



Material and genetic benefits of female multiple mating and polyandry

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The maintenance of female polyandry has traditionally been attributed to the material (direct) benefits derived from male mating resources (e.g. nuptial gifts) accrued by multiple mating. However, genetic (indirect) benefits offer a more robust explanation since only polyandrous, not monandrous, females may gain both material benefits from multiple mating and genetic benefits from multiple sires. Discriminating between material and genetic benefits is essential when addressing the mechanism by which polyandry is adaptively maintained, but are difficult to disentangle because they affect fitness in similar ways. To test the hypothesis that genetic benefits maintain polyandry, we compared four components of fitness (longevity, fecundity, hatching success and survivorship) between monandrous and polyandrous females in the ground cricket, *Allonemobius socius*. We discovered that females derived nongenetic benefits from mating multiply, in that the magnitude of the nuptial gift was positively associated with the number of eggs produced. However, polyandrous females had over a two fold greater hatching success and a 43% greater offspring survivorship, leading to a significantly higher relative fitness than the monandrous strategy. These results were independent of the confounding effects of material benefits, implying that genetic contributions play a large role in the maintenance of polyandry and potentially in the antagonistic coevolutionary relationship between polyandry and male nuptial gifts.

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Theory predicts a difference in mating frequency between the sexes when males and females differentially invest in offspring (Trivers 1972). In many systems with disparate parental investment, male mating frequency is largely constrained by the availability of mates, whereas female mating frequency is governed largely by the female's ability to store sperm. However, in many animal systems females mate repeatedly with a variety of males, exceeding the mating rate necessary to produce offspring continually prior to senescence. This polyandrous behaviour is unexpected in that superfluous mating often carries an associated cost. Aside from the energy and time expenditure required to engage in copulation (Thornhill & Alcock 1983), polyandrous females may be more vulnerable to predation (Arnqvist 1989), horizontally transmitted disease (Hurst et al. 1995), and/or caustic seminal fluids that ultimately reduce fitness (Fowler & Partridge 1989; Rice 1996).

A large body of empirical work suggests that these costs may be offset through the accrual of material benefits gained by the female from each mating (see Arnqvist & Nilsson 2000 for review). Material benefits are non-

genetic gains in female fitness (e.g. increased reproductive rate, reproductive longevity or fecundity) mediated through resources transferred by the male prior to, during, or following copulation. For instance, male nuptial gifts, which may consist of captured prey items, somatic tissue, or suicidal food transfers, have been shown to increase female fecundity and offspring fitness in some systems (Gwynne 1984; Reinhold 1999; Arnqvist & Nilsson 2000). Although material benefits provide a mechanism for the maintenance of female polyandry, most studies have ignored the role genetic benefits may play in this behaviour.

Genetic benefits are next-generation advantages gained through mating with numerous, genetically variable males (Yasui 1998). In essence, polyandry may reflect a bet-hedging strategy, whereby females actively seek a variety of males to lower the probability of mating with genetically incompatible, inferior or infertile mates as well as increasing next-generation genetic diversity and mean offspring fitness. A meta-analysis of 122 studies suggested that mechanisms above and beyond material benefits are unnecessary in explaining promiscuous behaviour due to the large impact these benefits have on female fitness (Arnqvist & Nilsson 2000). Unfortunately, genetic benefits are difficult to disentangle from material

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benefits, since both may affect next-generation mean fitness in similar ways. In other words, male nutrients that increase egg quality may have the same positive effect on mean offspring fitness as genetic benefits are predicted to produce, thereby obscuring potential genetic contributions. Discriminating between genetic and nongenetic effects is essential when addressing the mechanism by which female polyandry is adaptively maintained.

The striped ground cricket, *Allonemobius socius*, is an ideal organism to investigate the evolution and maintenance of female polyandry and male nuptial gifts. Not only do females mate with many different males, but male *A. socius* possess a specialized tibial spur that acts as a somatic nuptial gift chewed by the female during copulation (Mays 1971). Previous studies of *A. socius* suggest that the tibial spur provides direct access to the male's haemolymph (Fedorka & Mousseau 2002). Furthermore, the duration of tibial spur chewing was shown to be an excellent predictor of nuptial gift size, which can be as much as 10% of the male's mass prior to copulation. Gift size was also positively related to the duration of spermatophore attachment.

