

EVOLUTION UNDER RELAXED SEXUAL CONFLICT IN THE BULB MITE *RHIZOGLYPHUS ROBINI*

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Abstract.—The experimental evolution under different levels of sexual conflict have been used to demonstrate antagonistic coevolution in muscids, but among other taxa a similar approach has not been employed. Here, we describe the results of 37 generations of evolution under either experimentally enforced monogamy or polygamy in the bulb mite *Rhizoglyphus robini*. Three replicates were maintained for each treatment. Monogamy makes male and female interests congruent; thus selection is expected to decrease harmfulness of males to their partners. Our results were consistent with this prediction in that females from monogamous lines achieved lower fecundity when housed with males from polygamous lines. Fecundity of polygamous females was not affected by mating system under which their partners evolved, which suggests that they were more resistant to male-induced harm. As predicted by the antagonistic coevolution hypothesis, the decrease in harmfulness of monogamous males was accompanied by a decline in reproductive competitiveness. In contrast, female fecundity and embryonic viability, which were not expected to be correlated with male harmfulness, did not differ between monogamous and polygamous lines. None of the fitness components assayed differed between individuals obtained from crosses between parents from the same line and those obtained from crosses between parents from different lines within the same mating system. This indicates that inbreeding depression did not confound our results. However, interpretation of our results is complicated by the fact that both males and females from monogamous lines evolved smaller body size compared to individuals from polygamous lines. Although a decrease in reproductive performance of males from monogamous lines was still significant when body size was taken into account, we were not able to separate the effects of male body size and mating system in their influence on fecundity of their female partners.

Key words.—Acari, antagonistic coevolution, enforced monogamy, experimental evolution, mating systems, sexual selection, sperm competition.

Received February 7, 2006. Accepted June 19, 2006.

Male reproductive success is typically limited by the access to mates, rather than by the numbers of sperm they produce, whereas reproductive success of females is mostly limited by their fecundity (Bateman 1948). As a consequence of this asymmetry there is strong selection on males to improve their access to females (and their gametes), that is, sexual selection (Darwin 1871; Andersson 1994). Such selection on males can favor traits that increase their reproductive competitiveness even if the same traits cause harm to their female partners (Parker 1979; Rice 1996; Chapman et al. 2003; Arnqvist and Rowe 2005). On the other hand, females are likely to evolve counter-adaptations that decrease male-inflicted harm. If these female counter-adaptations affect male mating or fertilization success, then selection on males is expected to favor traits that overwhelm female defenses, leading to a perpetual arms race between sexes (Parker 1979; Holland and Rice 1998).

Antagonistic coevolution is difficult to observe, but has nevertheless been convincingly demonstrated in a few studies employing a comparative analysis or experimental evolution. In water striders, a relative measure of male structures aiding in grasping females and female antigrasping structures has been shown to be associated with the outcome of sexually antagonistic interactions, such as premating struggle (Arnqvist and Rowe 2002). Rice (1996) used cytogenetic methods to arrest female evolution in *Drosophila melanogaster*. Males, adapting to nonevolving females during 30 generations of the experimental evolution, increased their fitness, achieved higher remating rates, and were more harmful to their mates. In another experiment, monogamy was experimentally enforced in *D. melanogaster* lines, such that male and female

interests coincided and thus sexual conflict was reduced (Holland and Rice 1999). Males evolving under monogamy became less harmful to females compared to polygamous males. Interestingly, Holland and Rice (1999) also found that females evolving under relaxed sexual conflict became more susceptible to harm caused by polygamous males. A similar design was applied to other fly species, *Scatophaga stercoraria* (Hosken et al. 2001), *Sepsis cynipsea* (Martin and Hosken 2003), and *Drosophila subobscura* (Crudginton et al. 2005) and the authors arrived at generally similar conclusions (but see Crudginton et al. 2005).

