes' context, functioning as an extension of the diversifying nature of sexual reproduction itself. These females should behave so as to acquire a set of sires representing a wide range of morphological, physiological, or behavioural life-history strategies.

When females control sperm precedence as well as mate selection, they are free to engage in secondary matings for direct benefits, followed by cryptic sire selection to boost genetic benefits. This is important, because if the females' mate selection is modulated so as to augment phenotypic benefits, it may not be well designed to produce maximal diversity of offspring genotypes (or other genetic benefits). This is especially true when, as in the sierra dome spider, mating with any male brings direct benefits (see above). Thus, random or equitable sperm use are not necessarily effective ways

for females to transmit the widest range of genetic variation to offspring. Convincing support for the diversity hypothesis would entail female sperm use resulting in an even distribution of fertilizations among subsets of mates that are substantially different from one another, regardless of the number of males in each subset. Any unique mate would obtain a certain proportion of the available fertilizations for himself, while common mates would share a similar portion with other mates of their phenotypic subset. This would result in higher mean fertilization success for unique males, regardless of their position in the female's mating order. Most important is the prediction that a given mate's fertilization success be governed mainly by how unique he is, whether or not this is based on large or small values of the relevant phenotypic trait. Diversifying females display bidirectional or disruptive selection.

Genetic Bet-hedging

Under this hypothesis, females mix sperm from several mates in order to reduce the detrimental effects of occasional faulty choices of sires. The bet-hedging hypothesis pertains when females possess and apply consistent sire selection criteria that increase the probability of delivering good genes to offspring. However, either because these criteria are imperfect or the circumstances for implementing them are suboptimal, mistakes can be made. Bet-hedging females behave as though they know the limitations of their sire selection criteria.

The hypothesis predicts that male fertilization success will be unidirectionally related to values of male fitness-related traits, because bet-hedging females do not seek genetic diversity per se in their offspring. They act to reduce correlations in viability among offspring only to limit the number of offspring disabled by a poor choice of sire. The largest correlation reductions occur just when a female's sire selection criteria have led to a particularly bad decision. In contrast, diversifying females use every mating to minimize viability correlations among offspring.

METHODS

The data I use to evaluate correlates of male fertilization success are based on comprehensive sexual histories of 44 marked, free-living, multiply mated

females, followed by protein-electrophoretic estimates of paternity for their 113 mates (Watson 1991). These data were collected in 1982, 1984 and 1985 at the Flathead Lake Biological Station, Polson, Montana, U.S.A., using frequent scan sampling (Watson 1991). Since all fertile matings (i.e. those including an 'insemination phase'; see Appendix) last over 2 h and occur during daylight, the hourly scans I performed between 0800 hours and nightfall every day, usually with the help of two assistants, enabled me to observe all matings. Each female mated with two to five males (25 with two mates, 14 with three, three with four, and two with five, $\bar{X} \pm SD = 2.8 \pm 0.94$). Females either mated ad libitum with spontaneously visiting males ($N=24$), or were constrained to two matings with males I chose on the basis of body size ($N=20$; termed controlled-mating females: Watson 1991). All matings were observed and males captured for 42 (95.5%) of the females, while one to three mates eluded capture for two females (0.5%). I determined electrophoretic phenotypes at one or more isozyme loci for an average of 20.4 offspring per female ($SD = 10.1$).

I collected experimental data on phenotypic correlates of male fighting ability at the same site in 1989 (see below). Morphologies of genitalia were studied in 1983 (dissections of *L. marginata* and *L. litigiosa* epigyna, which includes the female copulatory organ and spermathecae), 1988 (serial sections of *L. litigiosa* epigyna) and 1989 (dissections of male pedipalps; both species).

Paternity Estimates

Starch gel electrophoresis of mothers, mates and offspring formed the basis for the allozyme studies used to estimate paternity (Watson 1991). Six polymorphic loci were used (esterase (two alleles), isocitrate dehydrogenase (2), triose phosphate isomerase (2), guanine reductase (2), 6-phosphoglucose dehydrogenase (3) and adenosine deaminase (2)), but only one or two allozyme systems were variable among the two to five mates of individual females. Consequently, only 10% of all offspring could be assigned a father through direct inspection of allozyme phenotypes. I therefore employed two statistical algorithms, denoted 'Bipat' and 'Empat', to estimate each male's fertilization success. Bipat yields a unit-free, relative index of paternity (Watson 1991). Empat is a maximum likelihood estimator (Dempster et al. 1977; Dickinson 1986;

Dickinson & McCulloch 1989), which is interpreted as the percentage of a brood sired by a given male (e.g. see Kukuk & May 1988).

Regression Procedures

To identify male traits associated with fertilization success, I used multivariate regression of estimated paternity on: (1) mating circumstances including information about the sexual and foraging history of individual females (Appendix); (2) measured male phenotypic characters (Appendix); and, in analyses concerning the genetic diversity hypothesis, (3) estimates of unmeasured male phenotypic 'factors' (sensu Crespi 1990), such as overall body size or copulatory vigour. Regression-based approaches to studying fitness/phenotype relationships are discussed in Lande & Arnold (1983), Mitchell-Olds & Shaw (1987), Crespi & Bookstein (1989) and Crespi (1990). Grafen (1988) discussed the effectiveness of the method for understanding biological adaptations. Various changes in my analytical procedures have led to small changes from the results in Watson (1988): statistics reported here take precedence.

Residuals from linear models with Empat as the dependent variable consistently deviated from normality. Therefore I performed logistical regression (logit) analyses (Steinberg 1985; Hosmer & Lemeshow 1989) using a trichotomous categorization of Empat as the dependent variable, denoted below as 'C\Empat' (C\Empat = 1 when $Empat \leq 0.33$, 2 when $0.34 \leq Empat \leq 0.66$, or 3 when $Empat \geq 0.67$).

