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Sexual Conflict in the Wild: Elevated Mating Rate Reduces Female Lifetime Reproductive Success

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ABSTRACT: Sexual conflict over mating rate is suggested to play a pivotal role in male-female coevolution, and females are predicted to reject superfluous mating attempts. Recent work suggests that direct effects of multiple mating on female fitness are not fully understood. A major concern in studies of sexual conflict is how well the data obtained under controlled laboratory settings relate to natural conditions. We tested the effect of female multiple mating on reproductive success in a natural population of a polyandrous spider, *Stegodyphus lineatus*. Previous studies show that a male who succeeds in entering a female nest also mates with her; therefore, we used male encounter rate as a proxy of female mating rate. We further elevated female mating rate by introducing males into females' nests. Female lifetime reproductive success was assessed as the likelihood of successful reproduction, offspring production, and juvenile offspring body mass. Increased mating rate increased the time to oviposition and reduced the likelihood of successful reproduction. Female mating rate negatively affected offspring body mass. Manipulated females produced fewer offspring than control females. The observed patterns imply a net cost of polyandry to females and suggest that natural mating rates can be suboptimal for females under natural conditions.

Keywords: mating rate, direct selection, polyandry, *Stegodyphus lineatus*, evolution of mating systems.

The divergence in reproductive interests between males and females is a potent cause of selection that can affect the evolution of life-history traits and generate female preference for specific male genotypes and drive speciation (Parker 1979; Rice 1992; Stockley 1997; Holland and Rice 1998; Lessels 1999; Gavrilets et al. 2001; Arnqvist and Rowe 2002; Martin and Hosken 2003; see Chapman et al. 2003*b* for review). Female avoidance of male-imposed costs of mating forms the basis of sexual selection via sexual conflict. The genetic model of sexual conflict over mating rate predicts rapid evolution of male sexual traits in response to female resistance, resulting in sexually antagonistic coevolution (Holland and Rice 1999; Gavrilets et al. 2001). The costs of mating and the costs of resistance at equilibrium mating rates may be substantial.

A large number of studies have successfully identified various direct costs of mating in different taxa, such as increased predation risk (Moore 1987; Arnqvist 1989; Fairbairn 1993; Hosken et al. 1994; Rowe 1994), disease transmission (Daly 1978), energy costs (Cordts and Partridge 1996; Watson et al. 1998), toxic accessory gland products (Chapman et al. 1995), and physical injuries (for extensive references on various types of costs, see Michiels and Newman 1998; Crudgington and Siva-Jothy 2000; Stutt and Siva-Jothy 2001; Blanckenhorn et al. 2002). Yet females commonly mate with multiple males, and this pattern is nearly universal in nature (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Hosken and Stockley 2003). The meta-analysis conducted by Arnqvist and Nilsson (2000) suggests that an almost ubiquitous occurrence of polyandry in insects is accompanied by large direct benefits of multiple mating to females. Nevertheless, it further suggests the existence of female remating optima above which matings tend to be deleterious to females, which in turn renders conflict over mating rate between sexes to be prevalent in mating systems (Arnqvist and Nilsson 2000). The exact form of the relationship between mating rate and female fitness depends on the interaction between costs and benefits associated with multiple mating (Arnqvist and Nilsson 2000; Arnqvist et al. 2004) and may therefore vary under different environmental conditions (e.g., Chapman and Partridge 1996). Hence, it is essential to relate the natural mating rates to female fitness in wild populations

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(Chapman and Partridge 1996; Chapman et al. 2003*a*, 2003*b*; Cordero and Eberhard 2003).