However, the evidence in support of the significance of antagonistic coevolution driven by sexual conflict is quite restricted and limited taxonomically. Here, we use experimental evolution to investigate the importance of antagonistic coevolution in the bulb mite (*Rhizoglyphus robini*, Acari, Acaridae). The bulb mite is characterized by a promiscuous mating system (Radwan and Siva-Jothy 1996), and both costs and benefits of mating have been documented. Mating with many partners was found to increase fecundity of polyandrous females' daughters compared to daughters of females that copulated repeatedly with the same male (Konior et al. 2001). Thus, promiscuity, requiring high mating rates, may indirectly benefit females (Kozielska et al. 2004). In contrast, experimentally decreased mating frequency increased female lifetime fecundity (Kołodziejczyk and Radwan 2003), suggesting that mating is associated with direct fitness costs to females. Here, we test whether these costs arise as a by-product of male adaptation to reproductive competition. Monogamy makes male and female interests congruent: males harming their mates pay costs in terms of decreased fitness

of their sole partners, whereas benefits of increased sexual competitiveness do not apply. Thus, it can be expected that males in lines with enforced monogamy will evolve decreased harmfulness to females, which should be coupled with lower male sexual competitiveness (Holland and Rice 1999).

The main criticism of some of the earlier experimental evolution experiments is that monogamous and polygamous lines undergo different degrees of inbreeding during many generations under limited population size (Snook 2001; but see Rice and Holland 2005). Therefore, we also assessed the degree of inbreeding depression in polygamous and monogamous lines by comparing fitness components of individuals obtained from crosses within lines (possibly homozygous for some recessive deleterious mutations due to inbreeding) with fitness components of individuals obtained from crosses between lines (made heterozygous for those mutations).

MATERIALS AND METHODS

Culturing

The laboratory population used in this study was established in 1998 from about 200 individuals obtained from onions. It was then maintained as a large population (>1000 individuals) for more than 100 generations before commencement of this research. Culturing conditions were 22–26°C, >90% humidity, and food consisted of a 3:1 mixture of powdered yeast and wheat germ ad libitum (see Radwan et al. 2004 for details). The same feeding, humidity, and temperature conditions were maintained throughout the procedures described below. Individually isolated mites, pairs, and small groups of mites were kept in 0.8-cm diameter vials (2 cm high) with plaster of paris bases soaked with water, and were provided with food ad libitum. Larger groups were kept in similar 2.5-cm diameter vials.

The Lines

Three lines with sexual selection experimentally removed (henceforth monogamy lines, M1, M2, and M3) and three with sexual selection retained (henceforth polygamous lines, P1, P2, and P3) were established in January 2002. Each line consisted of 100 males and 100 females, mated one to two days after emergence. In monogamous lines, each female remained paired with one randomly assigned male for a week in an 8-mm diameter vial. In polygamous lines, five males and five females were housed together for a week. This allowed for the operation of sexual selection, as evidenced by increased variance in male mating success in excess of random expectation (Radwan et al. 2004). On the eighth day, all females from each line were placed in a common 2.5-cm diameter vial where they oviposited for one day. The eggs were left until larvae emerged on day 7, at which time fresh food was provided. Five days later 300 nymphs were collected at random, and isolated individually to obtain virgin males and females. The isolated individuals were left in the cells for another four days, which is 1–2 days longer than required for adults to emerge. Thus, natural selection could act on female fecundity and offspring survival in both M and P lines, but not on the development rate of offspring. One

hundred individuals of each sex were used to establish the next generation.

The lines were maintained for 37 generations until April 2005, when we carried out experimental crosses to control for maternal effects and to test for inbreeding depression. To reduce maternal effects of polyandry (Kozielska et al. 2004), both M and P lines were passed through two generations of monogamous mating. Males and females were paired at random, except that mating with siblings was avoided. Unlike previous generations, each female oviposited in an individual cell, and contributed exactly one male and one female to the next generation. This change was introduced to avoid natural selection, such that frequencies of genes after two generations of monogamy should change very little compared to M and P lines of the 37th generation.

