

# Good genes and the maternal effects of polyandry on offspring reproductive success in the bulb mite

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Genetic benefits are potentially the most robust explanation of the controversial issue of evolutionary maintenance of polyandry, but the unambiguous demonstration of such benefits has been hindered by the possibility of their confusion with maternal effects. Previous research has shown that polyandrous bulb mite females produce daughters with higher fecundity than monandrous females. Here, we investigate whether this effect arises because polyandrous females invest more in their offspring, or because their offspring inherit 'good genes' from their fathers. Females were mated with either one or four (different) males. However, by sterilizing three of the four males with ionizing radiation, we eliminated any chance of sexual selection (in the polyandrous treatment) so that any differences in the female mating regimes must have been owing to maternal effects. Polyandry had no significant effect on daughter fecundity, thus indicating that any previously documented effects must have been genetic. This was further supported by a significant association between fathers' offensive sperm-competitive ability and the fecundity of their daughters. The association with fathers' sperm defensive ability was not significant, and neither was the association between fathers' sperm competitiveness and sons' reproductive success. However, sons of polyandrous females had lower reproductive success than sons of monandrous females. This shows that the maternal effects of polyandry should be taken into account whenever its costs and benefits are being considered.

**Keywords:** sexual selection; sperm competition; mating systems; parental investment; differential allocation

## 1. INTRODUCTION

Over the past decade, the evolution of polyandry has attracted much attention (reviewed by Jennions & Petrie 2000; Arnqvist & Nilsson 2000; Hosken & Stockley 2003; Radwan 2003). This interest was prompted by the apparent contradiction between the expectation that female reproductive success should not depend on their number of mates (Bateman 1948) and the common occurrence of multi-male mating (Birkhead & Møller 1998). Several benefits that select for female polyandry were identified. Females may benefit directly, e.g. when they receive nutrients during copulation (Gwynne 1988; Wiklund *et al.* 2001), or when they replenish sperm after mating with a sub-fertile partner (Arnqvist & Nilsson 2000; Radwan 2003). Because polyandry extends the scope for sexual selection (see reviews in Eberhard 1996; Birkhead & Møller 1998), indirect genetic benefits can also be expected to play a role. The progeny of polyandrous females may inherit their fathers' high sperm competitiveness (Keller & Reeve 1995; Bernasconi & Keller 2001) or other beneficial traits that are correlated with sperm competitiveness (Yasui 1997; Watson 1998; Evans & Magurran 2000; Konior *et al.* 2001) and polyandry may facilitate cryptic female choice (Eberhard 1996; Ward 2000). Mating with many males may also serve to avoid genetic incompatibility (Newcomer *et al.* 1999; Simmons 2001), inbreeding (Tregenza & Wedell 2002) or fertilization by older males' sperm that is burdened with deleterious mutations (Radwan 2003).

However, because mating also incurs costs, e.g. in terms of decreased female lifespan (Stutt & Siva-Jothy 2001) or fecundity (Kołodziejczyk & Radwan 2003), it is possible that polyandry is a result of sexual conflict that is won by males who can coerce or persuade females to mate suboptimally (Holland & Rice 1998; Arnqvist & Rowe 2002). Thus, a careful analysis of costs and benefits is necessary to understand fully the complexities of polyandry evolution.

The genetic benefits are potentially more widespread than direct benefits. Provided that there is enough genetic variance for mate quality (or compatibility), genetic benefits will always accompany any direct benefits (Jennions & Petrie 2000; Fedorka & Mousseau 2002). Studies that have found some support for genetic benefits tested the prediction that polyandrous females should have fitter progeny than monogamous females (Madsen *et al.* 1992; Olsson *et al.* 1996; Watson 1998; Tregenza & Wedell 1998; Evans & Magurran 2000; Bernasconi & Keller 2001; Konior *et al.* 2001; Fedorka & Mousseau 2002; Pai & Yan 2002; Sakaluk *et al.* 2002; Kamimura 2003). However, the increased opportunity to choose a mate by polyandrous females could influence their investment in their progeny (Simmons 1987; Wedell 1996; Pearse *et al.* 2002). Maternal effects can affect many aspects of the fitness of progeny in a variety of taxa (reviewed in Mousseau & Fox 1998), including acarid mites (T. G. Benton, A. P. Beckerman, C. T. Lapsley and N. Koesters, unpublished data). In the context of sexual selection, there is evidence that maternal investment is influenced by mate attractiveness (reviewed by Sheldon 2000). However, the maternal effects of polyandry have been little studied. In a recent study, Tregenza *et al.* (2003) showed that in the