Several studies that attempted to quantify the net costs and benefits associated with increased mating rate (Arnqvist 1989; Byrne and Roberts 1999, 2000; Stutt and Siva-Jothy 2001; Maklakov and Lubin 2004) suggest that sexual conflict may be the driving force behind the observed matting patterns and that females are paying a considerable net cost for superfluous matings. Nevertheless, the generality and ecological relevance of these findings may be questioned. For instance, Cordero and Eberhard (2003) asked whether the reduction in lifespan in fruit flies *Drosophila melanogaster* and bedbugs *Cimex lectularius* has important fitness consequences under natural conditions. In laboratory populations, some measures of the cost of mating may depend on environmental conditions under which experiments are performed. Thus, Chapman and Partridge (1996) found an interaction between levels of nutrition and encounter rates with males for the cost of mating in females in *D. melanogaster*. Only under higher food levels did females that experienced high mating rates have reduced lifespan, and only at the highest food level did the flies show reduced lifetime fecundity. Thus, longevity is not always an adequate measure of the cost of mating (Chapman and Partridge 1996). Moreover, the data suggest that increased remating frequency became maladaptive only at a food level that was higher than those normally experienced by female flies in the rearing cages. Holland and Rice (1999) demonstrated the sexually antagonistic nature of male seminal fluids and increased harm to females under sexual selection in *D. melanogaster* (see also Martin et al. 2004 for similar results in the dung fly *Scathophaga stercoraria*); however, the generality of these findings under variable environmental conditions remains to be tested.

Another artificial selection experiment using polyandrous and monandrous lines of *Sepsis cynipsea* failed to identify measurable effects of selection on female lifetime reproductive success, although there were longevity costs to females congruent with sexually antagonistic coevolution (Martin and Hosken 2003). In another selection experiment, Martin and Hosken (2004) found, however, that female lifetime reproductive success decreased with increasing sexual conflict in *S. cynipsea*. In wild populations, the natural rates of encounter between the sexes are typically difficult to measure, and it is even more difficult to relate the natural mating rates to the lifetime reproductive success (Chapman et al. 2003*b*) or to manipulate the mating rates under otherwise natural conditions. Yet such data are urgently needed to enhance our understanding of how sexual conflict over mating rate interacts with life-history traits to affect female fitness in nature.

We studied the effect of sexual conflict on female fitness in a field population of the polyandrous web-building spider *Stegodyphus lineatus* (Eresidae). This is a well-studied system in which male-female conflict over mating is well documented (Schneider and Lubin 1996, 1997, 1998; Erez 1998; Schneider 1999; Maklakov and Lubin 2004). Females are sedentary and annual (Ward and Lubin 1993), which allows for estimation of lifetime reproductive success, while males can be individually marked and surveyed in the field (Schneider 1997).

Here we focus on the effect of mating rate, defined as mating frequency per reproductive bout, on female fitness in a natural population of *S. lineatus*. Specifically, we ask how increased mating rate affects net offspring production by females. We estimated natural rates of polyandry for females in the field and manipulated female mating rate by introducing additional males to females' webs (see below). Previous studies confirm that males that succeed in entering a female's retreat invariably copulate with her later on (Schneider and Lubin 1996; Maklakov et al. 2004). Therefore, we used male occurrence rate in the female's retreat as a proxy for female mating frequency, that is, the number of males a female mates with.

Methods

Stegodyphus lineatus Latreille 1817 (Eresidae) is a web-building spider that is widespread in arid and semiarid habitats around the Mediterranean basin. Females occupy thick conical silk retreats built on shrubs, and irregular capture webs radiate from the retreat (Ward and Lubin 1993). Males leave their nests after the final molt to adult stage and wander in search of females. Males cohabit with females for several days prior to or between copulations (see below). The mating season begins in March and lasts until June (Schneider 1997; Schneider and Lubin 1997). The females produce a single egg sac during their lifetime and provide maternal care to their young. The clutch size therefore represents the female's lifetime fecundity. Mothers release the young from the egg sac, feed them by regurgitation (Kullmann et al. 1971), and are invariably consumed by the offspring approximately 2 weeks after hatching (Schneider 1995). Therefore, offspring production to the stage of matriphagy represents the female's lifetime reproductive success.

