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Postmating Sexual Selection Favors Males That Sire Offspring with Low Fitness

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Despite the costs of mating, females of most taxa mate with multiple males. Polyandrous females are hypothesized to gain genetic benefits for their offspring, but this assumes paternity bias favoring male genotypes that enhance offspring viability. We determined net male genetic effects on female and offspring fitness in a seed beetle and then tested whether fertilization success was biased in favor of high-quality male genotypes in double mating experiments. Contrary to expectations, high-quality male genotypes consistently had a lower postmating fertilization success in two independent assays. Our results imply that sexually antagonistic adaptations have a major and unappreciated influence on male postmating fertilization success. Such genetic variation renders indirect genetic benefits an unlikely driver of the evolution of polyandry.

Our understanding of the evolution of multiple mating by females (i.e., polyandry) in the face of the costs of mating is limited (1, 2), despite a massive empirical effort (3, 4). Polyandry is adaptive in cases where females receive material benefits from males (3), but in many cases such direct benefits are lacking. Thus, it is commonly believed that females gain genetic (or indirect) benefits for their offspring by mating with multiple males (4). Theory suggests that genetic benefits in the form of genetic diversification or genetic bet-hedging (i.e., various forms of genetic risk-spreading) are unlikely to contribute to the evolution of polyandry (5). Instead, the genetic benefits of polyandry rely on a positive relationship between male postmating fertilization success and the viability of offspring carrying his genes (5, 6). Cryptic female

choice, which occurs through the success of certain males over others by female traits that bias postmating fertilization (7), would promote this relationship if it favors males carrying alleles with high fitness or alleles that are more compatible with the female genotype because of epistatic interactions (1, 6, 8). Females can maximize offspring fitness by choosing both types of genetic variation in fitness simultaneously (8). We thus define male genetic quality as the net viability effects of his genes in the offspring of a given female genotype. Under this wide definition, male genetic quality may vary across female genotypes and will be the sum of additive (i.e., good genes) and nonadditive (i.e., compatibility) genetic quality (8).

The relationship between male genetic quality and fertilization success plays a key role for the evolution of polyandry (9–12). Polyandrous females can reduce the cost of inbreeding by cryptic female choice for genetically compatible males (12–14). However, except for documented cases of inbreeding avoidance, very limited evidence supports the assumption that fertilization is generally biased toward males with a genotype that enhances offspring viability (1, 11, 15).

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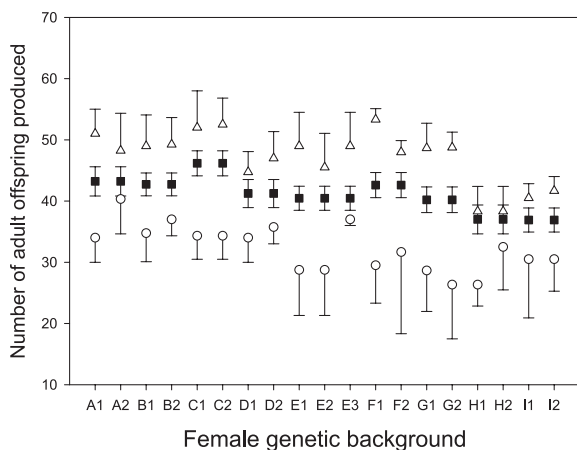


Fig. 1. The average number of adult offspring produced ($\blacksquare \pm SE$) (lifetime reproductive success, LRS) by isogenic females across all isogenic males. Male genotypes that conferred a high lifetime offspring production ($\triangle +SE$) were considered high-quality males, and those that conferred a low lifetime offspring production ($\circ -SE$) were designated low-quality males. Females enjoyed higher fitness when reproducing with high- compared with low-quality males (mixed model analysis of variance, effect of male quality: $F_{1,108} = 68.13$, $P < 0.001$).

We tested whether males of high genetic quality are also favored in postmating sexual selection in the seed beetle *Callosobruchus maculatus*. This species is polyandrous and shows both differential sperm competition success across male genotypes and cryptic female choice, as evidenced by the fact that sperm competition success of specific male genotypes varies across female genotypes (16, 17). Reciprocal crosses between a large number of discrete isogenic genotypes were used to establish both female fitness and female offspring fitness (lifetime reproductive success) in crosses between genotypes (18). For each female genotype, we ranked males according to their net genetic quality, that is, the net additive and nonadditive effect of a male genotype on fitness (18). Focal females were then mated with two males, each representing a high- and a low-quality male, in two independent assays of postmating fertilization success (19). In the first assay, male quality rank was assessed from paternal effects on the lifetime number of adult offspring produced by a given female genotype (Fig. 1). In the second, male quality rank examined paternal effects on the lifetime number of adult offspring produced by the daughters of a specific cross (18). Paternal genetic effects on the fitness of their mates and parental genetic effects on the fitness of their daughters are sizeable and significant in this species (18).