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yellow dung flies maternal environment interacts with the female mating regime (monandrous or polyandrous) to affect progeny fitness. Here, we simultaneously test for genetic and maternal polyandry effects on offspring fitness in the bulb mite, *Rhizoglyphus robini* (Acari, Astigmata, Acaridae).

The bulb mite is characterized by a promiscuous mating system, resulting in mating frequencies that are as high as  $8 \text{ day}^{-1}$  (Radwan & Siva-Jothy 1996). Both the costs and benefits of mating have been documented. Experimentally decreasing the mating frequency increased female lifetime fecundity (Kołodziejczyk & Radwan 2003). However, daughters of polyandrous females had increased fecundity compared with daughters of females that copulated repeatedly with the same male. Because other fitness components of offspring did not differ between polyandrous and monandrous treatments, Konior *et al.* (2001) concluded that polyandry is likely to benefit females genetically. However, their result could also be explained by the maternal effects of the mating regime. Unlike monandrous females, polyandrous females could choose a male, either directly or indirectly, and the possibility of making a choice could affect their maternal investment (see Simmons 1987). Here, we describe a design that allows us simultaneously to detect the genetic and maternal effects of polyandry. We collected the progeny of males mated sequentially with two females. One female in such a pair was monandrous and one was polyandrous, but because they shared the same sire, any consistent differences in the quality of their progeny could arise only via non-genetic effects. The same experiment allowed us to quantify the correlation between male success in sperm competition and progeny fitness, thus providing a test of the genetic benefits of polyandry. We have confirmed the importance of such benefits, but we have also demonstrated the maternal effects of the female mating system on progeny fitness.

## 2. MATERIAL AND METHODS

The mites came from a population of approximately 200 individuals isolated from a single onion in May 2002, i.e. *ca.* eight months (*ca.* 16 generations) before the commencement of these experiments. They were cultured in the laboratory as a large population (more than 500 individuals) under standard conditions (more than 90% r.h.,  $24 \pm 1 \text{ }^\circ\text{C}$ , fed with a 3 : 1 powdered yeast and wheat germ mixture).

The polyandrous and monandrous treatments were similar to those described in Konior *et al.* (2001). Virgin females were obtained from larvae individually isolated from the stock culture. The experiments began 1–2 days after their final moult. Males were obtained in the same way, but were kept with females for 36 hours before they were used for the experiments. This was done to standardize their semen reserves (Radwan 1997). Males of the bulb mite are dimorphic (Radwan 1995). In a similar fashion to Konior *et al.* (2001), only the more common fighter morph was used.

Both polyandrous and monandrous females were kept with a male for 48 hours, but in the former treatment the male was replaced every 12 hours (i.e. females were mated with four different males), whereas monandrous females remained paired with the same males for the whole period. Such a procedure results in similar numbers of copulations in both treatments

(Konior *et al.* 2001). However, unlike in Konior *et al.* (2001), the possibility of genetic benefits of polyandry was eliminated by allowing only one, randomly chosen male to sire the offspring of polyandrous females. This was achieved by irradiating three of the male partners of each female with 20 krad from a Co60 source. This dose prevents the eggs fertilized by the sperm of irradiated males from hatching (with 100% effectiveness,  $n = 54$ ) without significantly compromising the sperm competitiveness of irradiated males (Radwan 1997). We will further refer to this female mating regime as pseudo-polyandry, to stress that post-copulatory sexual selection was eliminated.