Male Encounter Rate as Proxy for Female Mating Rate

Males that encounter female webs initiate courtship behavior that can result in immediate copulation, in male cohabitation with the female inside the retreat, or in female rejection of the male, in which case the male leaves the web immediately (Maklakov et al 2003; Bilde et al. 2005). If copulation does not occur immediately after entering a female's retreat, males invariably succeed in copulating later. This is backed up by several earlier studies. In a study of sperm precedence, Schneider and Lubin (1996) introduced two males sequentially to a female's web but did not observe the actual copulations. The second male sired on average 50% of the offspring, demonstrating unequivocally that subsequent males that are accepted into the female's retreat copulate later. In a second study, two males were introduced sequentially, and immediate copulation was not always observed; however, when the female accepted male presence in her retreat, repeated copulations were observed at a later stage (Maklakov and Lubin 2004). Finally, we performed two studies in which second and third males were observed by constantly following their placement on the female's web. In all cases, males that were accepted into the female retreat were later observed in copula with the female. Males that were rejected by aggressive females were not permitted entrance to the retreat, and such males always tried to escape from web (A. A. Maklakov, T. Bilde, and N. Schilling, personal observation, March–May 2002 and 2004). A mating pair that copulated more than once was still considered to be only one mating event.

Males that successfully mate with a female stay in her nest on average 2 days, and the cohabitation period ranges from 1 to 18 days (Schneider 1997). During this period, males can obtain prey from webs of females (kleptoparasitism; Erez 1998; Maklakov et al. 2004). The cohabitation period may serve as mate guarding because resident males often fight with intruding males (Maklakov et al. 2004).

Virgin females usually accept any male into their retreats, whereas mated females lose receptivity and behave aggressively toward subsequent males (Maklakov et al. 2003, 2004). Encounters between mated females and males may result in fierce fights (Schneider and Lubin 1998), and the outcome of the fight is determined by the relative cephalothorax size of the contestants (Schneider and Lubin 1996; Schneider 1997). Hence, large males can force unreceptive females to mate and large females can prevent subsequent males from mating, rendering relative body size between the sexes an important role in intersexual conflict (Schneider and Lubin 1998). The cephalothorax of males is slightly smaller than females, but there is an overlap in size range (Schneider 1997).

Experimental Procedure

We conducted the study in a population of *S. lineatus* spiders in the Negev Desert, Israel in March–August 2003. The population consisted of 500–700 subadult spiders in early March. Daily mortality of *S. lineatus* is very high (Schneider 1996), and many subadult spiders that overwinter successfully do not survive to maturation. We monitored the population two to three times a week until the first spiders matured. Males are protandrous (Schneider 1997), and the first males appeared in the end of March, while the first females matured in the beginning of April. Once females became adult, we monitored our population on a daily basis for 48 days (from April 1 to May 18) until all males had disappeared from the population. These daily inspections gave a good approximation of the realized mating rate, although we could have missed successful males with cohabitation periods shorter than 1 day. Therefore, the effects of possible shorter cohabitations were not examined. We estimated relative male cohabitation time as residuals from least squares regression of total time males spent with females on total number of male visits because the relationship between cumulative male cohabitation time and male number is linear ($R^2 = .676$, $F = 266.06$, $\mathrm{df} = 1, 126$, $P < .001$).

Following the mating season, we monitored the population three times a week for three additional months to collect the data on time to oviposition, reproductive success, and offspring production. Time to oviposition was defined as day count from April 1 to the date of egg laying. Once the offspring consumed the mother, we collected the nest and brought it to the laboratory to count and weigh the offspring using an analytical balance. We returned the nest with the young to the field after the measurements were taken.

