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SEXUAL CONFLICT OVER MATING IN A SPIDER: INCREASED FECUNDITY DOES NOT COMPENSATE FOR THE COSTS OF POLYANDRY

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Abstract.—Female multiple mating (polyandry) is a widespread but costly behavior that remains poorly understood. Polyandry may arise when whatever benefits females accrue from multiple mating outweigh the costs, or males manipulate females against the females' best interests. In a polyandrous spider *Stegodyphus lineatus* females may mate with up to five males, but behave aggressively toward additional males after the first mating. Female aggressiveness may act to select for better quality males. Alternatively, females may try to avoid superfluous matings. To test these alternatives, we allocated females into single-mating (SM) and double-mating treatments. Double-mated females either accepted (DM) or rejected (RE) the second male. DM females laid more eggs, but did not produce more offspring than SM and RE females. Offspring of DM females were smaller at dispersal than offspring of SM and RE females. Also, nest failure was significantly more common in DM females. Paternal variables did not influence female reproductive success, whereas maternal body condition explained much of the variation. We show that polyandry is costly for females despite the production of larger clutches and suggest that multiple mating results from male manipulation of female remating behavior.

Key words.—Antagonistic coevolution, direct selection, multiple mating, sexual selection, *Stegodyphus lineatus*.

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Female multiple mating (polyandry) is a widespread but costly behavior that remains poorly understood. Polyandry may arise when (1) whatever benefits females accrue from multiple mating outweigh the costs, or (2) males manipulate females against the females' best interests. Traditional evolutionary explanations have centered on benefits to females as a result of multiple mating. Females may trade copulations for material benefits, such as nest sites, parental care (Davies 1992), and courtship feeding (Thornhill and Alcock 1983). Genetic benefits of polyandry constitute a whole class of ideas (Jennions and Petrie 2000), including improving on the previous matings (good genes models; Thornhill and Alcock 1983; Simmons 1987; Olsson et al. 1996), reducing the risk of genetic incompatibility (Zeh and Zeh 1996, 1997), inbreeding avoidance (Tregenza and Wedell 1998, 2002), and increased genetic diversity (Baer and Schmid-Hempel 1999). Genetic ''bet-hedging'' was put forward as yet another possible explanation for female multiple mating (Watson 1991); however, this strategy is likely to evolve only when polyandry is cost-free (Yasui 1998), which is unlikely in most systems. In species where males are actively searching for sedentary females, the value of sperm for females may be very high. Consequently, females may be expected to accept the first male indiscriminately, and become choosier with additional mates (Halliday 1983; Gabor and Halliday 1997).

Nevertheless, recent theoretical and empirical work indicates that female polyandry may result as a by-product of selection on males to increase their fitness (Holland and Rice 1998; Arnqvist and Nilsson 2000; Crudgington and Siva-Jothy 2000; Byrne and Roberts 2000; Stutt and Siva-Jothy 2001). Male fitness depends largely on the number of fertilized females. Females, however, often benefit from limiting the number of mates, thus creating a potential for conflict, and an evolutionary arms race over the mating rate can ensue (Parker 1979; Rice 1996; Gowaty 1996; Partridge and Hurst 1998; Arnqvist and Rowe 2002a,b). At any given point in evolutionary time, either sex may have an upper hand in the conflict (Parker 1979; Arnqvist and Rowe 2002a). When males forcefully impose copulations on females, the females must consider the costs of resistance versus the costs of superfluous copulations (Clutton-Brock and Parker 1995; Arnqvist 1997; Stockley 1998). If the cost is too great, the mating rate of a given population may stabilize above the optimal value for the females (reviewed in Arnqvist and Nilsson 2000).

We tested the ''female benefits'' versus ''male manipulation'' hypothesis in a polyandrous web-building spider *Stegodyphus lineatus* (Eresidae). In this system, females may encounter five or more males during the breeding season, but the average number of visiting males is about two (Schneider 1997). Males provide no material benefits, so that only genetic benefits of polyandry may apply. Egg sac-tending females respond aggressively towards males, and males succeed in mating only after subduing a female and destroying her egg sac (Schneider and Lubin 1996, 1997). Infanticidal males fertilize on average half of the females' replacement clutch, thus increasing their reproductive success at the expense of previous sires (Schneider and Lubin 1996). Females pay a fecundity cost since replacement clutches are smaller than the first ones (Schneider and Lubin 1996, 1997). Females fight against the intruding males and the size difference between the opponents influences the outcome of the encounter. However, female's resistance behavior suggests the possibility of quality testing. First, the fight involves the hooking of chelicerae as the opponents pull and push one another, which may function as a test of strength (Schneider and Lubin 1998). Second, defeated females retreat to the end of the nest and do not put up further resistance, nor do they prevent the

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male from removing and destroying the egg sac. Thus, females may put additional males through a test of vigor and accept the ones that are of higher quality than their first mate (Schneider and Lubin 1997).

