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ORIGINAL ARTICLE

Indirect genetic benefits of polyandry in a spider with direct costs of mating

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Abstract The search for the evolutionary explanation of polyandry is increasingly focused on direct and indirect selection on female resistance. In a polyandrous spider *Stegodyphus lineatus*, males do not provide material benefits and females are resistant to remating. Nevertheless, polyandrous females may obtain indirect genetic benefits that offset the costs associated with multiple mating. We manipulated the opportunity for females to select between different partners and examined the effect of female mating history (mated once, mated twice, or rejected the second male) on offspring body mass, size, condition, and survival under high- and low-food rearing regimens. We found that multiple mating, not female choice, results in increased female offspring body mass and condition. However, these effects were present only in low-food regimen. We did not find any effects of female mating history on male offspring variables. Thus, the benefits of polyandry depend not only on sex, but also on offspring environment. Furthermore, the observed patterns suggest that indirect genetic benefits cannot explain the evolution of female resistance in this system.

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Introduction

Females commonly mate with different partners within a reproductive cycle. Multiple mating with different males (polyandry) is a widespread phenomenon, which occurs in a broad range of taxa with a variety of mating systems (Arnqvist and Nilsson 2000; Jennions and Petrie 2000). It is clear that males will increase their reproductive success by mating with multiple females. But, the benefits to females from multiple mating are not so obvious. The costs of multiple mating to both sexes range from increased risk of physical injury, predation, and energy expenditure to sexually transmitted diseases, which are well documented in the literature (Daly 1978; Parker 1979; Arnqvist 1989; Hurst et al. 1995; Blanckenhorn et al. 2002). Therefore, whatever benefits females accrue from multiple mating should outweigh these costs.

Several hypotheses were put forward to explain the evolution of polyandry and its prevalence in animal mating systems (Choe and Crespi 1997; Arnqvist and Nilsson 2000). These hypotheses can be divided broadly into those based on direct or indirect fitness consequences to females as a result of multiple mating. Under direct selection, potential benefits to females include paternal care, nutritious ejaculates, and nuptial gifts provided by males and gonadotropic substances, which are commonly transferred to females with male ejaculate (Eberhard 1996; Vahed 1998; Arnqvist and Nilsson 2000).

Polyandry may evolve solely as a result of selection on males to increase their reproductive success, i.e., females may be forced, seduced, or otherwise manipulated by males to remate against females' best interests (Clutton-Brock and Parker 1995; Arnqvist 1997; Holland and Rice 1998; Chapman et al. 2003). Even when certain levels of polyandry are currently beneficial to females, males will be selected to increase the mating rate above the female optimum (Arnqvist and Nilsson 2000), creating ample opportunity for conflicts of interest between sexes. Under this scenario females are expected to evolve counter-adaptations and both sexes may enter an evolutionary arms race over mating rate (Parker 1979; Holland and Rice 1998; Arnqvist and Rowe 2005).

It is therefore not surprising that female resistance to male mating attempts is very common in nature (Chapman et al. 2003; Arnqvist and Rowe 2005). There is considerable experimental and comparative evidence to suggest that direct costs of mating are substantial and may be sufficient to explain the evolution of female resistance in terms of direct fitness tradeoffs (reviewed in Arnqvist and Rowe 2005). Another hypothesis regarding the evolution of female resistance argues that resistance is maintained by indirect genetic benefits to females and that resistant females are screening males for genetic quality (Eberhard 1996; Cordero and Eberhard 2003). Indirect genetic benefits to "choosy" females are often considered to be a weak selection force (Kirkpatrick 1996; Kirpatrick and Barton 1997; Cameron et al. 2003) that may only reinforce the evolution of female resistance via avoidance of direct fitness costs (Gavrilets et al. 2001; Chapman et al. 2003; Arnqvist and Rowe 2005). Empirical data from the well-studied *Drosophila melanogaster* system support the notion that indirect genetic benefits to females do not compensate for male-induced direct costs (Oreiza et al. 2005; Stewart et al. 2005). Recently, however, Head et al. (2005) suggested that the indirect genetic benefits of mate choice that female house crickets (*Acheta domestica*) accrue via increased attractiveness of their sons are high enough to outweigh the direct costs associated with choice. We clearly need more experimental data to assess the extent of indirect genetic effects on female net fitness, especially in species where sexual conflict over mating was documented.