Furthermore, the progeny of females from pseudo-polyandrous and monoandrous treatments shared the same sires. This was achieved by mating the non-irradiated male from the pseudo-polyandrous treatment with another female from the monogamous group. These males mated with a pseudo-polyandrous female either as her first mate, and then paired with a female from the monogamous group, or as their last mate, after being mated with a monogamous female. The sperm-competition success of the latter group was related to the ability of males to assure the advantage of their own sperm over that of the preceding males (see Radwan & Witaliński (1991) and Radwan (1997) for the details of the biology of reproduction), whereas with the former group it was related to the ability of males to defend their own sperm against the sperm of the female's subsequent partners. We will thus refer to these groups as 'offensive' and 'defensive', respectively. Because competitors of these males were irradiated, we could also determine their sperm-competition success using the sterile male technique (Parker 1970). Because nearly all eggs fertilized by non-irradiated males normally hatch, their success could be estimated by counting the proportion of hatched eggs (Radwan & Siva-Jothy 1996; Radwan 1997).

We counted all eggs laid by females for 5 days after mating and then recorded the proportion of eggs that hatched in the polyandrous treatment. Ten larvae from each female were collected for fitness assays and reared to maturity. However, this was not always possible with the pseudo-polyandrous treatment, where sometimes all or most of the eggs were fertilized by irradiated males. Whenever this occurred, the family from the monogamous treatment (i.e. sired by the same male) was discarded. Retaining the monogamy-derived progeny of males that were unsuccessful in sperm competition in the pseudo-polyandrous treatment, perhaps owing to their lower genetic quality, could have confused our estimation of maternal effects with genetic effects. Thus, our aim was to compare the reproductive success of pairs of progenies obtained from females belonging to different mating regimes but that shared the same sire. After the larvae matured, we randomly selected three individuals of each sex (or as many as available if we obtained fewer than three adults of a given sex) from each family for the fitness assays.

We measured the fecundity of female progeny beginning 1–2 days after emergence, for 9 days during which they were mated with three different, randomly selected males. The male was replaced on the second day, and then on the fifth day, with the aim of decreasing any variance to any male influences of female fecundity. A period of 9 days is representative of female lifetime fecundity, lasting on average 3–4 weeks (Konior *et al.* 2001).

The reproductive success of each male progeny was measured in competition over two females with another, randomly selected, irradiated male. The test started 1–2 days after emergence, and lasted for 5 days. The eggs laid during that time and the

Table 1. Repeated-measures analysis of variance with progeny reproductive success as the dependent variable, father as a subject, female mating regime (monandry or pseudo-polyandry) as the repeated-measure factor, father's mating order (as the first mate or as the last) as a fixed factor and block as a random factor.

source	sons				daughters			
	d.f.	MS	F	p	d.f.	MS	F	p
♂ mating order	1	0.088	0.981	0.325	1	298	0.097	0.756
block	1	0.745	8.259	0.006	1	66139	21.608	< 0.001
♂ order × block	1	0.003	0.029	0.864	1	18387	6.00	0.016
error (between subjects)	66	0.090			71	3061		
♀ mating regime	1	0.385	6.845	0.011	1	1134	0.400	0.528
♀ regime × block	1	0.070	1.250	0.267	1	3204	1.201	0.277
♀ regime × ♂ order	1	0.001	0.018	0.893	1	272	0.096	0.757
♀ regime × ♂ order × block	1	0.092	1.625	0.207	1	29	0.010	0.920
error (within subjects)	66	0.056			72	2794		

larvae hatched were counted. Male success was measured as the proportion of hatched eggs. In the following analyses we use family means for either son or daughter reproductive success.

For logistical reasons, the experiments were done in three blocks. With the first block, we lost mites from the monandrous treatment owing to a chance event so the pseudo-polyandry data from this block were used to analyse only relationships between the sperm-competition success of fathers and the reproductive success of their offspring. Statistical tests were done with STATISTICA 6.1.