To investigate whether M and P lines differed in inbreeding depression, during the second generation of monogamous crossings we mated females outside their lines, but within the same mating system. We performed the following replicated crosses: female P1 × male P3, female P2 × male P1, female P3 × male P2, and similar combination of M lines. If M or P lines had fitness decreased due to inbreeding depression, we expected a significant effect of cross type (within or outside line).

Fitness Assays

Male reproductive success was estimated in assays in which a male from the experimental line competed with two males from the stock culture over access to two females for five days. The females were obtained from the stock culture at their nymphal stage and were virgin, one to two days old at the beginning of experiment. Of the two morphs occurring in this species (aggressive heteromorphs and benign homeomorphs; Radwan 1995), the latter was rare in the stock culture. The proportion of homeomorphs in our lines ($n = 55$ males/line morphed on average) was also low (see Results). We therefore used only heteromorphs in all experiments. Twenty males from each line were tested. All males (including those from the stock culture) were one to two days old when used for the experiments, and each was kept with a female from the stock culture for two days before the experiment began. To enable their recognition, stock culture males were fed food mixed with Blue Nile (BDH Chemicals, Poole, England) for two days prior to experiments. The dye lasts for several days and does not affect male behavior or survival (Woodring and Cutcher 1968). The cells were inspected three times a day (at 800 h, 1400 h, and 2000 h) and survival, copulations, and fights were recorded. To allow estimation of fertilization success of experimental males, stock culture males were irradiated with 20 krad gamma rays. This dose causes 100% embryonic mortality, without significantly compromising competitiveness of irradiated males' sperm (Radwan 1997). On the fifth day of the experiment, the mites were removed from each vial, and eggs laid by the females were counted. The proportion of eggs that hatched, which measured the fertilization success of nonirradiated experimental males, was then determined.

Even though only the eggs laid on the eighth day were used to start a new generation during the experimental evo-

TABLE 1. Means (\pm standard errors) for three fitness components to test for differential inbreeding depressing between lines. Individuals used for tests were obtained from parents crossed either within lines (W) or between lines (B) within the same mating system (P, polygamous; M, monogamous). *P*-values based on *t*-tests with 4 df.

Cross type	Mating system	Lifetime eggs		Eggs days 7–12		Embryo viability		Male success	
		Mean \pm SE	<i>P</i>	Mean \pm SE	<i>P</i>	Mean \pm SE	<i>P</i>	Mean \pm SE	<i>P</i>
W	M	284.3 \pm 13.6	0.53	86.7 \pm 5.2	0.66	97.8 \pm 0.1	0.18	0.431 \pm 0.013	0.58
B		278.0 \pm 7.9		90.7 \pm 6.8		97.4 \pm 0.2		0.476 \pm 0.073	
W	P	286.8 \pm 15.6	0.81	95.5 \pm 5.8	0.40	97.5 \pm 0.3	0.52	0.617 \pm 0.014	0.82
B		284.4 \pm 5.1		102.4 \pm 4.6		96.6 \pm 1.2		0.634 \pm 0.071	

lution procedures, we used lifetime fecundity as the main index of female fitness. The advantage of using lifetime fecundity was that it allowed us to trace long-term effects of our experimental treatments. Female bulb mites oviposit continuously, starting about 24 h after the first insemination, and the egg-laying rate remains nearly constant throughout the first two to three weeks (Konior et al. 2001). Thus, evolution of a steep increase in the fecundity at day 8 seems unlikely. Nevertheless, we additionally analyzed the number of eggs laid by females at about the eighth day of the experiment.