In the present study, we assess long-term indirect genetic benefits of multiple mating in a polyandrous spider *Stegodyphus lineatus* (Eresidae). In this species, females are commonly visited by several males both before and after oviposition (Schneider 1997; Schneider and Lubin 1997; Maklakov et al. 2005). Mated females often actively resist mating attempts by coercive males, while males fight with resistant females to achieve copulation. Females vigorously defend the entrance to their nests and spiders use their chelicerae to bite the opponent and their cephalothorax and front legs to push each other in and out of the nest during the contest (Schneider and Lubin 1997, 1998; Maklakov et al. 2004). Males are either chased away from the nest or gain entrance and copulate with the female. Larger males are more likely to succeed in mating with previously mated females (Maklakov et al. 2004).

It is reasonable to assume that direct costs associated with mating—infanticide (Schneider and Lubin 1996), kleptoparasitism (Maklakov et al. 2004; Erez et al. 2005), reduced offspring production (Maklakov et al. 2005)—are the reasons for female resistance in this species. Yet male–female combat may also be viewed as a test of male vigor (Schneider and Lubin 1997, 1998) and females may use their aggressive behavior to "screen" for higher quality males (cf. Cordero and Eberhard 2003). There is no male order priority for paternity in this species (Schneider and Lubin 1996); therefore, a female that mated a second time can expect that half of her offspring will be fertilized by a superior male. So far, we found no evidence for short-term benefits of polyandry in this species—double-mated females did not increase their reproductive success in terms of the number or quality of juveniles produced to dispersal stage in comparison with single-mated females or with females that succeeded in rejecting the second male. On the contrary, the offspring body mass at dispersal was lower in broods from double-mated females than single-mated females (Maklakov and Lubin 2004). Nevertheless, it is possible that double-mated females obtain indirect benefits via increased offspring viability and adult body mass. The negative effect of double mating on offspring body mass at dispersal is likely to be a result of maternal effects because the young are using their mother as a sole source of food during the early stages of development until they finally consume her completely (Schneider and Lubin 1998). Double-mated females produced larger clutches than single-mated females but suffered higher offspring mortality and produced smaller spiderlings (Maklakov and Lubin 2004). However, while maternal effects are prevalent early in life, their influence may attenuate with offspring age (Heath et al. 1999).

We tested for indirect genetic benefits of multiple mating by experimentally manipulating the ability of females to select between different partners by presenting them with either one (single-male group, SM) or two males. Females that were exposed to two different males could either accept (double-male group, DM) or reject (rejection group, RE) the second male. We reared offspring from clutches of DM, SM, and RE females into adulthood under low-food and high-food rearing regimens and seminatural climatic conditions. We used two different food regimes for offspring rearing because genetic benefits may in theory depend on offspring environment (Tregenza et al. 2003; Hunt et al. 2004; Uhl et al. 2005). We compared the effect of mating history together with parental body size and mass, offspring development time, clutch size and hatching success on offspring fitness measured as survival, and adult body mass, size, and condition of males and females under different food regimens. The "sequential female choice" hypothesis (Halliday 1993) predicts that females that were given an opportunity to mate with a second male (i.e., DM and RE groups) will have higher fitness than females that were exposed to only one male (Maklakov and Lubin 2004; Uhl et al. 2005). Alternatively, double mating per se may be beneficial to females (Uhl et al. 2005). We demonstrate positive effects of double mating on body mass and condition in adult female offspring under low-food regimen and discuss the potential role of genetic benefits for the evolution of polyandry and female resistance.