The evolutionary origin and contemporary maintenance of nuptial gifts has recently become the focus of debate (see Vahed 1998 for review). From the male's perspective the gift may function as a form of male mating effort by promoting copulation and/or increasing fertilization success (Thornhill 1979; Sakaluk 1984) or as paternal investment by increasing the number and/or fitness of the gift-giver's own offspring (Trivers 1972; Reinhold 1999), although these functions are not mutually exclusive (Vahed 1998). Even though both hypotheses facilitate female material benefits, the distinction between whether gifts function to increase egg quantity or quality is important because it sheds light on the gift's evolutionary origins. Considering the spur chewing and spermatophore attachment duration relationship previously established in *A. socius*, the gift may serve to elevate the number of sperm transferred during copulation, implying a mating effort function. Whether nutrients derived from nuptial feeding also act to increase immediate (e.g. reproductive longevity, fecundity, reproductive rate) or future female fitness (e.g. offspring viability) has not been tested directly in this system.

Considering these observations, we had three main objectives concerning nuptial gifts and the maintenance of polyandry in *A. socius*: (1) to determine whether nuptial feeding mediates material benefit resources; (2) to elucidate the functional significance of the nuptial gift (i.e. mating effort or paternal investment); (3) to ascertain whether genetic benefits, once disentangled from material benefits, can be invoked as a mechanism that adaptively maintains female polyandry. We predicted that the magnitude of any material benefit would be limited by the magnitude of the nuptial gift received. In other words, the duration of spur chewing would have a direct, positive effect on female fitness. We also predicted that the gift serves both as a form of mating effort and paternal investment. Finally, we predicted that polyandrous females would show a higher relative fitness

when compared to monandrous females, because while both strategies would theoretically accrue the same material benefits, only polyandry provides the additional opportunity to gain genetic benefits.

METHODS

General Maintenance

Experimental crickets were first-generation laboratory-reared individuals hatched from wild caught central South Carolina females. All crickets were maintained in plastic cages (10 × 10 × 8 cm) containing ground cat food, a carrot slice, dampened cheesecloth (water source and oviposition material) and strips of brown paper towel for cover. Every 3 days the food, carrot and paper towel were replaced. The adult female diet consisted of only carrots once the mating trials began under the assumption that a restricted diet would help accentuate the effects of nuptial feeding (Gwynne 1993). Cages were kept in a constant environment at 28°C and a 12:12 h light:dark cycle provided by a Percival incubator. The age of laboratory-reared experimental crickets was 12 ± 2 days posteclosion (final adult moult).

Mating System

In *A. socius*, males may mate multiple times and females do not discriminate based on the condition of the spur (unpublished data). Mating begins with the male performing a calling song that he uses to attract distant females. Once a potential mate is encountered, males switch to a courtship song and dance that culminates with the male orienting his abdomen towards the stationary female. If the female is receptive, she will briefly mount the male in a 'mock copulation' lasting only a few seconds. Once an effective mock copulation is achieved (this may take several attempts) the male will cease courting and begin to form a spermatophore (approximately 20 min). When complete, he will renew his courtship behaviour, again enticing the female to mount. At this time, the pair will adjoin abdomens as the male adheres the spermatophore to the female's seminal receptacle. The male will then bring his hind tibia forward allowing the female to chew on his spur until the pair separates (upwards of 30 min). Once apart, the female will remove and consume the spermatophore. Therefore, both the spermatophore and spur chewing may contribute to material benefit resources.