Females encounter multiple males also before oviposition, when they do not have the costs associated with the replacement clutch (Schneider 1997). Yet these females as well behave more aggressively towards additional males prior to oviposition (T. Erez, pers. comm. 1998). Male body mass largely determined the mating success of males with previously mated females (Maklakov et al. 2003). This further suggests that females may be employing a mate choice strategy, in which male success in combat indicates higher genetic quality (Schneider and Lubin 1997).

Female benefits and male manipulation hypotheses generate explicit predictions regarding the effects of multiple mating and rejection of additional males versus single mating on female fitness. Consider the case of female benefits. Under this hypothesis, female aggressiveness toward additional males is used to screen for genetically beneficial mates. Genetic benefits are understood here in a broad sense, in terms of good genes, genetic compatibility, or low relatedness. A female may use some cues in male appearance or behavior and will accept additional males if they are genetically superior, genetically more compatible or less related than their initial mates. The female benefits hypothesis assumes that females reject additional males if they are not better than their previous mates. Therefore, females that are provided a choice between two randomly selected mates will have, on average, higher fitness than females that are artificially restricted to mating with one randomly selected mate. Alternatively, in the case of the male manipulation hypothesis, females that are presented with only one male will achieve higher fitness than females that mated with two males. Moreover, females that succeeded in rejecting the second male will also have higher fitness than females that accepted the second male.

We tested these predictions by comparing the effects of female mating history on fitness measures of females and offspring, namely, time to oviposition, nesting success, clutch size, brood size, dispersal cohort size, egg hatching success and offspring body mass at dispersal. We estimated the brood size by counting the number of successfully hatched young and dispersal cohort size by the number of young that survived to dispersal.

MATERIALS AND METHODS

Study Species

Stegodyphus lineatus Latreille 1817 (Eresidae) is a web-building spider that is common in arid and semiarid habitats around the Mediterranean basin. Females are extremely sedentary. Males leave their nests after the final molt to adult stage and wander in search of females. The mating season begins in March and lasts until June (Schneider 1997; Schneider and Lubin 1997). Males are slightly smaller than females, but there is an overlap in size (Schneider 1997). Males cohabit with females for 1–18 days before leaving the nest in search of new females (Schneider 1997). This behavior may serve both as mate guarding and as sperm competition strategies, since resident males often fight with intruding males and continue to copulate with females during the first two to four days of cohabitation. Males do not build capture webs following maturity, but may obtain prey from webs of females (kleptoparasitism). Male presence negatively affects female body condition (T. Erez, pers. comm. 1998). Females may be visited by more than five males during the season prior to oviposition and over 50% are visited by more than one male (Schneider 1997; A. A. Maklakov, unpubl. data). Mean number of male visitors for 60 adult females in the field was estimated as 2.1 ± 1.4 (Schneider 1997). Schneider and Lubin (1996) used sterile male technique to test for order effect in paternity doubly mated *S. lineatus*. Two males were sequentially introduced to females and enclosed for a number of days, but without observing the actual copulation. The data showed that the first and second male sired on average 50% of the offspring suggesting complete sperm mixing (Schneider and Lubin 1996). Therefore, we expect that females will mate with males that are originally accepted into female's nest. Furthermore, in this species males mate repeatedly with their females during the time they cohabit in females' nests. This behavior is commonly observed in the field (A. A. Maklakov, unpubl. data). In this study, we observed matings on the second, third, and fourth day after the initial experiment. Given that males repeatedly copulate with the same female over a considerable period of time, it is of less importance whether they mated during the first three hours of observation or not, since accepted males copulate later on. The females produce a single egg sac during their lifetime and provide maternal care to their young. They may only produce a replacement clutch in case the first one was lost due to male infanticide or predation (e.g. by ants). Therefore, clutch size represents the female's lifetime fecundity. Spiderlings hatch and undergo a molt inside the sac. The females then release the young and feed them by regurgitation (Kullmann et al. 1971). Spiderlings molt another two to three times inside the natal nest and disperse approximately one month after hatching to start a solitary life. Females are invariably consumed by the offspring two weeks after hatching (Schneider 1995). The size of the young at dispersal influences their survival during the periods of low food availability (Schneider 1995).