### 3. RESULTS

The average (± s.d.) fecundity of monandrous and polyandrous females was, respectively, 97.9 ± 64.6 (n = 52) and 103.4 ± 69.7 (n = 52) in the first block and 117.1 ± 57.1 (n = 58) and 127.7 ± 61.4 (n = 47) in the second block. Analysis of variance revealed a significant block effect (F<sub>1,204</sub> = 5.986, p = 0.015), but the difference between female mating regimes was not significant (F<sub>1,2</sub> = 0.905, p = 0.342; male mating order, F<sub>1,2</sub> = 0.046, p = 0.829; interaction, F<sub>1,204</sub> = 0.356, p = 0.551).

The female mating regime significantly influenced the reproductive success of sons (table 1, figure 1a). However, neither the female mating regime nor the male mating order significantly influenced the fecundity of the daughters (table 1, figure 1b). There was a significant block by male mating order interaction effect on daughter fecundity, the biological interpretation of which is unclear.

The defence group fertilized a lower proportion of eggs than the offence group (F<sub>1,2</sub> = 148.44, p = 0.005, block, F<sub>2,119</sub> = 51.22, p = 0.019; interaction n.s.). The average proportion (± s.d.) of eggs fertilized by males in the pseudo-polyandrous offence and defence groups were, respectively, 0.543 ± 0.237 (n = 23) and 0.354 ± 0.197 (n = 24) in the first block, 0.446 ± 0.387 (n = 30) and 0.399 ± 0.332 (n = 28) in the second block and 0.495 ± 0.251 (n = 28) and 0.307 ± 0.255 (n = 30) in the third block.

ANCOVA with daughter fecundity as a dependent variable revealed a significant interaction between father's success in sperm competition and male mating order (table 2, figure 2b), and therefore we examined separate ANCOVAs for sperm offence and sperm defence. They revealed a significant association between daughter

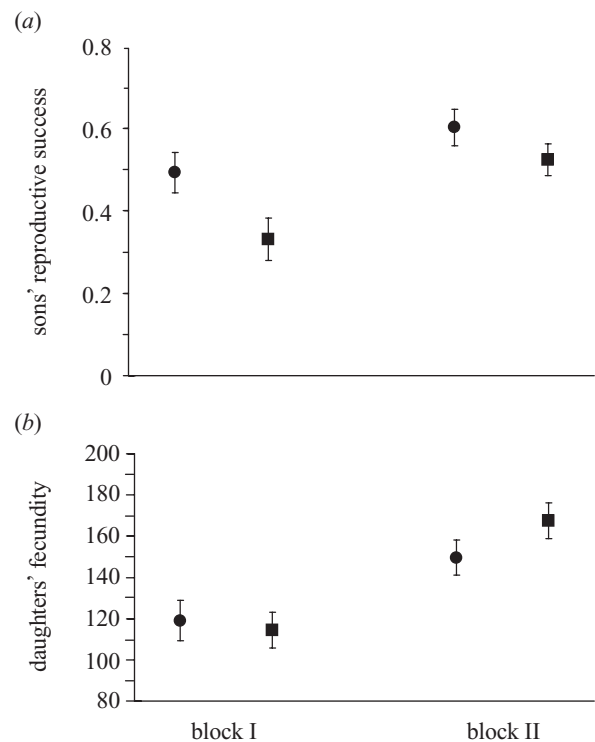


Figure 1. Mean ± s.e. reproductive success of (a) male and (b) female progeny of monogamous (circles) and pseudo-polyandrous (squares) females.

fecundity and the offensive sperm competitiveness of fathers (father's effect, F<sub>1,2</sub> = 27.15, p = 0.017, block, F<sub>2,56</sub> = 4.20, p = 0.019, interaction n.s.). However, the association with defensive sperm competitiveness was not significant (father's effect, F<sub>1,2</sub> = 0.08, p = 0.934, block, F<sub>1,59</sub> = 7.63, p = 0.001, interaction n.s.). We have found no significant effect of male success in sperm competition on the reproductive success of their sons (table 2, figure 2a).