Experimental Design

To investigate the functional significance of male nuptial gift giving and female polyandry, we established three female treatments consisting of a monandrous, polyandrous and a control group. Each monandrous and polyandrous female received a total of four matings. To create the monandrous treatment, we mated a female to the same male four times ($N=24$ females). Polyandrous females were mated to four different males one time each

($N=24$ females). Males were rotated within the polyandrous treatment so that each female was exposed to the full range of male mating experience (i.e. 0, 1, 2 and 3 prior matings). This allowed us to hold the number of matings constant for both sexes and to help control for variance in male experience. All individuals were mated only once per day, allowing males time to recuperate the cost of spermatophore and nuptial gift contribution. The control treatment consisted of females mated once to a single virgin male ($N=73$ females).

We conducted all mating trials ($N=265$) in a small petri dish (6 cm in diameter and 1.5 cm in height) lined with filter paper. After completing their mating schedule, we isolated the females and allowed them to oviposit until their death. Females that did not complete all matings within 1 week or that died before completing at least 2 weeks of oviposition were discarded from the analysis (the majority of eggs are laid within the first 2 weeks of oviposition, personal observation). For all treatments, we measured spur chewing duration (an estimate of gift size), spermatophore attachment duration (an estimate of sperm transfer) and relative fitness ($\omega_{\text{relative}} = \omega_{\text{individual}} / \omega_{\text{average}}$). We measured individual fitness as the number of each female's offspring that reached adulthood. Moreover, we used four variables of fitness to evaluate differences in fitness between treatments: female longevity (days from adult eclosion to death); fecundity; hatching success (proportion of eggs laid that hatched); and survivorship (proportion of hatched eggs that reached adult eclosion). Although some individuals in all treatments had missing data points (e.g. spermatophore attachment duration or longevity unknown), we still included them in the analyses where appropriate.

To test the hypothesis that male gifts are both a form of mating effort and paternal investment, we examined the effect of gift size on control treatment females only. Here, we considered a significant association between chewing duration (i.e. gift size) and female longevity and/or spermatophore attachment duration as evidence of male mating effort. Since, by nature of the mating ritual, a positive association between chewing duration and spermatophore attachment seems inherent, we also examined postchewing spermatophore attachment duration, assuming that larger gifts may satiate females and cause them to postpone removal and consumption of the spermatophore. Conversely, we considered a significant association between gift size and fecundity, offspring hatching success and/or survivorship as evidence of paternal investment.

To test the hypothesis that genetic benefits help maintain female polyandry, we compared individual fitness and its components between all three treatments. Gift-derived material benefits may affect all four fitness components. However, only hatching success (a measure of genetic compatibility between the parents) and survivorship (a measure of offspring viability) have the potential to be influenced by genetic effects. To test for the genetic consequences of polyandry appropriately, we must first determine whether material benefits are a confounding factor. A confounding effect would be indicated by a significant association between gift size and hatching

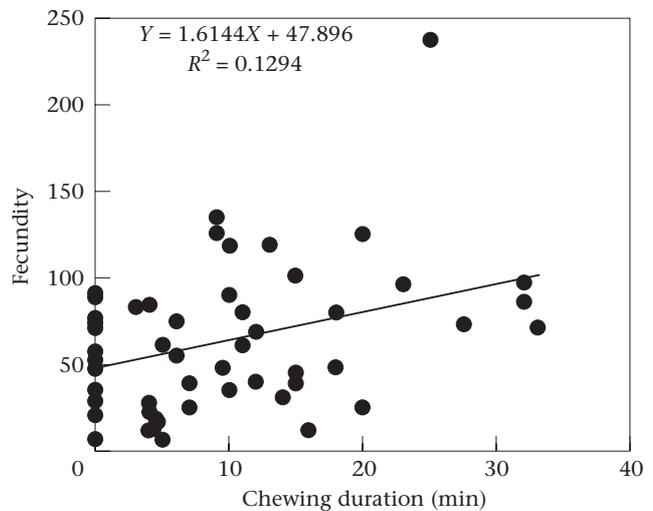


Figure 1. Fecundity as a function of tibial spur chewing duration. A least squares model predicted a 3.4% increase in fecundity for every additional minute of spur chewing, doubling reproductive output after 30 min. There was no significant association between spermatophore attachment duration and fecundity. These data support the hypothesis that the degree of material benefits are mediated by nuptial gift magnitude.

success or survivorship and/or by a difference in these variables between the monandrous and control treatments. Only in the absence of material benefits can we assess the existence of genetic effects accurately. All analyses were done using SAS version 8.1.