Materials and methods

Study species

S. lineatus (Eresidae) is a medium-sized [female body mass range (g)=0.266–0.739; male body mass range=0.079–0.355] web-building spider that occupies arid and semiarid habitats around the Mediterranean basin. The breeding season is from March to August and matings occur during the first 2–3 months of the season. Males mature on average 16 days before females over a period of 2–3 months after which they leave their nests in search of sedentary females (Schneider 1997; Schneider and Lubin 1998). Females may encounter several males during the breeding season (median=2; Maklakov et al. 2005; data from another population: mean=2.1±1.4; Schneider 1997).

Upon entering a female's nest, a male may copulate immediately or it may assume a "face out" posture at the entrance of the nest (Maklakov et al. 2003), thus blocking the entrance with its cephalothorax. Males may cohabit with female for 1 to 18 days (Schneider 1997). Male acceptance may be "peaceful" or it may follow a combat with a female. Alternatively, a male may be chased away from the nest by a resistant female, either after an intense combat or simply after the female showed signs of aggression, such as advancing toward an intruding male accompanied by leg waving and web plucking.

Subadult *S. lineatus* were collected in the Negev Desert in Israel in March 2000 and brought to Sede Boqer Campus of Ben-Gurion University. Spiders were kept individually in plastic containers with mesh lids (height 10 cm and diameter 5 cm) and reared to maturity on a diet of desert locusts (*Locusta* sp.), crickets (*A. domestica*), and flour beetles (*Tenebrio molitor*) (Maklakov and Lubin 2004). 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).

Experimental procedure

We mated 85 virgin females to virgin males (see Maklakov and Lubin 2004 for details). We left males with females for 5 days after the initial presentation. We randomly selected 43 females for double-mating group. A second male was introduced to each female 5 days after the removal of the first male. The second male was also left together with a female for a 5-day period. In this species, males that are accepted into females' nests often do not copulate straight away; rather, time to copulation may take hours or even days. However, accepted males do copulate repeatedly with the females later on (Maklakov and Lubin 2004). Thus, we can be confident that females in double-mated group mated with two different males, but the number of copulations was not controlled. We considered a male as "rejected" if he left the female's web by producing a thread and moving away from the vicinity of the nest. The pairs were fed three first instar desert locusts on the second day of each of the cohabitation periods. To standardize feeding conditions for all animals in the experiment, females that rejected the second male and singly mated females were also given three first instar locusts on the 13th day after the first mating. Consequently, only females that accepted the second male had to share their food with males during the second cohabitation period.

We raised the offspring from 38 SM, 20 DM, and 17 RE clutches. We randomly selected six young from each clutch for low-food regimen and six more young for high-food regimen. All spiderlings were kept individually in plastic containers as described above and were fed manually either once a week (high-food regimen) or once in 2 weeks (low-food regimen). Young spiderlings were fed with 4–5 *D. melanogaster* flies per feeding bout. As they grew older they were fed with first instar desert locusts *Locusta migratoria*, and finally with subadult locusts, crickets *A. domestica* and flour beetles *T. molitor*. All spiderlings built permanent nests attached to the walls of the container, which they enlarged as they grew. The prey was placed manually into the sticky capture webs attached to the nest entrance. We collected, measured and weighed adult males after their final molt. Adult females in this species are difficult to tell from subadult females even under a dissecting microscope (Schneider 1997). To standardize, we allowed all females to mature for two more months after the last male matured and collected and measured them all at the same time. Spider body size does not change with time after the final molt (Foelix 1996). Therefore, we use time from hatching to maturation for males and only the hatching date for females as an estimation of development time in our analyses. All measurements were done using digital calipers (precision ±0.02 mm) and analytical balance.