In total, we marked the nests of 218 freshly molted females and subadult spiders that we assumed may become females. Until the final molt, it is impossible to distinguish males from females in this species, so we sexed the spiders after maturation. All males were individually marked with four color dots on the abdomen using a nontoxic water-based paint. Overall we marked 183 males. Females are extremely sedentary and will not leave the nest unless disturbed. Females with egg sacs never leave their nests nor do they relocate their egg sacs (A. A. Maklakov, personal observation). Therefore, we measured body size only of females that succeeded in producing an egg sac. We excluded females that overwintered from the previous year (i.e., did not molt prior to egg sac production), females that were located only after maturation, females whose location we lost during part of the experimental period (i.e., some male visits could have been missed), subadult spiders that molted into males, and females that were predated or parasitized prior to mating with at least one male. In the end, our data set comprised 136 females, 35 of which we randomly allocated to be treated with additional males. Eight females were further excluded because experimental males used for the manipulation of mating rate in other females wandered into their nests. Finally we had 128 females (93 control and 35 experimental) that we monitored from the day of maturation until their death or successful reproduction.

For manipulation of female mating rate we used males from three neighboring subpopulations of *S. lineatus* in the Negev Desert. We chose to use males from separate subpopulations in order to avoid changing the natural operational sex ratio in the subject population. We used the following rationale in our manipulation of female mating rate. The time lag from mating to egg sac production is very variable (15–53 days [Schneider 1999]; 19–92 days in this study; see "Results") and females continue to encounter males during much of this period (Schneider and Lubin 1996; Schneider 1997; this study). To imitate the natural situation, we elevated female mating rate by adding males to experimental females on a weekly basis until the females produced an egg sac. This was done both to standardize the manipulation and to avoid the introduction of males at the egg stage because it would carry additional costs as a result of male infanticide (Schneider and Lubin 1996, 1997). If the focal female had a male in her nest, we postponed the introduction of an additional male for the next week. In this manner we elevated the mating rate in experimental females without interfering with the natural male encounters, and we could continue to do so throughout the entire breeding season. We strongly believe that such manipulation most closely resembles a natural increase in male encounter rate as might be experienced by females following an increase in population density or male bias in the operational sex ratio in a particular season. Median mating rate of control (unmanipulated) females was 2 (range 1–9), while median mating rate of manipulated females was 5 (range 2–10; Mann-Whitney *U*-test: $U = 550, N_1 = 93, N_2 = 35, P < .001$), which renders our manipulation successful. Schneider (1997) reported a mean mating rate in the field of 2.1 (number males found in females' nests), a similar number as found in the control females of our study.

Statistical Analysis

The data were analyzed using general linear models for time to oviposition, offspring production, and offspring body mass at matriphagy and generalized linear models for likelihood of oviposition and successful reproduction in SYSTAT 10 (SPSS, Chicago). We had to analyze the latter two variables separately rather than using multivariate analysis because certain variables were available only for a subset of individuals (e.g., female body size was collected only for females that produced an egg sac because the disturbance at an earlier stage of life cycle can lead to nest abandonment by a female; see above). Continuous variables in general models were log transformed prior to the analysis to normalize distributions. We present the results of full models throughout. The variables that entered into each model are specified directly in the text prior to presenting the statistics or are listed in the tables.

Results

Time to Oviposition

Fifty-one out of 93 control females (54.84%) survived to produce an egg sac within a mean of 57.02 days (±2.21 SE, minimum = 19, maximum = 92), compared with 26 out of 35 manipulated females (74.29%) that produced an egg sac within a mean of 60.89 days (±3.29 SE, minimum = 31, maximum = 92). When maturation date was accounted for, there was no difference between treatments in how likely females were to succeed in producing egg sacs (generalized linear model with treatment as discreet and maturation date as continuous predictors: LLR = 4.17, df = 2, χ^2 $P = .124$). Similarly, there was no difference in time to oviposition between control and manipulated groups when female body size and maturation date were accounted for in the model (ANCOVA: $F = 2.51$, df = 1, 73, $P = .118$ for treatment; $F = 5.06$, df = 1, 73, $P = .027$ for maturation date; $F = 19.16$, df = 1, 73, $P < .001$ for female body size). We then analyzed the effect of mating rate, residual male cohabitation time, female body size, and maturation date on time to oviposition and found highly significant effects of mating rate, female body size, and maturation date (table 1; the inclusion of treatment in this, or any other, model does not change the qualitative conclusions about individual parameters, yet we did not use it in any of our models because of potential colinearity problems). In turn, late oviposition reduced the likelihood of successful repro-