RESULTS

Mating Effort and Paternal Investment

Our data suggest that the magnitude of the nuptial gift, as described by spur chewing duration, had strong reproductive fitness implications. Chewing duration was a significant predictor of total spermatophore attachment duration (analysis of variance, ANOVA: $F_{1,58}=7.37$, $P<0.01$) and fecundity ($F_{1,54}=7.88$, $P<0.01$; Fig. 1). However, spermatophore attachment duration and fecundity were not significantly associated ($F_{1,43}=0.44$, $P=0.5129$), implying that male and female reproductive fitness is mediated through variance in gift size and not through variance in sperm allocation. There was no significant relationship between chewing duration and postchewing spermatophore attachment ($F_{1,40}=0.69$, $P=0.4110$). Hence, larger gifts did not keep females from delaying spermatophore removal once chewing had ceased. Chewing duration also varied independently from female longevity, offspring hatching success and offspring survivorship ($F_{1,60}=3.46$, $P<0.07$; $F_{1,52}=2.72$, $P<0.11$; $F_{1,41}=0.05$, $P<0.82$, respectively). These data weakly support both the mating effort and paternal investment hypotheses.

Material and Genetic Benefits

The magnitude of material benefits received by the female is also positively related to her mating frequency.

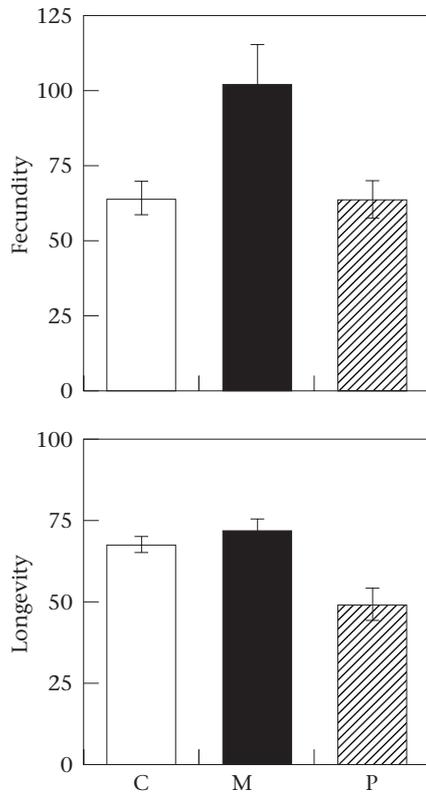


Figure 2. The material, nongenetic fitness effects of monandry and polyandry. Multiply mated monandrous females (M) possessed a significantly higher reproductive output compared with control females (C), further implying that females accrue material benefits from multiple mating ($\bar{X} \pm \text{SE}$: 102 ± 13.35 eggs versus 64.12 ± 5.40 eggs, respectively). Conversely, polyandrous females (P) incurred on average a 29% decrease in longevity when compared with both monandrous and control treatments (49.05 ± 5.14 days versus 71.51 ± 3.98 days and 67.45 ± 2.28 days, respectively).

When compared to the control treatment, monandrous females had a significantly greater reproductive output (Tukey Studentized range test: $P < 0.005$; Fig. 2). This result is consistent with the gift size, fecundity and spermato-phore relationships established above, implying that females who received larger gifts, or who received multiple gifts, gained material benefits through an increased number of offspring. Monandrous female longevity was not affected by an increased number of matings when compared to that of control females (Fig. 2). Contrary to these patterns, polyandrous females received no fecundity benefits from multiple mating when compared to control females ($F_{1,79} = 0.14$, $P < 0.72$; Fig. 2). Moreover, polyandrous female longevity was significantly shorter than both control and monandrous females (Tukey Studentized range test: $P < 0.01$; Fig. 2), suggesting a fitness cost to polyandry with regard to same-generation material benefits.