Our aim was to examine how the mating system under which a male evolved affects fitness of his female partner. However, evolution within lines could have a variety of consequences for reproductive biology of both sexes, some of which might not be associated with sexual conflict. For example, evolving within the same line could affect the perception of kinship and thus influence mating preferences: same line individuals might be perceived as more related and discriminated against. To avoid confounding the effect of evolving within the same or a different line with the effect of the mating system, fecundity and progeny viability were estimated for females that were always paired with males from a different line than the female but evolved either under the same mating system as the female or a different one. Thus, we had the following replicated pairings for P females within the same mating system: female P1 \times male P3, female P2 \times male P1, and female P3 \times male P2. The pairings between mating systems, involving P females were: female P1 \times male M3, female P2 \times male M1, and female P3 \times male M2. Analogous pair combinations within and between mating systems were also applied to M females. Lifetime fecundity was measured for females housed in 0.8-mm vials with a single male throughout the experiments. If a male died, it was replaced by another male from the same age cohort and the same line. We recorded female survival every second day. Eggs laid by each female were counted every six days,

TABLE 2. Results of repeated measures ANOVA on male and female size, with mating system as a fixed factor and sex as a repeated factor.

Effect	df	MS	<i>F</i>	<i>P</i>
Mating system	1	2387	223.5	<0.001
Error	4	11		
Sex	1	64617	2288.2	0.001
Interaction	1	0	0.001	0.935
Error	4	28		

following transfer of a pair to new vial. Twenty females from each line were tested.

To estimate embryonic survival, eggs laid between 20th and 25th day of the experiment were counted for seven females from each line. The number of hatched eggs was recorded eight days after egg collection.

Statistics

As lines were independent observations, all analyses were done on line means (see Holland and Rice 1999; Radwan et al. 2004).

RESULTS

None of the tested components of fitness showed significant inbreeding depression. Individuals obtained from crosses between lines within each mating system performed equally well as individuals obtained from crosses within lines (Table 1). Further tests described below were carried out on individuals crossed within lines.

There was no significant difference in male morph ratios between monogamous (86.1% heteromorphic males, SD = 8%) and polygamous lines ($88.1 \pm 2\%$; $t_4 = 0.37$, $P = 0.731$). Male reproductive success was lower in monogamous lines than in polygamous lines (Table 1; $t_4 = 10.0$, $P < 0.001$), but both males and females from polygamous lines were larger than those from monogamous lines (Table 2, Fig. 1). To find out whether higher reproductive success of P males is explained by their larger size, the analysis of covariance was performed with male size as a covariate. However, the effect of the line remained significant ($F_{1,3} = 12.92$, $P = 0.036$),

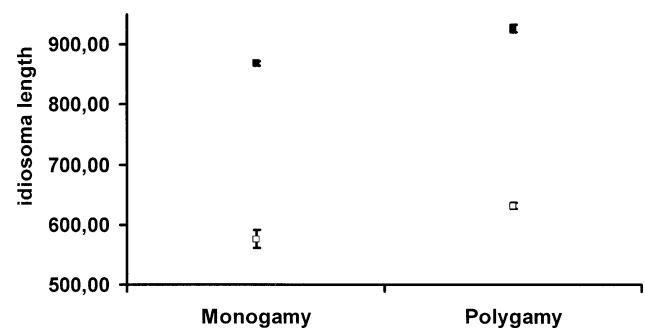


FIG. 1. Mean body sizes (idiosoma length \pm SD) of males (open symbols) and females (filled symbols) from monogamous and polygamous lines (μm).

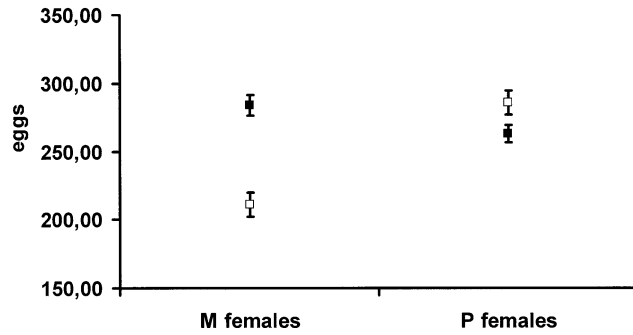


FIG. 2. Mean (\pm SE) fecundity of females mated to males from monogamous (filled symbols) or polygamous (open symbols) lines. M, monogamy lines; P, polygamy lines.

whereas the effect of male size was not significant ($F_{1,3} = 0.45$, $P = 0.550$).