Subadult *S. lineatus* were collected in their natural habitats in the Negev Desert in Israel in March 2000 and brought to the Sede Boqer Campus of Ben Gurion University. Spiders were kept individually in plastic containers with mesh lids (height 10 cm, diameter 5 cm) and reared to maturity on a diet of desert locusts (*Locusta migratoria*), crickets (*Acheta domestica*), and flour beetles (*Tenebrio molitor*; Bilde and Lubin 2001; Bilde et al. 2002). We kept spiders outdoors under natural temperature and light conditions protected partially against direct sun by shade cloth. After the final molt to maturity, the spiders were measured and weighed. We used prosoma width as a measure of male and female body size, following Schneider and Lubin (1997). See Schneider (1997) for details of measuring procedures. Female body condition was obtained by dividing female body mass by female size (Schneider 1999).

TABLE 1. The data on time to oviposition, total clutch size, brood size (number of hatchlings), the size of dispersal cohort, ratio of unhatched eggs, and offspring body mass in *Stegodyphus lineatus* with different mating history ($N = 75$; single-mated, double-mated, and double-mated females that rejected the second male) presented as number of cases, mean, and standard errors. We also provide data on body condition of the test subjects (both male and female).

	Single-mating (n = 38)		Double-mating (n = 20)		Rejection (n = 17)	
	Mean	SE	Mean	SE	Mean	SE
Fitness measured as:						
Time to oviposition	26.95	0.99	28.95	2.56	22.59	1.27
Clutch size	49.13	3.49	58.5	4.36	55.23	5.51
Brood size	38.89	2.58	48.1	4.21	42.82	4.44
Dispersal cohort	37.76	2.58	43.6	3.92	42.7	4.45
Unhatched eggs	0.17	0.03	0.14	0.05	0.2	0.04
Offspring body mass	4.3	0.26	3.32	0.28	4.29	0.26
Test subject body condition						
Male	0.049	0.003	0.049	0.002	0.043	0.003
Female	0.112	0.004	0.108	0.004	0.115	0.006

Experimental Procedure

We randomly mated 85 virgin females by placing virgin males onto their webs. Males were left with females for five days to simulate the effect of male cohabitation. The pair was fed three first instar desert locusts on the second day of the five-day cohabitation period. Three females molted after the first mating and were excluded from the analysis. Forty-three females were selected randomly to be presented with a second male. A second male was introduced to each female five days after the removal of the first male (i.e. 10 days after the first mating). We observed the mating behavior of the pair for three hours. During this time, females copulated with the males, accepted the males into their nests, or rejected them by chasing them out of the nest and from the web. We concluded that a female accepted the male if it entered the nest of the female and assumed a ‘‘face out’’ position, with its abdomen toward the female inside the nest and its prosoma blocking the entrance to the nest. Although the male is vulnerable to the female in such position, we never observed females trying to attack a male that assumed a ‘‘face out’’ position, even if there were aggressive interactions between a male and a female prior to that. All single-mated females that accepted males into their nests but were not observed mating within the first three hours of male presence produced viable egg sacs. Therefore, we considered both copulation and nest entering as successful mating events (see also Study Species). We considered a male as rejected if it left the female’s web by producing a thread and moved away from the vicinity of the nest. If the male succeeded in copulating with a female or entering her nest, it was left with the female for five additional days. Thus, the whole experimental procedure for doubly mated females lasted for fifteen days. There was no difference between body size and body condition among females from three treatment groups prior to the experiment (size: ANOVA: $F_{2,72} = 0.38$, $P = 0.687$; condition: ANOVA: $F_{2,72} = 0.43$, $P = 0.651$). Similarly, there was no difference between males selected for either single- or double-mating treatment (size: ANOVA: $F_{1,73} = 0.07$, $P = 0.795$; condition: ANOVA: $F_{1,73} = 0.68$, $P = 0.412$). Nevertheless, we included male and female body size and body condition as predictors in all subsequent analyses. The pair was fed three first instar desert locusts on the second day of the cohabitation period. In order to standardize food treatment for all animals in the experiment, females that rejected the second male and singly mated females were also given three first instar desert locusts on day 13 after the first mating. All females were fed one flour beetle per week from the end of the 15-day experimental period until oviposition. Five days after the female released the young from the egg sac (Schneider 1995) we cut open the nest and counted the spiderlings to estimate the size of the brood. We returned the young to the mother and sewed the nest to allow for maternal feed care to continue. We estimated the clutch size by adding the number of unhatched eggs inside the egg sac to the number of hatchlings. We collected all of the young again when approximately 75% of the brood had left the maternal nest and started building retreats on the container mesh lid (dispersal cohort), counted and weighed them, using an analytical balance.