Although monandrous females gained greater material benefits from multiple mating, polyandrous females were the exclusive recipients of genetic benefits, as predicted. The eggs of polyandrous females had a 2.4-fold greater hatching success than either the monandrous or control

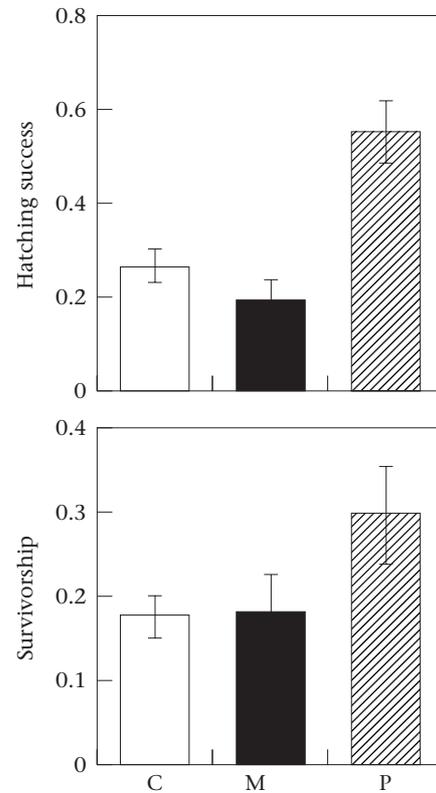


Figure 3. The genetic effects of polyandry. Polyandrous females (P) experienced an approximate 2.4-fold increase in hatching success compared with monandrous (M) or control (C) treatments ($\bar{X} \pm \text{SE}$: $0.55 \pm 0.06\%$ versus $0.19 \pm 0.04\%$ and $0.26 \pm 0.04\%$, respectively). Polyandrous females also had on average a 43% greater survivorship than did the other two treatments, however this was not significant. Thus, female fitness was positively related to the genetic diversity of the male mates.

females (Tukey Studentized range test: $P < 0.001$; Fig. 3). In addition to an increased hatching success, the coefficient of variation (CV) for polyandry was approximately 41% lower than the other treatments ($CV_P = 62.02\%$, $CV_M = 107.85\%$, $CV_C = 103.42\%$), suggesting that polyandry acts as a bet-hedging strategy to reduce the possibility of an unsuccessful mating with infertile or genetically incompatible males. Offspring of polyandrous females also had an approximately 43% higher rate of survivorship than did the other groups (Fig. 3), although these comparisons were not significant.

Despite no significant association between gift size and longevity, hatching success or survivorship, some of these variables were only marginally nonsignificant (see the univariate analyses above). Therefore, we reanalysed the treatment comparisons with an analysis of covariance (ANCOVA), using male body size as the covariate to control for potential differences in nuptial gift contribution between the monandrous and polyandrous treatments (body size is a significant predictor of nuptial gift size: Fedorka & Mousseau 2002). (Chewing duration was not used as the covariate because these data were incomplete for the monandrous treatment.) These results were consistent with our initial analyses, suggesting that

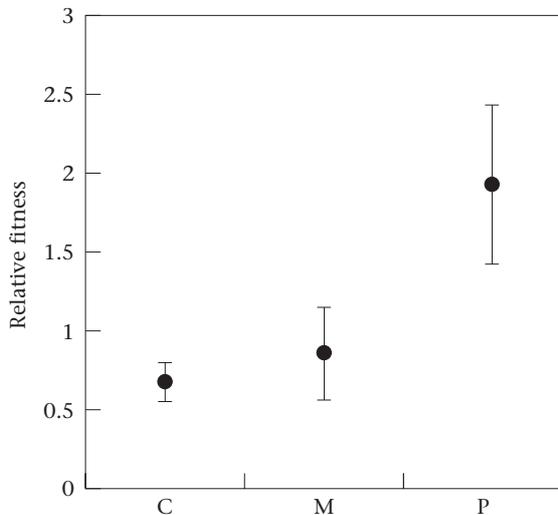


Figure 4. Relative fitness of female mating strategies. All four fitness components (longevity, fecundity, hatching success and survivorship) directly influence the number of offspring that reached adulthood in the next generation (relative fitness). Here, the polyandrous strategy showed on average a 2.5-fold increase in fitness compared with both the monandrous and single mating strategies (1.94 ± 0.5 versus 0.86 ± 0.29 and 0.68 ± 0.12 , respectively).

the genetic response variables (hatching success and survivorship) were free of confounding material benefits.