Table 1: Statistics from general linear model testing the effect of mating rate, residual male cohabitation time, female body size, and maturation date on time to oviposition for control females and for all females pooled together

Factor	Coefficient	SE	*t* ratio	*P*
Control females:[a]				
Mating rate	.174	.058	3.017	.004
Cohabitation time	.064	.065	.982	.331
Female body size	−.374	.086	−4.365	<.001
Maturation date	.211	.069	3.038	.004
All females:[b]				
Mating rate	.168	.046	3.87	<.001
Cohabitation time	.03	.061	.536	.632
Female body size	−.348	.074	−4.876	<.001
Maturation date	.204	.061	3.668	.001

Note: Time to oviposition, mating rate, cohabitation time, and maturation date were log transformed prior to the analysis.

[a] $F = 9.61$, df = 4, 46, $P < .001$.

[b] $F = 11.612$, df = 4, 72, $P < .001$.

duction (generalized linear models: LLR = 5.5, df = 1, χ^2 $P = .019$ for control females; LLR = 7.48, df = 2, χ^2 $P = .006$ for all females pooled together), and reproducing females that oviposited later produced fewer young (linear regressions: $R^2 = 0.263$, df = 1, 22, $P = .006$ for control females; $R^2 = 0.27$, df = 1, 75, $P = .001$ for all females pooled together).

Likelihood of Successful Reproduction

Twenty-four out of 93 control females (25.8%) had reproduced successfully compared with 11 out of 35 manipulated females (31.43%). There was no difference between control and manipulated females in how likely they were to reproduce (Pearson $\chi^2 = .405$, df = 1, $P = .525$). However, when we analyzed data for all females that succeeded in producing an egg sac, we found significant negative effect of mating rate and significant positive effect of female body size on the likelihood of successful reproduction (generalized linear model: LLR = 8.018, df = 2, χ^2 $P = .018$; see table 2 for standard errors and *t* ratios of the single parameters).

Table 2: Statistics from generalized linear model testing the effect of mating rate on the likelihood of successful reproduction

Factor	Coefficient	SE	*t* ratio	*P*
Mating rate	−.259	.128	−2.029	.042
Female body size	1.414	.661	2.140	.032

Net Offspring Production

Control females that succeeded in reproducing had significantly more offspring (45.58 ± 5.26 SE; $n = 24$) than successful manipulated females (29.36 ± 6.76 SE; $n = 11$; ANCOVA with female body size as a covariate: $F = 6.31$, df = 1, 32, $P = .017$ for treatment; $F = 14.4$, df = 1, 32, $P = .001$ for female body size; fig. 1).

Offspring Body Mass at Matriphagy

Females that mated at a higher rate prior to oviposition produced smaller offspring when accounting for maturation date, female body size, number of offspring, and relative cohabitation time (table 3). However, there was no difference between manipulated and control females (ANOVA: $F = 0.29$, df = 1, 33, $P = .592$).

Discussion

Our results consistently show negative effects of increasing mating rate on female fitness, measured as time to oviposition, likelihood of successful reproduction, and offspring body mass prior to dispersal. Our main result, however, is that manipulated females experiencing an elevated mating rate suffered a 35% loss in the number of offspring produced compared with control females. We find that natural mating rates can be suboptimal for *Stegodyphus lineatus* females under field conditions and that an experimental increase of mating rate is detrimental to net offspring production. However, these results also highlight the value of estimating the relative importance of conflict over mating on female fitness under stochastic natural conditions as well as the difficulties associated with this approach (Chapman et al. 2003*a*; Eberhard and Cordero 2003). For example, only one of the measured fitness variables was significantly affected by experimental manipulation of female mating rate when analyzed separately.