Statistical significance

When presenting results of a set of statistical tests, I report the individual significance of each test as well as a combined significance level calculated via the sequential Bonferroni method (Rice 1989). Throughout the text, '*P*' refers to the significance level of an individual statistical test and '*P_{sb}*' to its Bonferroni adjustment. Since I evaluated the influence of many variables on paternity, I did not calculate all adjustments simultaneously. Instead, I broke the variables into five categories (see Appendix) and adjusted within each category.

Appreciable noise probably exists in the paternity estimates Bipat and Empat, because predicted electrophoretic phenotypes of the offspring sired by different mates of a female were usually not

qualitatively distinct (i.e. only expected offspring allomorph frequencies differed, and occasionally even these were identical among some mates). Thus I suggest that reasonable trends in the relationships between the paternity estimates and predictors are noteworthy, although some warrant further verification.

As an aid to interpretation of linear regression coefficients, I report the percentage of the residual variance explained by particular independent variables (denoted $\%R^2_a$). This quantity is defined as

$$\%R^2_a = \{[R^2_a(\text{full model}) - R^2_a(\text{base model})] / [1 - R^2_a(\text{base model})]\} \times 100$$

where R^2_a is the degrees-of-freedom adjusted coefficient of determination, and 'full' and 'base' refer to the model with the variable of interest included, and the covariate only model, respectively. For logit models I report independent variable derivatives (Steinberg 1985). These show how a unit change in an independent variable affects the probabilities of low, medium and high paternity.

Covariate selection

I screened 11 variables concerning female mating history and mating circumstances (Appendix) for use as covariates in models predicting paternity. Covariate selection was based on: (1) existence of a plausible reason why the variable might affect paternity independently of any process of female choice; (2) a significant partial regression coefficient; and (3) lack of 'degrading' collinearity with already chosen covariates or male phenotypic variables (see Belsley et al. 1980 and Wilkinson 1988 for collinearity diagnostics).

Evaluation of the Diversity Hypothesis

To test the prediction of the diversity hypothesis that unique mates of individual females have higher fertilization success than mates that resembled one another, I used data from females that mated three or more times ($N=20$) to analyse relationships between paternity and six male 'uniqueness indices'. I derived these indices from three groups of male phenotypic characteristics: (1) size, which incorporates weight, body length, cephalothorax width, body condition and the number of missing or deformed legs; (2) precopulatory courtship, which includes courtship intensity and duration, attentiveness towards the female and the number of missing or deformed legs; and (3) preinsemination

phase copulatory performance, which includes duration, rate of successful intromissions, estimated number of successful intromissions and the ratio of failed to successful intromissions. For each group of characteristics, I calculated the uniqueness indices in three steps: (1) reduction of the data in each character group via factor analysis; (2) calculation of continuous uniqueness descriptors from the factor scores; and (3) categorization of each male's descriptors as 'uniquely low', 'common', or 'uniquely high'.

In the factor analyses the first two principal components were retained, and final factor scores generated via varimax rotation (Kleinbaum et al. 1978). This generated six factor scores per male in the sample ($N=70$). For each male, I calculated two uniqueness descriptors from each factor score: (1) the average difference between the male's score and those of all the other mates of the same female ($\bar{X}D$); and (2) the corresponding standard deviation (SD). Descriptor pairs were taken as positive or negative based on the sign of $\bar{X}D$. Finally I assigned each male to one of three categories according to where his descriptors for a particular character group fell in relation to the upper and lower quartiles (LQ and UQ, respectively) of the distribution of such descriptors for all 70 males in the sample: 'common', if $LQ < \bar{X}D < UQ$, or $SD \leq LQ$; 'uniquely low', if $\bar{X}D \leq LQ$ and $SD > LQ$, or $\bar{X}D < 0$ and $SD \geq UQ$; 'uniquely high', if $\bar{X}D \geq UQ$ and $SD > LQ$, or $\bar{X}D > 0$ and $SD \geq UQ$.

To determine whether 'unique' mates attained greater fertilization success than 'common' mates, I estimated the following model

$$\text{Paternity estimate} = \beta_0 + \beta_1(\text{Numpalp}) + \beta_2(\text{Mating status}) + \beta_3(\text{Uniqueness category})$$

where Mating status coded whether a male was a first or secondary mate, and Numpalp the number of pedipalps (one or two) the male used in copulation. Since principal components 1 and 2 were used to represent variation in each of the three suites of traits, six models were estimated, once with Bipat, and again with C\Empat as the dependent variable. I followed each estimate with post hoc tests of the following pairs of hypotheses.

(1) Test 1. Ho: paternity of males with uniquely high index values = paternity of common males. Ha: paternity of males with uniquely high index values > paternity of common males.

(2) Test 2. Ho: paternity of males with uniquely low index values = paternity of common males.

Ha: paternity of males with uniquely low index values > paternity of common males.

I performed one-tailed tests, because the diversity hypothesis predicts that unique individuals will have greater fertilization success than common individuals. The hypothesis also predicts higher fertilization success for males with either uniquely high or uniquely low descriptor values. Thus if the diversity hypothesis is true for a set of male characters, the null hypotheses should be rejected in both post hoc tests 1 and 2.

Fights Between Males

To assess agreement between intrasexual and intersexual selection, I measured male preinsemination phase intromission rates and body weight followed (next day) by experimental fights between the males. All fights ($N=37$) took place on female-occupied webs in the field. Since I knew already that the relative weights of contestants is a strong predictor of the outcome of fights (Watson 1990), I minimized the influence of weight in these fights in the hope that this would help reveal the predictive value of intromission rate. I did this by selecting pairs of adversaries from the available pool of males that were similar in weight (mean \pm SD absolute difference between contestants was 1.2 ± 0.9 mg), but quite different in their intromission rates (mean absolute difference was 6.1 ± 3.9 intromissions/3 min). Also, in 33 fights (89%) I matched males such that the individual enjoying the residual weight advantage had the lower intromission rate, so that if intromission rate predicted the probability of winning a fight there would be no possibility of a confound with weight.

I obtained males and their intromission rates each day by (1) searching the study site for copulating pairs, (2) ensuring that the male had 30–40 min of 'warm-up' time to reach a steady intromission rate, (3) counting the number of successful and unsuccessful intromissions the male achieved in an undisturbed 3-min period, and (4) capturing the male, weighing him to 0.1 mg, and putting him in a petri dish with moist tissue.