Overall, polyandrous females had a higher relative fitness than either of the other two female treatments (Tukey Studentized range test: $P < 0.05$; Fig. 4). Even though the polyandrous strategy incurred an immediate fitness cost with regard to lower longevity and fecundity, the genetic fitness gains gave polyandrous females a 2.5-fold higher fitness advantage. Thus, genetic benefits provide a mechanism for the adaptive maintenance of female polyandry in this system.

DISCUSSION

Our present study suggests that female fitness is influenced by male nuptial gifts. A least squares model predicted a 3.4% increase in fecundity gained from every additional minute of tibial spur chewing, independent of spermatophore attachment duration. The model further predicted that females who chewed for 30 min would increase their reproductive output by 100%. These data support the hypothesis that the degree of female material benefits are mediated by the magnitude of the nuptial gift received during copulation, an association that has been observed in other orthopteran (Gwynne 1984, 1988; Butlin et al. 1987; Simmons 1988) and lepidopteran systems (Rutowski et al. 1987; Wiklund et al. 1993).

In *Allonemobius* and other orthopterans, the gift has traditionally been described to function solely as a form of mating effort (Gwynne 1983; Bidochka & Snedden 1985; Vahed 1998). Unfortunately, both hypotheses concerning the functional significance of the nuptial gift in *A. socius* are currently indefensible. The magnitude of the gift was a significant predictor of spermatophore

attachment duration, as predicted by the mating effort hypothesis. However, the duration of spermatophore attachment was not associated with fecundity. This is unusual since an increase in sperm transfer should operate to increase fertilization success. One explanation is the existence of a large variance in sperm transfer rate. This would seem likely if a large variance in spermatophore size also existed (assuming that transfer rate and spermatophore size were positively related); however, previous studies on spermatophore size do not support this relationship (Fedorka & Mousseau 2002), leaving the transfer rate hypothesis currently unsupported. Conversely, the number of eggs laid was predicted by the size of the nuptial gift, implying a parental investment function (e.g. Trivers 1972) although no offspring variables were associated with the nuptial gift. However, incorporation of donated nutrients is likely to be much slower than the female's reproductive refractory period (Wedell 1993), making it unlikely that these extra eggs would actually be fertilized by the gift-giver. If this is true, it would imply that the gift's evolutionary origins lay in mating effort, and that females secondarily coerce gift nutrients into their own reproductive maintenance.

This assertion is consistent with the more uncommon hypothesis that nuptial gifts evolved as the result of sexual conflict over female polyandry (Parker & Simmons 1989). To help reduce sperm competition in polyandrous systems, males of many species transfer chemicals that induce an extended refractory period in female receptivity (Arnqvist & Nilsson 2000). However, extended refractory periods may not be advantageous for the female because they reduce the potential for accruing material and genetic benefits. Thus, females should evolve resistance to male coercion, which may eventually lead to the female metabolizing and incorporating these chemicals into somatic or reproductive maintenance (e.g. Boggs 1990; Wiklund et al. 1993; Stockley 1997; Vahed 1998). This antagonistic relationship may lead to a continual exaggeration of the male ejaculate or nuptial gift in an attempt to circumvent female resistance. Additional support for the sexual conflict hypothesis comes from comparative studies in butterflies that suggest a positive association between nuptial gift size and the degree of polyandry (Svard & Wiklund 1989; Gage 1994; Karlsson 1995), implying a coevolutionary arms race motivated by female mating frequency.