Analysis

Data were analyzed using general linear model in SYSTAT 10 (SPSS Inc., Chicago, IL). We tested the variables for normal distribution using Kolmogorov-Smirnov one-sample test. When necessary, we used reciprocal power transformations (Wilkinson et al. 1996) to obtain normality. Proportional data were arcsine-transformed, using a formula by Freeman and Tukey (1950). Frequency data were analyzed using tests of independence. Two-tailed *P*-values are given throughout.

RESULTS

Female mating history had a significant effect on nesting success: of 25 double-mated females (DM), only 20 produced a viable egg sac, compared to 38 of 39 single-mated (SM) and 17 of 18 females that rejected the second male (RE; Pearson $\chi^2 = 0.045$).

Female mating history had a significant effect on female fecundity (Tables 1 and 2). Post-hoc comparisons reveal that DM females had significantly larger clutches than SM females ($P = 0.032$), but no difference was found between DM and RE females ($P = 0.361$, Bonferroni contrasts). Additionally, there was no difference in clutch size of SM and RE females ($P = 1$). Female body condition also had a sig-

TABLE 2. The effect of female mating history (single-mated, double-mated, and double-mated females that rejected the second male), male and female body size and body condition, and female age (Julian date) on time to oviposition (in days), clutch size, brood size, dispersal cohort, ratio of unhatched eggs, and offspring body mass at dispersal in *S. lineatus*. The results are presented as *F*-ratios and *P*-values of the respective general linear models.

	Time to oviposition		Clutch size		Brood size		Dispersal cohort		Ratio of unhatched eggs		Offspring body mass	
Source	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Mating history	2.262	0.112	3.454	0.037	2.863	0.064	1.412	0.251	0.766	0.469	5.094	0.009
Female size	10.739	0.002	0.594	0.444	0.033	0.857	0.386	0.536	0.433	0.513	0.21	0.648
Female condition	12.387	0.001	68.259	<0.001	21.996	<0.001	28.801	<0.001	7.933	0.006	11.778	0.001
Male size	2.501	0.118	0.064	0.802	0.008	0.93	0.188	0.666	0.826	0.367	0.105	0.747
Male condition	2.799	0.099	0.667	0.417	0.276	0.601	0.646	0.424	0.029	0.865	0.018	0.892
Female age	7.148	0.009	0.031	0.86	1.209	0.276	0.958	0.331	0.874	0.353	2.292	0.135

nificant positive effect on female fecundity (Table 2). Female body condition had a strong effect on brood size and on the number of dispersed young (dispersal cohort; Table 2), whereas the effect of female mating history on brood size was marginally non significant. Female mating history had no effect on the size of the dispersal cohort. Female mating history and female condition significantly influenced the size of the offspring at dispersal (Tables 1 and 2). Offspring of DM females were smaller than offspring of SM and RE females ($P = 0.013$ and $P = 0.03$, respectively, Bonferroni contrasts). Table 1 presents the untransformed data (means and standard errors) for offspring body mass. Adjusted least-squares (ALS) means and corresponding standard errors (SE) obtained using power-transformed offspring body mass while accounting for male and female body size and condition and female age look very similar (SM: ASL = −0.26, SE = 0.01; DM: ASL = −0.32, SE = 0.02; RE: ASL = −0.25, SE = 0.02). If we look at the effect of treatment on offspring body mass directly using only female body condition as a covariate, both factors are highly significant (ANCOVA: $F_{2,71} = 6.42$, $P = 0.003$ for treatment; $F_{1,71} = 17.42$, $P < 0.001$ for female body condition).

DISCUSSION

Doubly mated females produced larger clutches than singly mated females but not larger than females that rejected the second male. However, this pattern is less apparent for the brood size data, which reveal a nonsignificant trend. Moreover, we found no significant difference in offspring survival cohort. Therefore, the acceptance of a second male by females did not increase their net reproductive success as measured in this study. Females that mated with two males had smaller offspring than females that were restricted to one male only and than females that rejected a second male. This result is in accordance with predictions derived from the male manipulation hypothesis. Additionally, doubly mated females had lower overall nesting success than singly mated females. We did not find any effect of double mating on time to oviposition or hatching success. Surprisingly, female condition was positively correlated with the relative number of unhatched eggs (ratio). We did not find any significant effect of female mating history on time to oviposition, which was positively correlated with female size and negatively with female condition and female age at mating. Schneider (1999) suggested that the negative correlation between time to oviposition and female age stems from sexual conflict over mating, and represents a female strategy to avoid costly infanticide by additional males. In general, paternal variables—male size and male body condition—had no effect on any of the female fitness correlates we measured.