### 4. DISCUSSION

The results of our study indicate that the benefit of polyandry previously documented in the bulb mite (i.e. increased fecundity of polyandrous females' daughters; Konior *et al.* 2001) arises through genetic rather than maternal effects. First, we have not detected a significant

Table 2. Analysis of covariance with progeny reproductive success as the dependent variable, father success in sperm competition as a quantitative factor, father's mating order (as the first mate or as the last) as a fixed factor and block as a random factor.

source	sons				daughters			
	d.f.	MS	<i>F</i>	<i>p</i>	d.f.	MS	<i>F</i>	<i>p</i>
father	1	0.003	0.339	0.592	1	18676	3.423	0.203
mating order	1	0.086	1.961	0.226	1	18770	26.721	0.020
block	2	0.088	2.347	0.298	2	26204	41.008	0.023
father × order	1	0.067	0.847	0.449	1	21163	34.807	0.021
father × block	2	0.006	0.084	0.923	2	5484	9.410	0.096
order × block	2	0.037	0.571	0.566	2	639	0.251	0.778
father × order × block	2	0.079	1.204	0.303	2	582	0.228	0.796
error	113	0.066			115	2547		

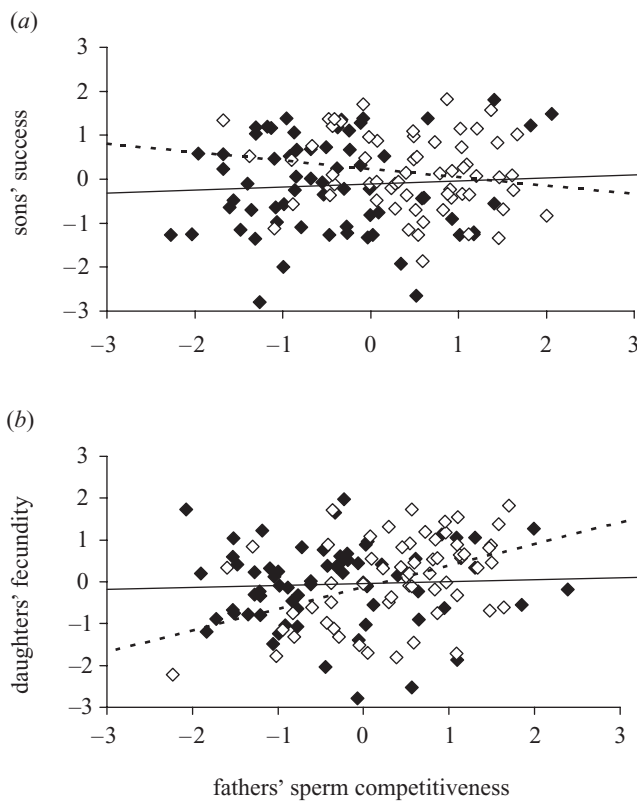


Figure 2. The association between fathers' success in sperm competition (defence: filled symbols, solid line; offence: open symbols, dashed line) and reproductive success of (a) male and (b) female progeny. Units = s.d. Regression slopes ( $\pm$  s.e.) on standardized data were  $0.518 \pm 0.140$  for sperm offence and  $0.044 \pm 0.124$  for sperm defence.

difference between pseudo-polyandrous and monandrous females in the fecundity of their daughters. Since progenies in both female mating regimes shared the same fathers, such differences were expected only if females increased their maternal investment in response to mating with multiple males. Second, we found a significant association between fathers' success in sperm competition and the fecundity of their daughters. The only other study of which we are aware that has demonstrated a similar effect was by Hosken *et al.* (2003) on dung flies (*Scathophaga stercoraria*), where fathers' sperm competitiveness was positively correlated with progeny development rates. In the bulb mite, the regression was significant

only for the group of males that were the last mates of polyandrous females, and not for the males that mated first. Because positive regression implies positive covariance (Lynch & Walsh 1998, p. 641), this result indicates that female fecundity is positively genetically correlated with male sperm-offensive ability. In the experiments of Konior *et al.* (2001), each polyandrous female mated with four males, so the sperm competition success of all but the first of them depended on their offensive ability, especially in the case of the last male. Thus, the higher fecundity of polyandrous females' daughters could result from a genetic correlation between fecundity and sperm-offensive ability.