There was no significant difference between mating systems in the mean number of copulations recorded ($t_4 = 0.03$, $P = 0.979$; mean \pm SE: 4.53 ± 0.38 for M lines and 4.51 ± 0.49 for P lines). Males from polygamous lines were involved in fights more often (mean \pm SE: 1.88 ± 0.02) than males from monogamous lines (1.50 ± 0.15), but the difference was not significant ($t_4 = 2.49$, $P = 0.067$). Survival of males relative to control males was tested in ANCOVA with survival of the experimental male as the dependent variable, mating system as a factor, and sum of days survived by control males as a covariate. However, the effect of mating system was not significant ($F_{1,3} = 1.30$, $P = 0.33$; average (\pm SE) days survived was 5.75 ± 0.13 for M males and 5.36 ± 0.36 for P males).

Unlike male reproductive success, there was no significant difference between polygamous and monogamous lines in female lifetime fecundity ($t_4 = 0.21$, $P = 0.846$), fecundity between days 7 and 12 (which included the day 8, when eggs were collected from females in all lines to start a new generation; $t_4 = 1.14$, $P = 0.317$) or embryonic mortality ($t_4 = 1.16$, $P = 0.311$; see Table 1 for means).

Lifetime fecundity of M females was significantly lower when they were paired with P males, compared to pairing with M males (Fig. 2, $t_4 = 6.14$, $P = 0.003$). However, the fitness of P females was not significantly affected by the origin of their partner (Fig. 2, $t_4 = 2.37$, $P = 0.077$). To find out whether the significant effect on M females resulted from their shortened life span on exposure to P males, or from their reduced egg production rate, we performed two analyses. The first revealed marginally insignificant effect of male mating system on female life span ($t_4 = 2.70$, $P = 0.054$; mean \pm SD: 24.6 ± 0.33 days for P males and 28.9 ± 2.78 for M males). However, in ANCOVA with longevity as a covariate, lifetime fecundity become marginally insignificant ($F_{1,3} = 8.54$, $P = 0.061$). These two complementary analyses thus suggest that longevity and egg production rate jointly contribute to the highly significant effect of male mating system on female lifetime fecundity.

In the next analysis we examined whether the effect of male mating system on female lifetime fecundity is correlated with male size, which differed between mating systems. When partner size was entered in the analysis, the effect was

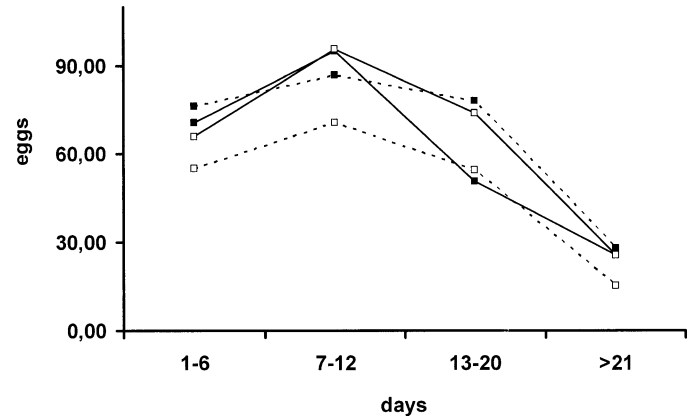


FIG. 3. Mean number of eggs laid by females mated to males from monogamous (filled symbols) or polygamous (open symbols) lines throughout the experiment (eggs were counted every six days). Broken lines, M females; solid lines, P females.

no longer significant ($F_{1,3} = 0.46$, $P = 0.547$). However, neither was the effect of male size ($F_{1,3} = 4.01$, $P = 0.138$), which indicates that the effects of male size and mating system are strongly correlated and cannot be separated statistically.