Analysis

Data on size-related variables were analyzed using multivariate analysis of covariance (MANCOVA) models and we tested the model residuals for deviation from normal distribution by plotting the observed values against the predicted values using normal probability plot in SYSTAT 11©. The effect of mating history on offspring condition was analyzed with ANOVA, with condition estimated as residuals from linear regression of body mass on body size (Schulte-Hostedde et al. 2005). Post hoc comparisons were conducted with Tukey honestly significantly different procedure as implemented in SYSTAT 11©, which controls for multiple comparisons. The effect of mating history on the proportion of offspring that survived to maturity were analyzed in GENSTAT 7© using EXTRABINOMIAL script for generalized linear models with binomial error distribution and logit link function with Williams correction for overdispersion (Crawley 1993). Frequency data were analyzed using contingency tables. We analyzed the effect of female mating history on offspring size and mass together with potentially important factors such as parent body size and mass, clutch size, number of unhatched eggs, and offspring development time. We averaged the mass and size values for male and female offspring separately from each family. We analyzed the data separately for each sex and each food regimen. We followed this procedure for two reasons. Firstly, some factors such as developmental time were estimated differently for males and females for reasons explained above. Secondly, spiderlings from different families in different food regimens did not survive until maturity, which would result in highly unbalanced design.

Results

Growth data

Conditions during growth had profound effects on offspring body mass and size at maturity both for male (t test for body size: t=11.119, df=96, and P<0.001; for body mass: t=12.971, df=96, and P<0.001) and female offspring (t test for body size: t=11.119, df=96, and P<0.001; for body mass: t=12.971, df=96, and P<0.001) with spiders from the high-food regimen being larger and heavier than spiders from the low-food regimen (see Table 1).

Offspring fitness-related variables

Low-food regimen

There was a significant effect of female mating history on female offspring size-related variables (Table 2). Univariate analyses reveal a significant effect of mating history on female offspring mass ($F_{2,\ 53}$=5.6 and P=0.006), but not on female offspring size ($F_{2,\ 53}$=3.13 and P=0.061). There was a significant effect of female mating history on female offspring body condition ($F_{2,\ 60}$=3.98 and P=0.024), but not male offspring body condition ($F_{2,\ 49}$=0.377 and P=0.688) (Fig. 1). Post hoc comparisons reveal that female offspring of DM females had higher body condition compared to offspring of SM (P=0.039) and RE females (P=0.048). There was no difference in body condition between female offspring of SM and RE females (P=0.929).

High-Food Regimen

There were no significant effects of female mating history on size-related variables of female or male offspring (Table 2). Similarly, female mating history did not affect offspring body condition (female offspring: $F_{2,\ 60}$=2.283 and P=0.111; male offspring $F_{2,\ 43}$=0.329 and P=0.722) (Fig. 1).

Offspring survival

Spiders from 70 families out of 75 survived to adulthood both in low-food and high-food regimen. In low-food regimen the numbers of families per experimental groups were as follows: 34 SM out of 38, 20 DM out of 20, and 16 RE out of 17; in high-food regimen the numbers were 35 SM, 19 DM, and 16 RE. There is no difference in the probability of family survival between food regimens (Pearson χ^2: df=2, χ^2=0.04, and P=0.98). In low-food regimen the mean percent offspring survival for different experimental groups was as follows: SM 65.2±3.61%, DM 62.5±6.03%, and RE 66.67±5.27%. In high-food regimen the mean percent offspring survival was lower than that of low-food regimen: SM 57.62±4.12%, DM 51.75±4.75%, and RE 52.08±4.78%. There was no effect of female mating history on offspring survival within low-food ($LLR_{2,\ 62}$=0.16 and P=0.849) and high-food regimens ($LLR_{2,\ 69}$=0.58 and P=0.559). All of the covariates used in the models were nonsignificant (all P>0.087 in both generalized linear models).