Males collected on a given day either fought on the next day or were released. Each male was marked, either blue or yellow, on the tibia of the posterior leg just before the trial. I introduced the males onto the female's web 15–25 min apart, the order of introduction being determined by coin flip, and observed them until one of the males was

forced from the web by his rival or was killed. The data were analysed by logistical regression with either fight outcome (i.e. blue male wins or loses) or degree of fight escalation (i.e. non-contact display only or contact fighting) as the dependent variable. See Watson (1988) for details of fighting behaviour.

RESULTS

Covariate Selection

The only variable that met the criteria for use as a covariate was the number of pedipalps used by a male in copulation (i.e. Numpalp; see Appendix). Thus, the base model used in analyses of the factors affecting the paternity of secondary mates was

$$\text{Paternity estimate} = \beta_0 + \beta_1(\text{Numpalp})$$

Relationships of all the other variables with the fertilization success of secondary mates (Appendix) were evaluated by adding them to the base model and re-estimating.

In analyses involving only first mates I did not use Numpalp as a covariate, because of its apparent irrelevance to first mate fertilization success. In tests of the genetic diversity hypothesis, for which I pooled data on first and secondary mates, mating status (i.e. first or secondary) was added to the above model as a second covariate. The influence of mating status on paternity has already been established (Watson 1991).

Paternity of First Mates

None of the 15 predictors of fertilization success potentially relevant to first mates (Appendix) had any relationship with the Empat or Bipat estimates of paternity (all $P \geq 0.125$). Thus, first mates achieve comparatively high fertilization success regardless of their size relative to secondary mates, absolute physical and behavioural attributes, or even their use of one versus two pedipalps in copulation.

Paternity of Secondary Mates

Bipat

With Bipat as the dependent variable there was marginal support for the influence of two factors on the fertilization success of secondary mates, namely, the duration of the preinsemination phase of copulation and cephalothorax width (Table I).

Table I. Predictors of paternity for secondary mates using linear analyses with the Bipat paternity estimate as the dependent variable and the number of pedipalps used in copulation (Numpalp) as covariate*

Male attribute or mating circumstance	β	SE	<i>N</i>	<i>P</i>	P_{sb}	% R^2_a
Covariate Numpalp	0.193	0.087	65	0.029	0.206	5.80
Duration of preinsemination phase copulation	-0.073	0.030	61	0.017	0.068	7.88
Cephalothorax width	0.353	0.161	57	0.033	0.130	6.51
Preinsemination phase intromission rate	0.008	0.005	54	0.074	0.221	4.29
Body condition	0.236	0.135	57	0.087	0.260	3.63
Weight	0.009	0.006	65	0.162	0.326	1.59
≥20% heavier than first mate	0.066	0.069	65	0.343	0.343	-0.11
Precopulatory courtship intensity	-0.014	0.043	56	0.748	1.000	-1.74
Days since last precipitation	0.001	0.006	65	0.924	1.000	-1.59

*Variables that were significant ($P < 0.05$) in logit analyses (see Table II) are included. P_{sb} are adjusted significance levels and % R^2_a are percentages of base model residual variance explained by each variate (see Methods).

Two additional male attributes had relationships with Bipat with fairly low *P*-values: preinsemination phase intromission rate and body condition. Scatterplots and box-whisker plots of Bipat versus all 23 variables tested are provided in Fig. 2.

C\Empat

In logit analyses with C\Empat as the dependent variable, there were strong indications that two variables concerning preinsemination phase copulation were related to paternity: duration and intromission rate. A male's absolute weight and his weight relative to his female's first mate, as well as precopulatory courtship intensity had marginally significant positive relationships with paternity. Finally, there was a suggestion that the number of days since the last precipitation might positively affect paternity (Table II). Considering the independent variable derivatives, these effects mostly apply to a male's odds of low versus high paternity; conclusions are weak with regard to the influence of male attributes on the odds of medium versus low or high paternity. Estimates of the logit models generally corroborated preliminary linear analyses of Empat. However, in the linear analyses neither (1) precopulatory courtship intensity nor (2) the number of days that had elapsed since the last precipitation showed an association with paternity. Table III provides correlations amongst the predictors listed in Tables I and II to help assess levels of redundancy.

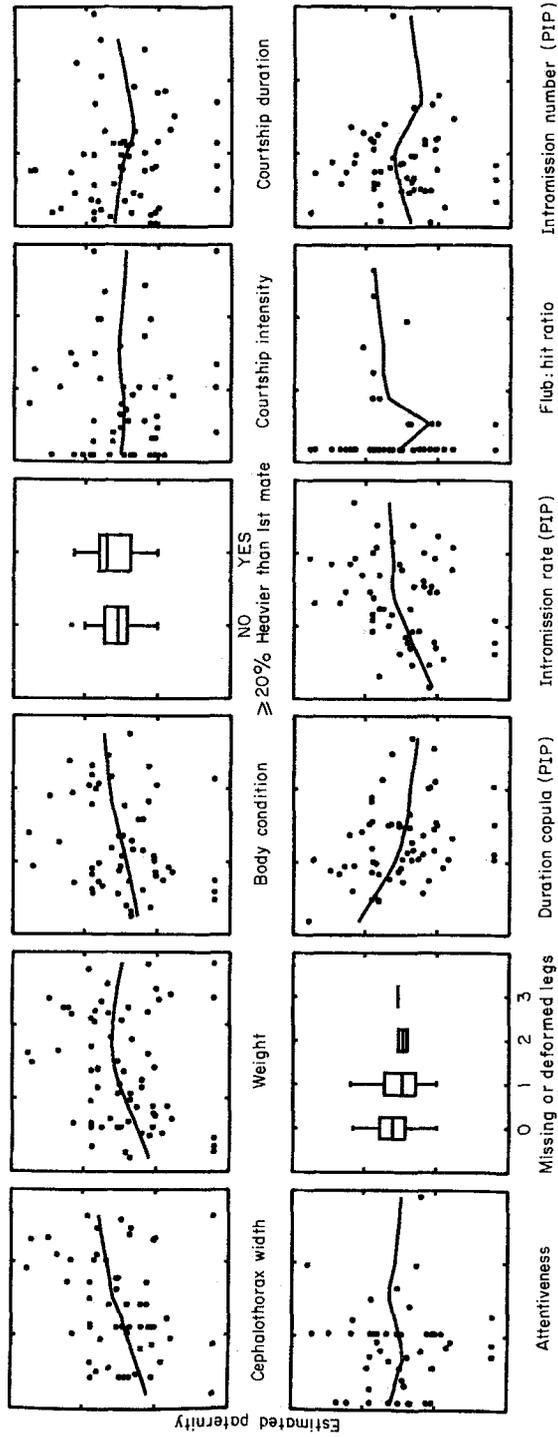
Overall, the duration of preinsemination phase copulation had the strongest link to paternity; this was a negative relationship that was not originally