The data on reproductive success are similar to those of Eady et al. (2000), who found that polyandry increases fecundity but decreases egg-to-adult survival in the bruchid beetle (*Callosobruchus maculatus*). The authors suggest that male ejaculate-derived ovipositional stimulants may have a positive effect on egg-laying response from females. The reasons behind reduced egg-to-adult survival in bruchids were unclear (Eady et al. 2000). Similar explanations may be applicable to other systems, including *S. lineatus*, although, due to suicidal maternal care there may be no conflict of interest between males and females regarding the optimal clutch size. Nevertheless, a positive effect of ejaculate-derived stimulants could be an unselected byproduct of multiple mating. As in many arthropods, the clutch size in *S. lineatus* is positively affected by female body mass (Ward and Lubin 1993; Schneider 1995). In *S. lineatus*, reduced egg-to-dispersal survivorship of young from polyandrous clutches may be due to the negative effects of multiple mating on female body condition via stress and kleptoparasitism (T. Erez, pers. comm. 1998). Females in the DM group and no others had to share their food with second males. Our approach was to address the question of polyandry in general, including direct material benefits and/or costs and indirect genetic benefits and/or costs. The main cost of mating in one of the best-studied polyandrous systems, water striders, comes from energy expenditure and exposure to predators while females are carrying around copulating males (Arnqvist 1997). In this system, males commonly cohabit with females and male presence has been suggested to negatively affect female condition. Therefore, we wanted to include this possible interaction in our experiment. We view male-induced reduction in female condition, which may be due to both stress and sexual kleptoparasitism as one of the potential costs of polyandry, which has to be included in any general estimation of a polyandrous mating system. Our design also allowed for direct testing of this interaction. Thus, females that rejected the second male avoided the costs of additional male presence.

Interestingly, doubly mated females had lower nesting success than singly mated ones due to egg sac hatching failure. Multiple insemination creates a potential for sperm competition between males, in which the most aggressive sperm wins (Birkhead et al. 1993; Eberhard 1996). The resulting arms race can lead to polyspermy and, consequently, to increased infertility (Eberhard 1996; reviewed in Morrow et al. 2002). However, the polyspermy hypothesis predicts low egg hatching success in polyandrous females (Morrow et al. 2002) rather than increased probability of failure of a complete clutch. Another possibility is that bodily contact with multiple partners can increase the chance of disease transmission (Hurst et al. 1995). *Stegodyphus lineatus* often suffers from fungus infections (A. A. Maklakov, pers. obs.), which might be transmitted to the female's nest by visiting males, and which then could infect the egg sac during the building process and lead to subsequent sac failure.

Offspring body mass at dispersal was positively influenced by female body condition, but not by paternal variables or female age. Since females provide prolonged brood care, which includes regurgitation feeding (Kullmann et al. 1971) and terminates with matriphagy (Schneider 1995), they may be considered as temporary food reserves that are gradually distributed among the young. The mass of young spiders is important for their endurance until the next breeding season—heavier animals have higher probability of survival during periods of low prey availability (Schneider 1996) and may have an initial foraging advantage, with a cumulative effect over their lifetime (Schneider 1995). Consequently, larger young are more likely to mature as large adults (Schneider 1996) and achieve higher reproductive success (Schneider and Lubin 1997). Therefore, the negative effects of multiple mating on offspring size at dispersal are highly important for offspring fitness, and may greatly reduce offspring survival and reproductive success.

In conclusion, our results demonstrate that females pay the costs of polyandry apparently without retaining compensating benefits. We suggest that polyandry in this system is maintained by sexual conflict over mating and that females are mating with additional males against their best interests. Whatever benefits females may accrue via sequential mate choice or any other ''good genes'' mechanism must be strong enough to outweigh the costs of multiple mating, which is unlikely given the absence of significant paternal effects on offspring body mass.

Sexual conflict has been proposed to be a main selective force determining the evolution of mating rate (Parker 1979; Holland and Rice 1998; Arnqvist and Nilsson 2000). Yet there are few empirical studies that directly demonstrate the importance of sexual conflict for the dynamics of the mating systems (Rowe and Arnqvist 2002). Our data suggest that female multiple mating may evolve via a sexual conflict scenario even when polyandrous females lay larger clutches. The costs of reproduction for females may outweigh the benefits, while strong selection on males to increase their reproductive success by imposing copulations on unwilling females may result in an elevated female mating rate.

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