One interesting result of our data is that polyandrous females did not gain the fecundity benefits accrued by the monandrous females. Moreover, polyandrous females suffered an approximate 29% decrease in longevity compared with the other treatments. These observations may also be the result of sexual conflict. As a genetic bet-hedging strategy, females seek sperm from a variety of male donors. However, this reduces the probability that a male's total mating effort will result in his offspring. As a countermeasure, males may transfer toxic chemicals along with sperm that reduce female receptivity (Eberhard 1996; Andersson et al. 2000) and stored sperm vitality (Clark et al. 1999) that, as a side effect, have a detrimental effect on female longevity (Fowler & Partridge 1989; Rice 1996; Clark et al. 1999). If male

A. socius could manipulate their ejaculate composition according to female mating history (i.e. higher sperm competition risk equals a more toxic ejaculate), the reduction in female longevity found here could be explained.

Evidence exists to suggest that male crickets can manipulate their ejaculate contribution based on sperm competition. In a recent study by Gage & Barnard (1996), male crickets modified their spermatophore content by increasing the number of sperm when the threat of intermale competition was increased. Given the large amount of time from initial courtship to the completion of spermatophore production in *A. socius*, there is ample opportunity for the male to adjust his ejaculate. Thus, increased polyandrous behaviour may come at the cost of an increasingly toxic internal female environment.

The most significant aspect of our data suggests that a female's fitness increases with the genetic diversity of her male mates. The offspring of polyandrous females had a higher hatching success rate and higher survivorship than did the offspring of females in the other two treatments. These results appear to be independent of the confounding effects of material benefits since no relation existed between these variables and gift size and no difference was detected between the monandrous or control treatments. Moreover, under the conditions imposed by our experiments, polyandrous females had on average a 2.5-fold greater relative fitness than did females in the other treatments, implying that polyandrous behaviour was the most fit strategy. Thus, these data suggest that polyandry may be adaptively maintained through genetic benefits.

The underlying mechanisms that may account for this observation are numerous. Polyandry may promote intra-sexual selection between the sperm of various males with the most fit sperm fertilizing the greatest proportion of eggs (intrinsic male quality hypothesis: Birkhead & Møller 1992; Madsen et al. 1992; Birkhead et al. 1993). Polyandry may also be a bet-hedging strategy whereby females seek a diverse store of sperm simply to lower the probability of mating with infertile or low-quality males (Wetton & Parkin 1991), or as a hedge against the uncertainty of future environmental conditions by increasing the genetic diversity of their offspring (Ridley 1993).

Recently, intragenomic conflict has also been recognized as a potential force in the evolution of polyandry. Here, selfish genetic elements such as cellular endosymbionts, transposable elements, segregation distorters and maternal-effect lethals can render parental genotypes incompatible (Zeh & Zeh 1996, 1997). The positive relationship between hatching success and polyandry in the field cricket, *Gryllus bimaculatus*, was suggested to be maintained through a bet-hedging strategy that minimized genetic incompatibility (Tregenza & Wedell 1998). Furthermore, Clark et al. (1999) found evidence that male fertilization success in *Drosophila* was dependent on the genotype of the male's female mate. This hypothesis is consistent with our data in that polyandrous females had a much lower coefficient of variation in hatching success than the other two treatments, which would be expected in a bet-hedging, genetic incompatibility scenario.

Genetic incompatibility is also consistent with a Red Queen hypothesis of antagonistic coevolution facilitated by sperm competition (Arnqvist & Nilsson 2000; Gavrillets 2000). In this system, both polyandry and nuptial gifts may have coevolved antagonistically due to sperm competition, leading to genetic incompatibility as a secondary result. If true, genetic incompatibility may have led to the selective reinforcement of polyandrous behaviour, exaggerating the size/complexity of the gift and the degree of polyandry to their present state. Regardless of the precise mechanism responsible for our results, we have shown that genetic benefits play an important role in the maintenance of female polyandry in this system. In addition, material benefits resources, mediated by the nuptial gift, appear to be of secondary importance in the maintenance of this behaviour.

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