predicted. The other predictors had relationships with paternity indicating that females favour larger, more active and dexterous secondary mates as sires.

Genetic Diversity Hypothesis

No analyses provided even tenuous support for the prediction of the diversity hypothesis that both 'uniquely high' and 'uniquely low' values of a given trait should be associated with greater male fertilization success than 'common' values. Logit analyses were not possible for three of the six factors, because certain levels of C\Empat were not observed under some uniqueness categories. Specifically, no individuals with high paternity had uniquely low values of the first principal component of size or the first principal component of courtship performance, and no males with medium paternity had uniquely high values of the second principal component of size. The three feasible analyses yielded predicted probabilities of low, medium and high paternity that did not differ between the uniqueness categories (pairwise comparisons using the Tukey-Kramer test; all $P \geq 0.25$).

There are strong indications that mates with unusually high values of the first principal component of size had greater paternity than common individuals within the same mate group ($P_{sb} = 0.012$ and $P_{sb} = 0.024$ under Bipat and C\Empat, respectively), and marginal support that mates with low values of this factor had lower paternity ($P_{sb} = 0.057$ and 0.075). This factor loaded heavily on cephalothorax width and body length, and moderately on body weight. There was also marginal



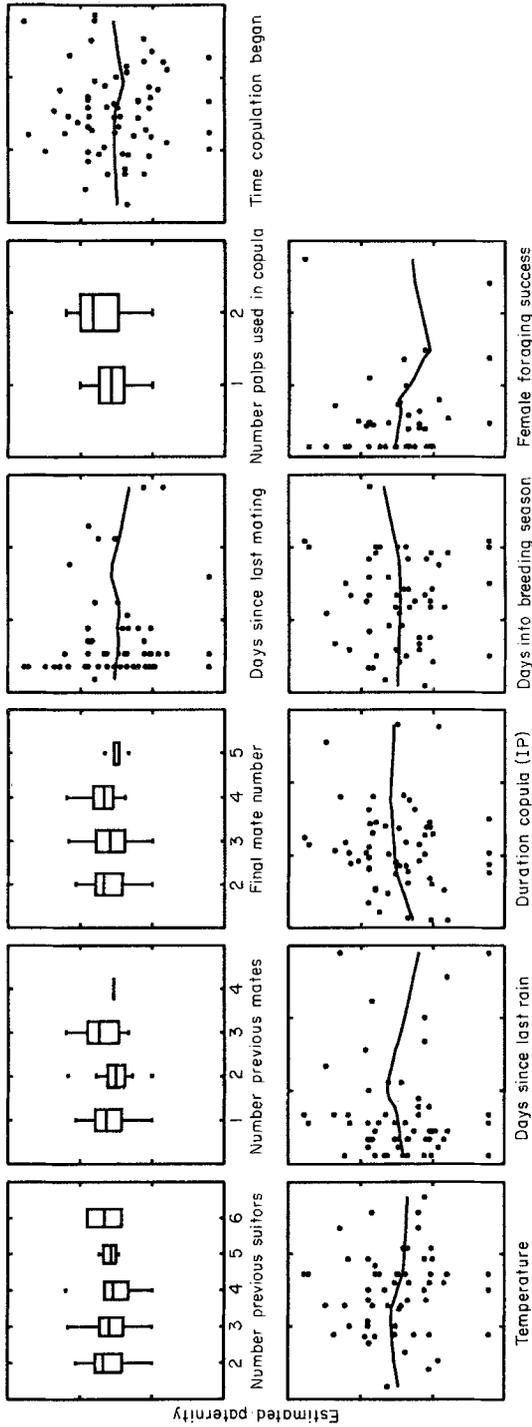


Figure 2. Raw data plots of estimated paternity (Bipat) versus the 23 variables examined in this study. (The plots appear in the same order as in the Appendix, where they are defined.) The X and Y axes of all plots have low values positioned nearest the origin. The scatterplots include a line drawn according to the 'LOWESS' algorithm (Cleveland 1979, 1981). This produces a smooth of the data by running along the X-values and calculating predicted Y-values from a distance-weighted average of observed Y-values (90% of all points were used to calculate each predicted value). LOWESS does not force a model to the data and thus helps reveal the true form of the X: Y relationship, such as features that could suggest stabilizing or disruptive sexual selection (i.e. an intermediate peak on the Y-axis or two peaks on the Y-axis at widely divergent values of X, respectively). Box-whisker plots (Velleman & Hooglin 1981) are drawn for categorical variables. These show medians (marked by centre vertical line), hinges (box edges), and values 1.5 and 3 times distant from the interquartile range (whisker ends and black dots, respectively). PIP: Preinsemination Phase; IP: Insemination Phase.