Discussion

Female multiple mating in *S. lineatus* resulted in increased body mass in female offspring, but not male offspring, under a low-food feeding regimen. Double-mated females produced heavier female offspring than females that mated with one male only (SM and RE groups). This effect remained when female offspring body mass was scaled by

Table 1 Mean body mass and body size (±SE) for males and females raised under low-food and high-food raising conditions

	Low-food		High-food	
	Number of spiders	Mean±SE	Number of spiders	Mean±SE
Male body size	52	3.24 mm±0.03	46	3.88 mm±0.05
Male body mass	52	0.161 g±0.005	46	0.289 g±0.009
Female body size	63	3.77 mm±0.03	63	4.2 mm±0.03
Female body mass	63	0.267 g±0.007	63	0.369 g±0.011

See text for analysis

body size, suggesting that double mating resulted in improved body condition of female offspring. There was no effect of female mating history on offspring size-related variables or condition under high-food regimen. These results suggest that the benefits of polyandry depend not only on sex, but also on offspring rearing environment. Female mating history had no detectable effect on offspring survival and none under high-food or low-food regimen (*cf*. Ivy and Sakaluk 2005).

Indirect benefits of polyandry were shown in previous studies (reviewed in Jennions and Petrie 2000; also see Konior and Radwan 2001; Sakaluk et al. 2002; Ivy and Sakaluk 2005; Uhl et al. 2005). Thus, polyandrous female crickets *Gryllodes sigillatus* produced larger sons, though no effect on female offspring was detected (Sakaluk et al. 2002). Sakaluk et al. (2002) suggested that sexual asymmetry in the effect of mating history on offspring mass implies a genetic benefit of polyandry, although direct benefits could not be ruled out. In *S. lineatus* males do not present females with nuptial gifts, nor do they deposit sperm in spermatophores. Moreover, males function as kleptoparasites on females' webs (Maklakov et al. 2003); consequently, male presence on the female's web reduces female body condition (Erez et al. 2005). It is important to note that mating with two different males resulted in reduced offspring body size at dispersal (i.e., early in life) compared to offspring of SM and RE females (Maklakov and Lubin 2004). Collectively, these arguments speak against the direct benefits of polyandry in this system.

Double-mated females did acquire indirect benefits in terms of increased female offspring mass and condition in our study. However, the effects were detectable only in low-food regimen and not in high-food regimen, suggesting a genotype × environment interaction (reviewed in Hunt et al. 2004). These results differ from the data on crickets *G. sigillatus* where the effect of polyandry on body mass of

Table 2 The effect of female mating history on offspring body size and body mass

Statistical variables	Low-food			High-food		
	df	Wilks' lambda	*P* value	*df*	Wilks' lambda	*P* value
Females	*n*=63			*n*=63		
Mating history	4, 104	0.797	0.018	4, 104	0.901	0.244
Female size	2, 52	0.979	0.572	2, 52	0.973	0.496
Male size	2, 52	0.966	0.409	2, 52	0.985	0.677
Female mass	2, 52	0.912	0.091	2, 52	0.971	0.467
Male mass	2, 52	0.980	0.588	2, 52	0.912	0.092
Clutch size	2, 52	0.991	0.787	2, 52	0.972	0.481
Unhatched eggs	2, 52	0.900	0.064	2, 52	0.990	0.765
Development time	2, 52	0.868	0.025	2, 52	0.930	0.151
Males	*n*=52			*n*=46		
Mating history	4, 82	0.877	0.244	4, 70	0.962	0.851
Female size	2, 41	0.901	0.119	2, 35	0.998	0.383
Male size	2, 41	0.997	0.939	2, 35	0.933	0.295
Female mass	2, 41	0.828	0.021	2, 35	0.992	0.875
Male mass	2, 41	0.992	0.854	2, 35	0.982	0.734
Clutch size	2, 41	0.838	0.027	2, 35	0.934	0.305
Unhatched eggs	2, 41	0.699	0.001	2, 35	0.973	0.620
Development time	2, 41	0.795	0.009	2, 35	0.977	0.670