The first assay showed that males that conferred a relatively low fitness on their mates had a significantly higher rate of fertilization success [generalized linear mixed models (GLMM), $F_{1,266.4} = 15.44$, $P < 0.001$] (Fig. 2). Studies of the genetic architecture of fitness among these genotypes (18) showed that variance in the effects of male genotype on female fitness (i.e., female lifetime offspring production) is due both to direct effects, such as variance in ejaculate composition (20) or costs of mating (21, 22), and to indirect genetic effects affecting juvenile survival (18). On

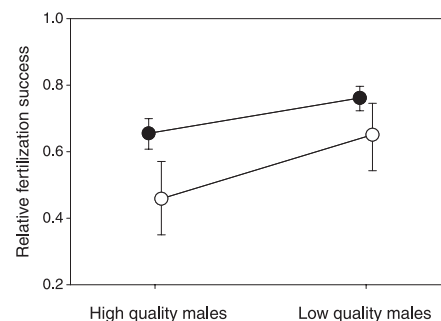


Fig. 2. Estimates of the average (with 95% confidence intervals) proportion of eggs fertilized by a second male mated with a female. Males were categorized as high or low quality on the basis of either their net effect on female lifetime offspring production (\bullet) or their paternal net genetic contribution to offspring fitness (\circ). In both assays, low-quality males sired a higher proportion of offspring.

average, females were 18% more fit (95% confidence interval = 13 to 28%) when reproducing with high-quality males relative to low-quality males. We expect then that females would benefit if they biased paternity toward high-quality males. This is supported by the fact that cryptic female choice for specific male genotypes has been demonstrated in this species (17, 23). Yet, the pattern of paternity bias that we observed was the opposite of what is expected to benefit females. In fact, our data show that males that confer a low fitness on their mates gain the highest share of paternity. This observation is consistent with the fact that male traits that increase success in sperm competition may, as a direct negative pleiotropic side effect, depress the fitness of their mates. Such sexually antagonistic male sperm competition adaptations are known from many different taxa (24), including seed beetles (21). Both male effects on female lifetime offspring production (18) and male postmating fertilization success (17, 23) are partly determined by male genotype-by-female genotype interactions in seed beetles. Our data suggest that these two types of interactions may be related, given the causal link between the paternal effects affecting a particular female genotype, and thus female fitness, and sperm competition success in that female genotype. We note that we expect to observe similar results whenever the efficacy of a sexually antagonistic male sperm competition adaptation (e.g., an accessory gland protein in the male seminal fluid) depends on the female traits with which it interacts (e.g., female receptors) (24).

In the second assay, males that fathered offspring with relatively low fitness sired a significantly higher proportion of eggs than did males of high quality. This was true whether females that did not produce any offspring of the second male to which they were mated were excluded (GLMM, $F_{1,58.9} = 8.9$, $P = 0.004$) or included (GLMM, $F_{1,162.3} = 15.9$, $P < 0.001$) (Fig. 2) in the analyses. On average, females produced daughters with 17% (95% confidence interval = 13 to 23%) higher lifetime reproductive success when reproducing with high-quality compared with low-quality males (18). A quantitative genetic study of the genetic architecture of fitness with these genotypes show that the fitness of daughters is dominated by both additive and nonadditive (dominance/epistatic) genetic variance (18). Females can gain indirect genetic benefits when their daughters have elevated reproductive success, and they can influence this by favoring genetically compatible males and/or males with a higher breeding value for offspring fitness (8). Thus, our results are again opposite to that expected under cryptic female choice for males carrying good or compatible genes for general viability (1). The apparent lack of precopulatory female mate choice in this species (25) strongly suggests that females are unable to negate this detrimental effect by exercising control before mating.

The observed negative relationship between male postmating fertilization success and the fitness effects of his genes in female offspring could be due to genes with either additive or nonadditive effects (18). If additive effects dominate, our results support that some degree of intralocus sexual conflict is occurring: the presence of sexually antagonistic genes with opposite effects on fitness when expressed in the two sexes (26). Intralocus sexual antagonism has been documented in other insects (27, 28). If common, such genes will result in successful males siring unsuccessful daughters (29). This predicts that the relationship between male quality and offspring fitness would be negative in daughters but positive in sons. However, the quantification of sex-specific genetic effects was not the aim of this study: Our primary goal was to determine the scope for nonrandom fertilization success among males to build genetic associations (i.e., linkage disequilibrium) between alleles coding for polyandry and those encoding high viability, thus generating indirect selection on female mating rate by a “good genes” process (5, 15, 18). Although intralocus sexual conflict can nullify indirect genetic benefits in one sex (28, 29), it is highly unlikely that sex-specific indirect effects would alter our main result. Because indirect selection is generally weak relative to direct selection (18, 30) and because males successful in sperm competition fathered offspring with low juvenile survival in both sexes and with low fitness in daughters (18), sex-specific benefits to sons would need to be very large indeed to result in appreciable net indirect selection for polyandry (15, 30). This possibility lacks empirical support (31). If nonadditive genetic effects dominate the fitness effects seen, they involve interactions between maternal and paternal genotypes affecting fertilization success in the parental generation and offspring fitness in the next generation. This could occur if, for example, particular combinations of sex-specific traits associated with high male paternity within a female reproductive tract are also associated with low fitness in daughters at other developmental stages.

Classic cryptic female choice (1, 7) and theory based on sexual antagonism (24, 26) make contrasting predictions with regards to the relationship between male genetic quality and paternity bias. If sexually antagonistic adaptations and/or sexually antagonistic alleles (i.e., where the direction of selection on a given allele expressed in both sexes depends on the sex in which it resides) are common and polymorphic, as is apparently the case in seed beetles, postmating sexual selection will not reward polyandrous females with the genetic benefits required to outweigh the costs of mating. Females may even suffer genetic costs from mating with multiple males in such situations, and any female benefits of polyandry must come from elements other than the paternal genetic contribution to offspring.

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Materials and Methods
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