Table II. Predictors of paternity for secondary mates using logistic regression analyses with C\Empat as the dependent variable and the number of pedipalps used in copulation (Numpalp) as covariate*

Male attribute or mating circumstance	Statistics				Derivatives		
	χ^2	<i>P</i>	<i>P</i> _{sb}	<i>N</i>	1	2	3
Covariate Numpalp	9.22	0.010	0.070	68	-0.40	0.15	0.24
Duration of preinsemination phase copulation	12.26	0.002	0.009	64	0.22	-0.10	-0.12
Preinsemination phase intromission rate	8.38	0.015	0.045	56	-0.02	0.01	0.02
Precopulatory courtship intensity	6.98	0.031	0.122	59	-0.04	0.09	-0.05
≥20% heavier than first mate	6.70	0.035	0.140	68	-0.28	0.09	0.18
Weight	6.38	0.041	0.140	68	-0.02	0.01	0.02
Days since last precipitation	6.10	0.047	0.284	68	-0.01	0.00	0.01
Cephalothorax width	4.09	0.129	0.259	60	-0.56	0.24	0.32
Body condition	3.99	0.136	0.259	60	-0.28	-0.03	0.30

*Variables that were significant ($P < 0.05$) in linear analyses (see Table I) are included. Independent variable 'derivatives' show predicted effects on the probability of low, medium or high paternity (i.e. C\Empat = 1, 2, 3, respectively). *P*_{sb} are adjusted significance levels (see Methods).

support that mates scoring unusually high in the second principal component of copulatory performance, which loaded mostly on the duration of preinsemination phase copulation and the number of intromissions, had lower fertilization success (under Bipat only; $P_{sb} = 0.088$). These results corroborate the findings that intersexual selection is directional.

All females included in the above analyses of the genetic diversity hypothesis mated three or more times. For twice-mated females, the genetic diversity hypothesis would be bolstered by evidence of a more equitable distribution of fertilizations when the two mates differ greatly than when they are similar. (If the mates are similar an ancillary influence upon sperm precedence might predominate, such as a first versus secondary mating status.)

This prediction was refuted for size-related male traits by a controlled-mating experiment (Watson 1991). The first and second mates of 20 controlled-mating females were extremely different in size compared to those of six females that mated twice ad libitum. Nevertheless, the paternity of first mates of controlled-mating females was indistinguishable from that of first mates of the ad libitum mating females under Bipat ($\bar{X} \pm SD = 0.996 \pm 0.303$, $N = 20$ versus 1.023 ± 0.188 , $N = 6$, $P = 0.67$) and Empat (0.625 ± 0.393 , $N = 20$ versus 0.787 ± 0.401 , $N = 6$, $P = 0.39$).

Selection on First Versus Secondary Mates

Relative weight was a predictor of the outcome of 37 staged fights ($\chi^2 = 4.04$, $df = 1$, $P = 0.044$). I

was surprised by the strength of the effect given that the contestants in these fights were much more closely matched in weight than in my earlier observations (Watson 1990). Thus male weight appears to have a positive association with fertilization success under both intrasexual and intersexual selection (see Table II).

Perhaps because males with higher intromission rates were at a weight disadvantage in 89% of the fights, relative intromission rates did not predict winners of fights ($\chi^2 = 0.78$, $df = 1$, $P = 0.380$). However, the intromission rate of lighter contestants was a predictor of whether a fight advanced from the non-contact display stage with which all fights begin, to full-contact wrestling or grappling/biting (Fig. 3; $\chi^2 = 4.17$, $df = 1$, $P = 0.041$). Indeed, the most stunning 'comebacks' and 'determination' witnessed in the course of these fights involved males that, though underdogs by weight, had very high preinsemination phase intromission rates. By favouring secondary mates with high intromission rates, female choice may be promoting paternity by males that are more likely to fight ferociously.

By using both weight and intromission rate as sire selection criteria for secondary mates, females might pick up on independent suites of traits that together comprise powerful predictors of male fighting ability. Indeed, male weight and preinsemination phase intromission rate are uncorrelated ($r = 0.115$, $N = 39$, $P = 0.487$, and $r = 0.090$, $N = 51$, $P = 0.528$ for males copulating with two pedipalps or one, respectively).

Table III. Spearman correlations among predictors of paternity (covariate and variates) shown in Tables I and II

	Numpalp	Cephalothorax width	Weight	Body condition	≥20% heavier	Courtship intensity	Duration copula	Intrmission rate
Numpalp	—							
Cephalothorax width	0.262*	—						
Weight	0.136	0.848†	—					
Body condition	-0.021	0.506†	0.872†	—				
≥20% heavier than first mate	0.171	0.558†	0.701†	0.583†	—			
Precopulatory courtship intensity	-0.063	-0.211*	-0.231*	-0.200*	-0.276*	—		
Duration of preinsemination phase copulation	-0.101	-0.030	-0.019	-0.018	0.134	-0.538†	—	
Preinsemination phase intrmission rate	0.313**	0.229*	0.170	0.055	0.046	0.119	-0.224*	—
Days since last precipitation	-0.067	0.301**	0.272**	0.180*	0.084	0.159	-0.205*	0.158

* $P \leq 0.05$; ** $P \leq 0.01$; † $P_{sb} \leq 0.05$.

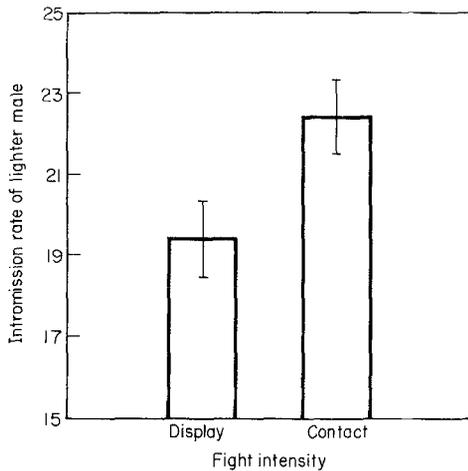


Figure 3. Mean intromission rates (\pm SE) of lighter weight contestants in fights that ceased after non-contact display versus fights that escalated to a contact match ($N=12$ and 24 , respectively; pooled variance $T=2.053$, $df=34$, $P=0.048$).