The data were analyzed as MANCOVA models for spiders reared under low-food and high-food regimen with mating history as a factor and parent body size and body mass, clutch size, unhatched eggs, and relative development time as covariates. Note that development time is estimated differently for males and female (see "Materials and methods")

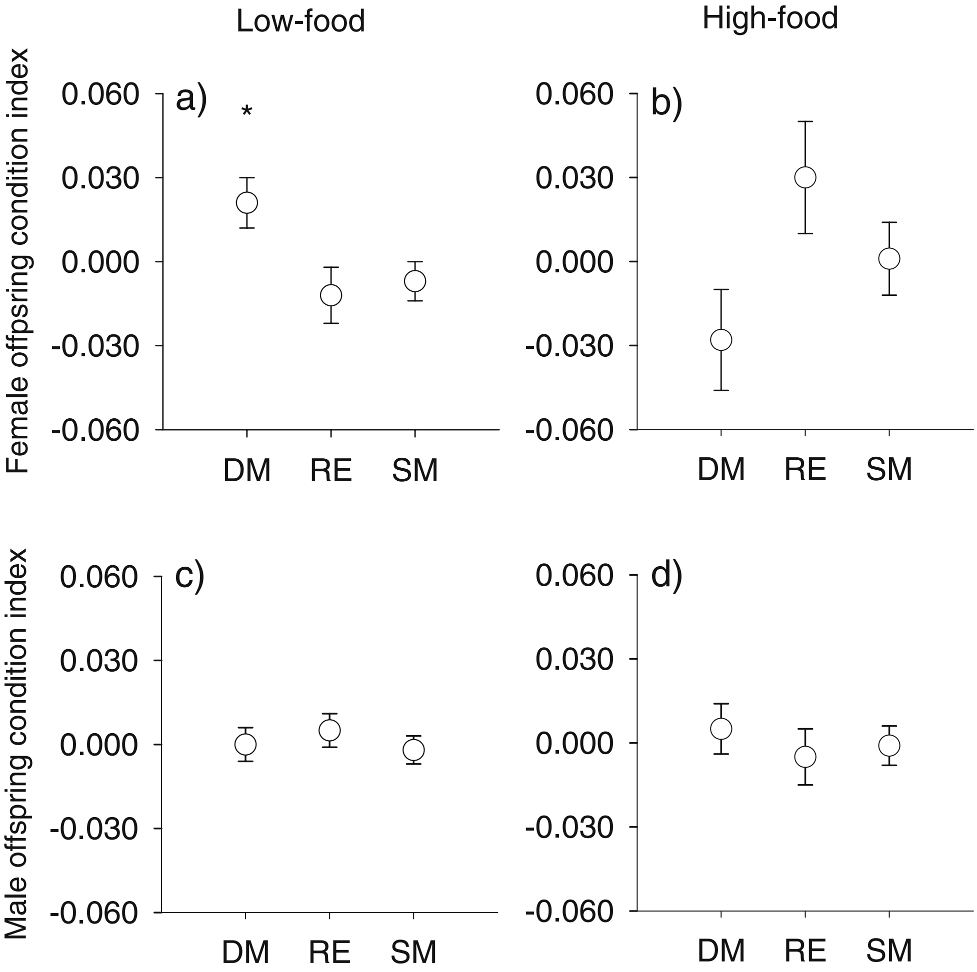

Fig. 1 The effects of female mating history on female and male offspring body condition index (residuals from linear regression of body mass on body size) reared under low-food or high-food regimen. Female offspring of double-mated (*DM*) females had higher body condition compared with single-mated (*SM*) females. Females that rejected the second male (*RE*) when reared under low-food regimen (**a**), but not when reared on high-food regimen (**b**). No effects of female mating history were found for male offspring neither on low-food (**c**) nor on high-food (**d**) rearing regimen. The *asterisk* indicates a group that was significantly different from the other two groups. See text for statistics