Similar results were obtained when we analyzed the number of eggs laid by females between days 7 and 12 (Fig. 3). Fecundity during this period was significantly correlated with lifetime fecundity ($r = 0.80$, $n = 12$, $P < 0.002$). Females from M lines paired with M males laid more eggs between day 7 and 12 (mean \pm SD: 90.8 ± 7.6) than those paired with P males (83.0 ± 15.3 ; $t_4 = 2.84$, $P = 0.046$). However, fecundity of females from P lines was not affected by the line of origin of her partner (M males: 94.9 ± 12.6 ; P males: 95.5 ± 10.0 ; $t_4 = 0.93$, $P = 0.401$). The effect of male line on fecundity of M females become insignificant when male size was entered as a covariate ($F_{1,3} = 0.87$, $P = 0.419$; male size effect: $F_{1,3} = 0.02$, $P = 0.907$).

In contrast to fecundity, there was no significant effect of male mating system on embryonic viability. Proportions of hatched eggs for M females were (means \pm SD) 0.978 ± 0.003 when paired with M males and 0.975 ± 0.0023 when paired with P males ($t_4 = 1.30$, $P = 0.262$); for P females, 0.973 ± 0.0094 when paired with M males and 0.974 ± 0.0032 when paired with P males ($t_4 = 0.15$, $P = 0.885$).

DISCUSSION

We found that, in accordance with the antagonistic co-evolution hypothesis, enforced monogamy resulted in deterioration in male sexual competitiveness. This decline was accompanied by a reduction in harmfulness to females, as revealed in higher lifetime fecundity of monogamous females when mated to monogamous males (Fig. 2). This effect was also significant for fecundity measured around the day 8 (i.e., the day on which selection on female fecundity was exercised in our experimental evolution lines), indicating that harmful effects of P males were already detectable in the short-term egg production rate. There was also a marginally insignificant effect of male mating system on longevity of M females, suggesting that the long-term effect on female survival also

contributed to a decrease in lifetime fecundity on exposure to P males.

Our results are thus consistent with those obtained in similar experiments in muscids, in which males evolving under monogamy had lower reproductive success (Holland and Rice 1999; Hosken et al. 2001) but were more benign to females compared to males evolving under polygamy (Holland and Rice 1999; Crudgington et al. 2005; but see Wigby and Chapman 2004). These results suggest that monogamous males are less harmful to their mates, and that the decline in sexual competitiveness could be a side-effect of their decreased harmfulness.

The decrease in fecundity of females exposed to males from polygamous lines was observed for monogamous, but not polygamous, females. This suggests that polygamous females were largely resistant to male harm; thus, mating with more harmful polygamous males did not detectably decrease their fitness compared to mating with monogamous males. The resistance of polygamous females probably resulted from the retention of the mechanism originally present in the stock population. Indeed, in this naturally highly promiscuous species (Radwan and Siva-Jothy 1996) it could be expected that polygamous lines would remain relatively static, whereas evolution could proceed under a novel situation of enforced monogamy. The lack of negative effect of polyandrous males on polyandrous females' fecundity, even though the males came from different lines than the females, is in agreement with the hypothesis that female resistance mechanisms in all polygamous lines were inherited from the original population.

Kołodziejczyk and Radwan (2003) found that experimentally reduced exposure to males increases female lifetime fecundity, implying a cost of mating to females. This could be the cost of mating per se, cost of male harassment (e.g., Rowe 1994), or the result of higher exposure to substances passed by males during copulation (Chapman et al. 1995). In the present study we found that males from monogamous and polygamous lines did not differ in the frequency of mating or in survival. This suggests that decreased competitiveness of monogamous lines, coupled with their lowered harmfulness to females, might result from a reduction in transfer of seminal fluids, which in acarid mites seem to play a role in removal or incapacitation of sperm deposited in spermatheca (Radwan and Witaliński 1991). Whether these substances harm females remains to be investigated.