Table IV. Numbers of fights between males that ended after a period of non-contact display or after escalation to contact fighting behaviour on webs of nearly-mature/virgin versus mature/mated females

Fight intensity	Female status	
	Virgin	Mated
Display only	2 (5.5)	9 (5.5)
Contact fighting	14 (10.5)	7 (10.5)

$\chi^2=7.20$, $df=1$, $P=0.007$. All virgin females were showing 'associative' behaviour (sensu Watson 1990) prior to the fight. Numbers in parentheses are expected values.

Data from these fights also revealed that contests on webs of nearly mature females are more intense than on webs of mature, already-mated females (Table IV). This effect adds to a previously established mechanism whereby nearly mature females enhance competition between males by eliciting prolonged guarding attempts (Watson 1990), and further reduces the importance of intrasexual selection in influencing the paternity of secondary mates compared with its crucial role for first mates.

Internal Genitalia

In female sierra dome and filmy dome, *L. marginata*, spiders, a pair of long spiralling sperm

ducts, far longer than necessary to accommodate the short intromittent organs of the male, lead towards each of the spermathecae. These ducts seem to be formed from folds on the inside wall of the heavily sclerotized epigynum. As the ducts approach the spermathecae they become fleshy. Dissections of female *L. marginata* revealed an anatomical feature in the ducts, very near the spermathecae, suggesting a mechanism whereby females could control sperm precedence, namely, a sharp elbow within a minute fleshy portion of the pre-spermathecal sperm ducts. The duct walls within the elbow region had fine radial striations. The layout of female *L. litigiosa* genitalia has so far prevented me investigating this species fully but serial sections of epigyna also revealed sharp pre-spermathecal curvatures of the sperm ducts. Note that both these species are very similar in overall morphology, mating system and ecology and are likely to have comparable mechanisms of sperm control.

DISCUSSION

Evaluation of Hypotheses

Best male

The most stringent system that female sierra dome spiders have of testing a male's quality is probably that to which first mates are subjected (Watson 1990, 1991). Conservatively low estimates indicate that first matings, on average, are preceded by two rounds of fighting (i.e. sequential encounters amongst three males on the penultimate female's web). The highest estimates of fighting between males preceding secondary matings indicate that, at most, 59% of secondary mates fight once before mating. Individual fights are also more intense on webs harbouring penultimate instar or mature unmated females. The intersexual courtship that precedes secondary matings is unlikely to test male vigour as well as intrasexual fighting does. If females were using a best male strategy, there would be no reason for them to use the sperm of later males. Thus, the hypothesis is refuted by the observed frequency of multiple paternity.

Further, the existence of a selection strategy such as the sierra dome spider's consisting of two choice mechanisms with different powers of quality control, is hard to interpret under the best male hypothesis. When would it ever be advantageous to bias fertilizations in favour of a mate subjected to

the weaker test? One circumstance might be when a weakly tested mate seems vastly superior to a male that passed the more stringent test. But, for the sierra dome spider this idea is contradicted by experiments in which females mated first with a small male and then with an exceptionally large, vigorous male: first mates were still favoured (Watson 1991).

Genetic diversity

Paternity estimates for mates with uniquely high or low values of phenotypic traits versus mates with relatively redundant phenotypes did not differ. This finding is not in line with the prediction of the diversity hypothesis that unique males should fertilize more eggs. This conclusion is limited, of course, to the traits of size, courtship vigour and preinsemination phase copulatory performance.

An additional point against the diversity hypothesis came from comparing sperm use by ad libitum and controlled-mating females that had mated twice. Controlled-mating females had mates that differed far more in size-related traits, but first mate sperm precedence in these females was not diminished (Watson 1991). The diversity hypothesis would have been supported if sperm use had been more equitable when the phenotypes of mates differed greatly. Overall, multiple paternity must increase the genetic diversity of broods, but there is no evidence that this is more than a secondary effect in sierra dome spiders, because of the apparent lack of specific design in female behaviour to produce disruptive sexual selection.

Genetic bet-hedging

Unidirectional sexual selection for large size and weight, and high intromission rates during preinsemination phase copulation, coupled with multiple paternity, is in line with the bet-hedging hypothesis. The hypothesis that fertilizations by secondary mates is a female tactic to compensate for modest uncertainty surrounding the quality of her first mate is the best supported explanation for the function of genetic polyandry in sierra dome spiders.

Further Support for Bet-hedging

In mating systems where individual females use more than one mechanism for screening potential sires, the bet-hedging hypothesis predicts that these

mechanisms will be in agreement, that is, males that do well under one test will be more likely to fare well under the alternative. Further, a given male's fertilization success should be influenced by the stringency of the mechanism by which he was assessed, because males that pass harder tests are better bets. Finally, interesting examples of bet-hedging, that is, behaviour that functions to reduce fitness variance, should demonstrate an inherent sacrifice in mean fitness; in the absence of such costs, variance-reducing mechanisms are always favoured (Seger & Brockmann 1987).

Selection of sires by female sierra dome spiders operates via temporally separate processes of competition between males and direct female choice. Females depend completely on the outcome of intrasexual competition to determine their first mate (Watson 1990), usually the main sire of the offspring (Watson 1991), a conclusion now corroborated by analyses that show no associations between fertilization success and phenotypic attributes of first mates. In contrast, the fertilization success of secondary mates is associated directly with male attributes, while fighting plays a minor role. As expected under the bet-hedging hypothesis, these two mechanisms of sire selection agree in one, and possibly two, ways. Their clearest concordance concerns male body size. Size has a positive influence on the fertilization success of secondary mates, and is also a correlate of fighting ability and thus the probability of becoming a first mate. The second area of agreement rests on a correlation between male preinsemination phase intromission rates and male fighting performance. Intromission rates are positively correlated with (1) the paternity of secondary mates and (2) how vigorously and riskily males fight. The latter plausibly affects the probability of becoming a first mate.

There is a suggestion that the sire selection strategy of female sierra dome spiders reduces mean fitness, because multiple paternity reduces the proportion of fertilizations by the female's most harshly tested (i.e. first) mate. As expected under the bet-hedging hypothesis, paternity is principally biased towards first mates (Watson 1991), while ancillary biases exist among secondary mates.