male offspring was similar across food regimens (Sakaluk et al. 2002). Our data, however, are in line with the study on the cellar spider *Pholcus phalangioides* where female offspring from double-mating group had higher body condition index compared with offspring from single-mating groups under low-food, but not high-food, regimen (Uhl et al. 2005). The genetic benefits of polyandry could potentially be masked by high body condition of spiders in high-food group. This finding strengthens the importance of testing the genetic benefits over a range of different environments (Hunt et al. 2004). The life history of web-building spiders is characterized by stochastic food acquisition (Vollrath 1987) and spiders are known to be well adapted to long periods of starvation (Foelix 1996). We believe it is unlikely that *S. lineatus* spiders enjoy consistent high-food supply during their development from the first instar until adulthood in nature. We therefore suggest that low-food regimen more closely reflects the rate of food acquisition by juvenile *S. lineatus* under natural conditions.

Size-related variables are important life history components that have pronounced effects on offspring fitness (Stearns 1992). Large females are generally more fecund (Reznick 1985), including spider females (Marshall and Gittleman 1994) and *S. lineatus* (Schneider 1995). Nevertheless, sexual selection is expected to favor large body size in males as well (Andersson 1994). Small difference in body size between males and females promotes male success in combat with egg-tending females (Schneider and Lubin 1997) and heavier/larger males are more successful in mating with previously mated females (Maklakov et al. 2003, 2004). Large body size confers success in male–male combat (Riechert 1978), and we found the same in *S. lineatus* (Maklakov et al. 2004).

Indirect genetic benefits could be acquired via polyandry when males successful in sperm competition can pass this trait to their male offspring ("sexy-sperm model") (Curtsinger 1991) or when there is an additional increase in offspring viability ("good-sperm model") (Yasui 1998). Because heavier/larger males are more successful in mating with previously mated females (Maklakov et al. 2003, 2004) and double-mated females tend to produce heavier offspring, it is reasonable to assume that larger males produce larger offspring and that female resistance functions to screen for larger mates. However, we argue that this is unlikely to be the case. Firstly, size and mass of the sire have no effect here and our data indicate that maternal and other environmental effects are important in defining offspring size at adulthood. Secondly, the observed pattern of the effect of female mating history on offspring fitness suggests that double mating per se results in genetic benefits, rather than the opportunity to choose between different partners (Uhl et al. 2005). Indeed, the sequential polyandry model assumes that females remate when their additional mate is better than their initial mate and reject remating if an additional mate is of lower genetic quality than the initial mate. Under this scenario, the females that are given an opportunity to improve their initial mate choice, i.e., females that are presented with two males sequentially, are predicted to have higher fitness compared to females mated to one male only. We found fitness benefits to double-mated females compared to both single-mated females and females that rejected the second male; at the same time, we found no difference between single mated females and females that rejected the second male. Therefore, it is unlikely that female resistance functions to screen for high quality males (cf. Uhl et al. 2005). We suggest that female resistance to remating evolved to reduce the direct costs associated with mating and male cohabitation in this system (Schneider and Lubin 1996; Maklakov et al. 2005; Erez et al. 2005).

Sakaluk et al. (2002) and Uhl et al. (2005) suggested that levels of polyandry in laboratory studies underestimate those found in nature. *S. lineatus* females encounter on average two males during breeding season in nature (Schneider 1997; Schneider and Lubin 1997; Maklakov et al. 2005), thus, our experimental mating rates were reasonable. Still, it is potentially rewarding to trace the changes in fitness returns with different levels of polyandry (e.g., Arnqvist et al. 2005). The challenge is to quantify the direct and indirect effects of multiple mating on female fitness in different taxa under conditions that reflect the recent evolutionary history of the organisms.

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