The decline in reproductive success of males from monogamous lines might, conceivably, be an effect of general fitness decline in those lines, rather than the side-effect of adaptation to the situation in which sexual conflict is removed. The first factor that could potentially cause such a decline is differential inbreeding depression between monogamous and polygamous lines (Snook 2001; Wigby and Chapman 2004). However, if inbreeding affected performance of our lines, we expected individuals obtained from crosses between lines (within the same mating system) to outperform those obtained from crosses within lines. This was not the case of male reproductive success, or indeed any other fitness components measured (Tables 1, 2). This result thus provides an experimental confirmation of calculations presented by Rice and Holland (2005) who argued that effects

of differential inbreeding at effective population sizes similar to that used in our study, should be negligible.

Another possibility is that experimental removal of sexual selection leads to a faster rate of accumulation of deleterious mutations in monogamous lines compared to polygamous lines. However, although sexual selection was shown to affect the rate of removal of experimentally induced mutations (Radwan 2004), no detectable effect was demonstrated when spontaneous mutations were accumulated for 12 generations (Radwan et al. 2004). Furthermore, the decline we recorded in reproductive success of males from monogamous lines was not observed for other fitness components we measured (Table 1). This implies that removal of sexual selection did not cause a general decline in fitness of monogamous lines.

Finally, we need to consider the possibility that both the decline in male reproductive success, and the accompanying male effects on fecundity of their mates, result from inadvertent selection pressures resulting from our experimental design. In particular, inadvertent selection for body size was suggested to be a possible confounding factor influencing performance of males from *Drosophila melanogaster* lines selected by Holland and Rice (1999; Pitnick and Garcia-Gonzalez 2002; but see Rice and Holland 2005). Such selection could result from selection for fast development (and maturation at lower size), which in polygamous lines could be opposed by sexual selection for increased body size (Pitnick et al. 2001). Indeed, we found that after 37 generations of experimental evolution both males and females from monogamous lines were smaller than those from polygamous lines. However, we believe that this difference is unlikely to result from inadvertent selection, because our lines were not selected for fast maturation: we picked progeny from eggs laid on a single day, and the time to reach adulthood exceeded the average development time by one to two days. Rice and Holland (2005) extended analyses of their original data to show that effect sizes of enforced monogamy were considerably larger than the effects of male size. Our analyses showed that, in the case of male reproductive success, the effect of mating system remained significant after we statistically controlled for male size, which suggests that sexual selection for large body size was not very strong in our study. However, using male size as a covariate in the analysis of fecundity of monogamous females rendered the effect of male selection regime insignificant. Thus, although we find the hypothesis of inadvertent evolution unlikely to explain our results, we acknowledge that we cannot separate the effect of male size on female fecundity from the effect of mating system. However, these effects may be intrinsically correlated. In fact, the "inadvertent selection" alternative implies that mating with large males is more harmful to females, otherwise there would be no reason to expect inadvertent selection for low body size to produce a correlated response in terms of decreased harmfulness. Indeed, the existence of such association was experimentally corroborated in *Drosophila melanogaster* (Friberg and Arnqvist 2003). Thus, in the absence of inadvertent evolution for reduced body size, it seems that smaller size of monogamous males could result from selection for reduced male harmfulness, rather than the other way round.

It is not clear why female body size decreased simulta-

neously. Body size may be genetically correlated between sexes; thus, selection for a decrease in male body size could cause a correlated response in females. Although female body size is (weakly) associated with increased fecundity in this species (Radwan et al. 2003), fecundity selection might not be efficient enough in opposing a correlated decrease in female body size if benefits of mating with small, less harmful males outweighed costs associated with producing smaller daughters. A decrease in the size of glands or other structures that are used to resist harmful effects caused by males might be another factor that could potentially contribute to a decrease in the body size of M females. This latter possibility remains to be explored, since the physiological and morphological mechanisms of female resistance to harm caused by sexually selected male adaptations is unknown.

ACKNOWLEDGMENTS

We thank D. Hosken, M. Konior, Associate Editor L. Rowe, and two anonymous referees for their useful comments on the earlier versions of the paper. This work was supported by the State Committee for Scientific Research (KBN 0408/P04/2001), Poland.

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