Advantages of Bet-hedging

For sierra dome spiders it is merely likely that a given female's first mate has passed a stringent intrasexual test of size and vigour. Since the

stringency of these intrasexual tests probably surpasses that of intersexual evaluations to which secondary mates are subjected, a degree of first mate sperm precedence is understandable. However, intrasexual selection is fallible via sampling error: if a female's luck is bad, only low quality males may find her during those days when she elicits the prolonged guarding necessary for effective intrasexual competition (Watson 1990). This may lead to a first mate that is merely the best of an unimpressive group and a poor sire. Thus female sierra dome spiders could be under pressure to bet-hedge owing to a small unavoidable risk that their first mate was of low quality.

Advantages of Female Choice

If active female choice is a weaker method of sire selection than direct competition between males, why do females use it at all? The answer may lie in the nutritional costs of intrasexual competition for females. Since males are kleptoparasitic, the continuous multi-day guarding connected with effective competition between males imposes a drastic and prolonged restriction on the foraging efficiency of females (Watson 1988, unpublished data). The different mechanisms of sexual selection used to screen first and secondary mates both favour large, vigorous males. However, the intersexual mechanism has reduced foraging costs, because any male guarding a non-virgin female departs within a day, affording the female a break in foraging interference that lasts until another male finds her web, which may be several days hence. Moreover, the act of remating itself decreases prey-stealing by males (Watson 1988), whereas males performing precopulatory courtship or guarding remain kleptoparasitic. Mature females probably cannot afford to employ intrasexual selection to filter prospective mates, because they are under pressure to form eggs quickly, before a predator, cold autumn weather, or disease ruins their reproduction.

Problems in Assessing Males

Sexual behaviour patterns designed to reduce correlations in viability among offspring must arise because sire selection, at least sometimes, yields uncertain results. Several bases for imperfect systems exist, and one or another of these problems probably crop up in most mating systems where females are choosy. Biotic unpredictability rooted

in rapid coevolution between parasites and hosts could render it impossible for a host female to choose a particular male and be sure of having captured all the disease resistance genes necessary to promote survival of her brood (Sherman et al. 1988). Variation in abiotic environmental factors could also lead to unreliable predictions about the value of mate genotypes to future generations (Williams 1975). Genotype-environment interactions can aggravate such difficulties, even reversing the fitness value of certain genotypes in different years or environments.

The expression of traits marking genetic fitness may depend upon the environment in which a male develops. Females will commonly lack information necessary to perform appropriately 'adjusted' assessments of male quality, because relevant aspects of male developmental history are beyond the female's perception. Thus, to a degree, the fitness of a prospective sire will be unknowable.

A female's ability to implement mechanisms of sexual selection might be weakened under certain circumstances. For example, the efficacy of any intrasexual sorting process is limited by the number and quality of males that discover the female during the period of intrasexual competition (as in the sierra dome spider for determination of first mates). Many species-specific scenarios exist.

Non-additive genetic variance in male traits is another problem faced by choosy females, because it can eliminate heritability and cause phenotypic correlations among offspring in the absence of parent-offspring correlations (Maynard Smith 1989). The problem of non-additive variance is aggravated if different combinations of alleles at more than one genetic locus all result in development of a favourable phenotypic trait, but some combinations do so through additive effects while others act non-additively. If females cannot tell whether a male's apparent quality is based on additive or non-additive genetics, then predictions about the value of male genes for the next generation will be less reliable.

Female Control of Sperm Precedence

Linyphiid spiders have a conduit-style sperm transport and storage system (Austad 1984). I have verified this for the sierra dome and the filmy dome spiders. Although conduit morphology may encourage first mate sperm precedence via a first-in first-out mechanism, it cannot explain how such

a bias would be maintained in spite of potential perturbations, such as displacement or mixing of ejaculates. Moreover, conduit morphology cannot explain why certain secondary mates obtain a majority of fertilizations. There is a variety of indirect evidence that female sierra dome spiders actively influence sperm precedence (Watson 1991).

If the pre-spermathecal sperm duct elbows of female linyphiid genitalia have a facultative valve-like function, females could regulate the amount of sperm each of their mates flushes out or injects during copulation. However, female structures that isolate male ejaculates not wanted for fertilizing eggs may accomplish more than a decoupling of mate and sire selection: they may also reduce the risk of venereal infections. In female sierra dome and filmy dome spiders, the long proximal section of the sperm ducts would probably easily hold an ejaculate blocked from passing into the spermathecae. The heavy sclerotization of the ducts might prevent both pathogens and sperm from leaving. The overall structure may be akin to an internal condom with a facultatively leaky tip; non-human organisms may also have discovered that such appliances can serve both birth-control and hygienic functions. Evolutionary analyses of genitalia (e.g. Eberhard 1985) should be extended from the perspective of their potential for venereal disease control. For instance, it would be interesting to know whether the distal tips of these condom-like structures, necessarily constructed of soft tissues, are especially well equipped with intracellular structures for destroying pathogens.

APPENDIX

Putative Predictors of Male Fertilization Success

An asterisk after a variate's name indicates that its influence on paternity was investigated for both first and secondary mates; absence indicates irrelevance to first mates.

Size-related male attributes

Cephalothorax width*: measured to the nearest 0.1 mm across the widest portion of the carapace viewed perpendicularly to the dorsal surface.

Weight*: measured to the nearest 0.1 mg within several hours of capture.

Index of body condition*: the quotient of observed over expected weight, where expected weight is calculated by entering the male's cephalothorax width (CW) into the following equation

$$\text{expected weight} = \exp(-0.230 + 2.744 \ln \text{CW})$$

The constants for this equation are based upon measurement of 111 males collected from the webs of random females over the entire breeding seasons of 1983 and 1984.

Weight class relative to the female's first mate: where the variable is a dichotomous indicator of whether the secondary mate was either (1) less than 20% heavier than the first mate or (2) at least 20% heavier than the female's first mate. The 20% level was chosen before any exploratory data analysis on the basis that this is a weight difference that usually guarantees that the heavier male will win a fight.