Much of the debate concerning the importance of sexual conflict over mating focuses on the two following points: “ecological relevance” and the balancing effect of indirect genetic benefits (Arnqvist 1989; Chapman and Partridge 1996; Holland and Rice 1998, 1999; Andres and Morrow 2003; Chapman et al. 2003*a*, 2003*b*; Cordero and Eberhard 2003; Cordoba-Aquilar and Contreras-Garduno 2003; Eberhard and Cordero 2003; Pizzari and Snook 2003). Collectively, our data support the hypothesis that direct costs resulting from sexual conflict over mating rate have measurable fitness consequences for females in nature. The question remains of whether “good genes” or “sexy son” processes are counterbalancing the negative effects of increased mating rate.

In *S. lineatus*, male body size or body mass are important predictors of male mating success with resistant females (Schneider and Lubin 1996; Maklakov et al. 2003, 2004) as well as of male success in gaining food from female’s webs (Maklakov et al. 2004), with larger/heavier males being more successful. However, neither male body size nor body condition had any effect on offspring body mass at dispersal in a laboratory experiment (Maklakov and Lubin 2004). In this study, we also did not find indirect benefits in terms of increased offspring viability or body mass of the young. Given the lack of evidence for early-life indirect benefits in *S. lineatus*, we suggest it is unlikely that indirect effects would be large enough to compensate the substantial costs of polyandry under field conditions as documented here. However, mitigating effects of indirect benefits to females via sexy sons or good genes effects cannot be ruled out, as neither of these studies on *S. lineatus* attempted to quantify indirect payoffs in the following generation (Cameron et al. 2003; Kokko et al. 2003; Tallamy et al. 2003), for example, whether the offspring of replacement males were particularly good at becoming replacement males in subsequent generations. Additionally, females may gain indirect benefits from multiple mating via inbreeding avoidance (Tregenza and Wedell 2002). Nevertheless, *S. lineatus* spiders are tolerant to inbreeding (Bilde et al. 2005) such that benefits via inbreeding avoidance are unlikely to outweigh the direct costs associated with mating.

A potential cost causing the reduction in female reproduction when females encounter subsequent males stems from struggles to prevent males from mating with females or for prey that are caught in the web. Therefore, the aggressive encounters between mated females and males (Schneider and Lubin 1996, 1998; Maklakov et al. 2004) could directly affect female fitness as well as being a predictor of female quality. Perhaps females that are less healthy or vigorous are less able to defend themselves and must tolerate more males on their webs than more vigorous females. This would imply that control females with higher mating rates may have lower fertility because of factors unrelated to copulation per se. This scenario is consistent with the idea that polyandry at least in part is driven by incomplete female control over mating (Maklakov and Lubin 2004). Nevertheless, the outcome of male-female combat in *S. lineatus* is influenced by the size difference of the contestants (Schneider and Lubin 1997), while female body size and, therefore, part of the variation in female fighting ability was accounted for in our models.

The possible mechanism by which additional matings reduce female reproduction in *S. lineatus* spiders appears to be subtle. We found no direct evidence of increased predation risk, although the chance of successful reproduction has previously been shown to decrease in late reproducing females as a result of parasitism by wasps (Ward and Lubin 1993). We have no information on sexually transmitted diseases and toxic seminal fluids, whereas physical injuries by males are unlikely (Maklakov et al. 2003; Bilde et al. 2005). The most plausible explanation is energy costs, which are probably a consequence of delayed oviposition and are also supported by the negative effect of mating rate on the body mass of young. Erez (1998) reported that male presence negatively affects female body condition when females were artificially con-

Table 3: Statistics from general linear model testing the effect of mating rate, residual male cohabitation time, female body size, maturation date, and number of offspring on mean offspring body mass

Factor	Coefficient	SE	*t* ratio	*P*
Mating rate	−.311	.144	−2.158	.039
Cohabitation time	.061	.186	.326	.747
Female body size	−.28	.261	−1.074	.292
Maturation date	−.046	.199	−.233	.817
Offspring number	−.001	.004	−.119	.906

Note: Mean offspring body mass, mating rate, cohabitation time, and maturation date were log transformed prior to the analysis.