By contrast, the ability of males to prevent the loss of paternity to subsequent mates of the female (sperm defence) was not associated with their daughters' fecundity. The lack of correlation between offensive and defensive aspects of sperm-competitive ability has been documented in fruitflies (Clark *et al.* 1995) and flour beetles (Bernasconi & Keller 2001). The higher paternity that we found in the offence group in the present study is consistent with the last-male sperm precedence reported for *R. robini* (Radwan 1997). In flour beetles, where last-male sperm precedence is high, the sons of polyandrous females had better sperm-offensive ability compared with sons of monandrous females, but there was no difference in sperm-defensive ability. The possible explanation for this pattern is that, in species with last-male sperm precedence, sperm-offensive ability has more impact on overall competitiveness than sperm-defensive ability (Bernasconi & Keller 2001). Another possibility is that there is more genetic variance in sperm-offensive ability than in sperm-defensive ability.

We did not find a significant correlation between fathers' success in sperm competition (either defence or offence) and the reproductive success of their sons. This might seem surprising given that sperm-competition success in *R. robini* was shown to be heritable (Radwan 1998). The significant genetic correlation with daughter fecundity documented in the present study implies that sperm competitiveness must have had a genetic component. Indeed, this population exhibits a polymorphism at the phosphogluconate dehydrogenase (PGDH) locus that is strongly associated with male success in sperm competition (M. Konior and M. Kolodziejczyk, unpublished data). However, the correlations that we analysed did not include fathers that failed in sperm

competition, and therefore the covariance between a father's sperm competition success and reproductive success of his offspring was probably underestimated by excluding the lower range of the distribution. Moreover, male reproductive success, as measured in this study, was the product of direct competition over access to females (Radwan *et al.* 2000), sperm competition (Radwan 1997) and, possibly, female preferences. If these components of male reproductive success are uncorrelated, the association between the sperm-competition success of fathers and the reproductive success of sons might be low, especially if the role of sperm competition in determining the total reproductive success is relatively smaller. Moreover, if these components of male reproductive success are negatively correlated genetically, the heritability of such measured reproductive success may be lower than the heritability of each component separately. These possibilities should be addressed in future research.

Another unexpected result that we obtained was that the reproductive success of sons of polyandrous females was decreased compared with the sons of monandrous females. As both groups shared the same fathers, the difference could be attributed to maternal effects. The mechanism underlying this effect is unclear. Kołodziejczyk & Radwan (2003) showed that increased mating frequency with the same male is detrimental to females and decreases their lifetime fecundity. One possible explanation for this finding assumes a detrimental role of seminal fluids, which seem to play a similar role in sperm competition in acarid mites (Radwan & Witaliński 1991) as they do in fruitflies, where their harmfulness is well documented (Chapman *et al.* 1995; Prout & Clark 2000). If the detrimental effects of seminal fluids from different males act synergistically (see Eady *et al.* 2000), polyandrous females could suffer increased costs of copulation compared with monandrous females, and these costs might affect their investment in progeny. A similar explanation was proposed for the beetle copwea weevil (*Callosobruchus maculatus*), where Eady *et al.* (2000) recorded a decreased egg-to-adult survival of the progeny of polyandrous females compared with the progeny of monandrous females. At the same time, Eady *et al.* (2000) recorded increased fecundity of polyandrous females, which suggests that multi-male mating stimulates female oviposition, perhaps at the cost of egg quality. However, neither our study nor that of Konior *et al.* (2001) has recorded a significant effect of the female mating regime on fecundity.

The detrimental maternal effect of polyandry affected only the reproductive success of sons, but not of daughters. Sex-specific effects of polyandry were also observed in flour beetles (Pai & Yan 2002) and in decorated crickets (Sakaluk *et al.* 2002), but in these studies it was the sons that benefited. However, these studies did not discriminate between maternal and genetic effects.

In conclusion, our results show that fathers who are successful in the offensive component of sperm competition sire more fecund daughters. At the same time, our study also proves that the maternal effects of polyandry can be important in determining offspring fitness.

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