Precopulatory courtship

Courtship intensity: the total number of courtship behaviour patterns performed by a male during one or more 30-s all-occurrence samples, divided by the total number of such samples on a given male/female pair. Courtship was observed during every regularly scheduled scan of a female's web. This final measure is based on scans performed between 0800 and 2000 hours and in which (1) the male was not feeding, (2) no fights between males were occurring, (3) no evidence of predator disturbance existed, and (4) copulation had not yet begun. Although courtship behaviour seldom occurs unless both male and female are within the dome of the web, the measure includes observations in which this was not the case. The courtship behaviour patterns used were: web strumming, abdominal twitching, pedipalp waving, touching or probing towards the female, and the silk-laying walk (see Watson 1988).

Duration of courtship: the number of hours lapsed between the male's arrival or 0800 hours (whichever was later) and the onset of copulation.

Attentiveness: the proportion of precopulatory scans in which the male was facing the female. The male was considered to be facing the female if, at the moment the scan began, any part of her body (not her legs) fell within an imaginary 30° wedge extending outwards from the male's face. Relevant scans were defined as for the courtship intensity index (see above), with the additional constraint that both the female and the male had to be present in the dome portion of the web. Since males consistently orient themselves towards the female during active courtship, attentiveness helps measure courtship intensity.

Male's number of missing or deformed legs*: the number of autotomized and improperly developed (e.g. stunted, abnormally long, bent, paralysed) legs. As much of precopulatory courtship involves web strumming displays performed with the anterior two pairs of legs, the number of missing legs should be negatively related to the male's ability to produce precise patterns of courtship strumming, if such exist. Missing legs may also affect the female's perception of male size.

Copulatory Courtship

Descriptions of linyphiid copulation have been presented by several authors (Prószyński 1961; van Helsdingen 1965; Rovner 1967; Austad 1982; Watson 1988). In the sierra dome spider copulation consists of a long series (i.e. hundreds) of separate intromissions. A single intromission involves: (1) precise positioning of a pedipalp upon the female's copulatory organ; (2) expansion of the pedipalp which forces the intromittent organ (i.e. the embolus) into the female; and (3) relaxation of the pedipalp and withdrawal of the embolus. Immediately after each intromission the male spends 1–2 s passing the pedipalp just withdrawn from the female through his mouthparts, probably lubricating the embolus with mucus. For males using both pedipalps to copulate, the subsequent intromission is performed using the opposite pedipalp, and continues with the male alternating regularly between his right and left. All copulations begin with a 2–6 h aspermic, preinsemination phase. The male then builds a sperm web, charges one or both pedipalps, and initiates the 0.5–1.4 h insemination phase of copulation. Intromission rates are 7–10 times higher in the preinsemination than insemination phase. All measures of copulatory courtship were taken during the preinsemination phase.

Duration of preinsemination phase copulation*: adjusted for break time and accurate to at least 1 h.

Intromission rate*: the number of successful intromissions per 3-min period: measured in the preinsemination phase, at least 45 min after the onset of copulation to ensure a standard 'warm-up'.

Flub to hit ratio*: the number of unsuccessful intromissions (i.e. obvious misses or incomplete penetrations ('flubs'), where the male's pedipalp does not completely expand), divided by the number of successful intromissions ('hits') recorded during the same 3-min period specified under Intromission rate above. This is a measure of the male's competency in copulation.

Number of intromissions*: the product of the preinsemination phase duration and intromission rate.

Female Mating History

Female's number of previous suitors: the number of males that courted the female prior to the current male's arrival.

Female's number of previous mates: the number of complete copulations the female engaged in prior to the current male's arrival.

Female's final number of mates*: the total number of complete matings accepted by the female between her sexual maturation and first oviposition.

Number of days since the female's last mating: the number of days lapsed between the female's prior mating and the arrival of the current male.

Mating Circumstances

Number of pedipalps used in copulation*: since males can gain access to both spermathecae only by using both pedipalps in copulation, it seems plausible that one-pedipalp copulations, whatever is behind them, could involve a sacrifice in fertilization success. It might seem that this factor should be considered under the heading of copulatory courtship, but it is unclear in individual cases why a male copulates with one pedipalp or two. Sometimes the basis of one-pedipalp matings is circumstantial; the male simply has a physically damaged pedipalp. There are also suggestions that much of the variation is related to female mating history and hence reproductive value (Watson 1988), but whether purely behavioural variation in pedipalp use is due to a free decision by the male or cryptic imposition by the female is unknown. If the former is true, then there are at least two ways in which males could have their fertilization success affected by this factor without the action of active female choice.

Time of day copulation began*: accurately measured to at least the hour.

Temperature*: taken at study site 0.6–2 h after the beginning of preinsemination phase copulation in 1984 and 1985; estimated from the biological station's daily weather records in 1982.

Numbers of days since last precipitation*: the number of days that have elapsed without rainfall

prior to the commencement of mating. This variable equals zero when precipitation on the day of mating is non-zero; from the biological station's records.

Duration of the insemination phase of copulation*: accurately measured to at least the hour, but often known to within 15 min. Estimates of the duration of the insemination phase, even if precise, may not help predict fertilization success, because although the insemination phase lasts between 0.5 and 1.5 h, most sperm may be transferred during the first few minutes as reported by Austad (1982) for the bowl and doily spider (*Frontinella pyramitela*: Linyphiidae).

Time of season*: the number of days since the first observed mating of the breeding season.

Female foraging success*: estimated female foraging success during the 4 days prior to the commencement of mating. Foraging scores are a weighted sum of prey items we saw the female capture, divided by the number of observations on the female during the 4-day period. The weightings are based on the typical number of hours an adult spider spent feeding on small (e.g. mosquito), medium (e.g. housefly) and large (e.g. large mayfly or crane fly) prey items. Small prey had a weighting of 1, medium prey 4 and large prey 8. Thus each foraging score equals

$$\frac{(\text{number of small prey} + (\text{number of medium prey})4 + (\text{number of large prey})8)}{\text{number of observations.}}$$

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