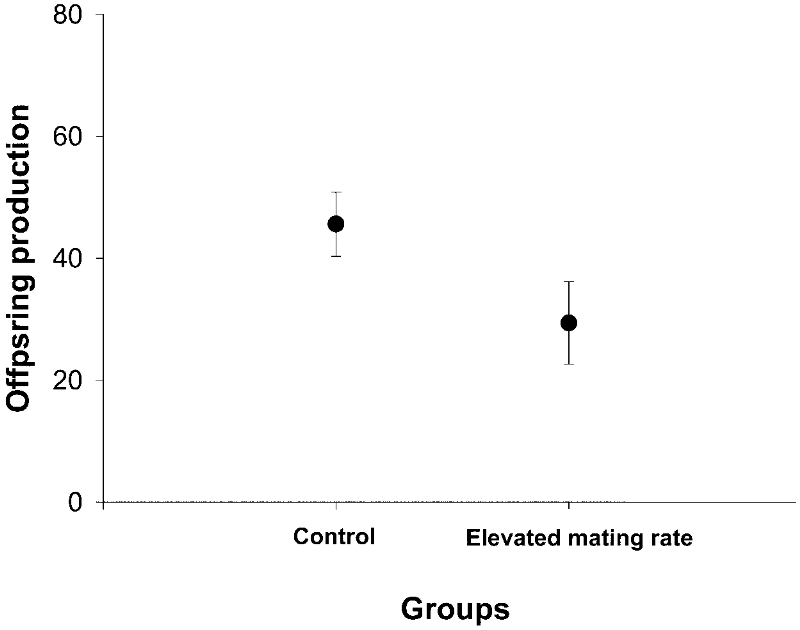

Figure 1: Effect of artificial elevation of female mating rate on female net offspring production. Females produced fewer offspring when mating rate was elevated. Dots represent mean values of the raw data unadjusted for female body size; bars represent standard errors. See text for details.

fined with males. In *S. lineatus*, female body condition strongly influences LRS (Maklakov and Lubin 2004; Bilde et al. 2005). In our study, the relative time that males spent in females' nests had no measurable effect on any of the fitness-related variables that we tested. This may be partly the result of the stochastic mode of food acquisition by females in the desert, in which the variation in female foraging success over time masks the effect of male presence on females. Multiple mating increased the time to oviposition in females under seminatural conditions (Erez 1998), which was confirmed in our field study by the positive relationship between mating rate and time to oviposition. The negative relationship between maturation date and oviposition means that early maturing females postpone oviposition, a pattern that was suggested to result from a female strategy to avoid infanticide by coercive males early in the season (Schneider 1999) and that indicates a trade-off between infanticide avoidance and risk of reproductive failure by delayed oviposition. Our data suggest that high male encounter rates drive females to delay oviposition to suboptimal parts of the reproductive season and therefore reduce their chances of reproducing successfully.

In conclusion, we demonstrated that increased mating rate reduces lifetime reproductive success in a natural population of *S. lineatus* spiders. While experimental manipulation of mating rate in wild populations is difficult, our data show a significant reduction in offspring production by reproducing females following an experimental increase in mating rate. Future studies of male-female interactions over mating in nature may want to focus on replicated populations to assess the impact of sexual conflict on net fitness. Another potentially rewarding approach is to study the interaction between sexual conflict and life-history traits for several generations because the magnitude of selection may vary between years.

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