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# Bet-hedging and the evolution of multiple mating

Charles W. Fox* and Claudia M. Rauter‡

*Department of Entomology, S-225 Agricultural Science Center North,*
*University of Kentucky, Lexington, KY 40546-0091, USA*

## ABSTRACT

Two related bet-hedging hypotheses have been proposed to explain the evolution of multiple mating by females. The first examines fitness of females within a single type of environment, and predicts that multiple mating can increase fitness by reducing the probability that all of a female's eggs are fertilized by a poor-quality male. The second examines fitness across environments and predicts that females who mate multiple times reduce the probability that all of their eggs are fertilized by a male that is unsuited to the current environment. We tested whether multiple mating actually provides the fitness benefits predicted by bet-hedging models by comparing the geometric mean fitness across generations of half-sib versus full-sib families of the milkweed bug, *Lygaeus kalmii*, reared on three different host plants. The variance in mean fitness (egg-to-adult survivorship) was always lower for offspring in half-sib families than for offspring of full-sib families. This translated into an average increase in geometric mean fitness of 4.1% within environments and 1.3% among environments for offspring of multiple-mated versus once-mated parents. These fitness increases are sufficient to produce rapid replacement of a once-mating genotype by a multiple-mating genotype. We conclude that multiple mating by parents reduces variation in offspring fitness and increases geometric mean fitness. We suggest that bet-hedging hypotheses are viable explanations for at least some of the variation in mating frequency observed in insects.

*Keywords*: bet-hedging, genetic benefits, geometric mean fitness, *Lygaeus kalmii*, multiple mating, polyandry.

## INTRODUCTION

Females of many insect species mate with more than one male during their lifetime. Although multiple mating has an obvious fitness advantage for males – each additional mating generally increases the number of eggs that a male fertilizes by at least some small amount – the fitness advantages to females are less clear. Numerous hypotheses have been proposed to explain multiple mating (polyandry) by females. For example, females often receive material benefits from males, which they use to increase their fecundity (Arnqvist and Nilsson, 2000; Wiklund *et al.*, 2001) and increase offspring fitness (e.g. Fox, 1993).

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* Author to whom all correspondence should be addressed. e-mail: cfox@uky.edu

‡ *Present address*: Department of Biology, 114 Allwine Hall, University of Nebraska at Omaha, Omaha, NE 68182-0040, USA.

Alternatively, females may mate multiple times to ensure that adequate sperm are acquired (especially if unable to detect sperm-depleted males; Jones, 2001), avoid male harassment (Lauer *et al.*, 1996; Galimberti *et al.*, 2000), exhibit mate-choice (e.g. Yasui, 1997; Savalli and Fox, 1998), encourage sperm competition (Curtsinger, 1991; Madsen *et al.*, 1992), avoid inbreeding (Hosken and Blanckenhorn, 1999), provide some type of genetic benefits (Walker, 1980; Evans and Magurran, 2000; Jennions and Petrie, 2000; for a review, see Newcomer *et al.*, 1999), such as increasing genetic diversity among their offspring (Loman *et al.*, 1988; Ridley, 1993; Hosken and Blanckenhorn, 1999; Baer and Schmid-Hempel, 2001), or simply as a consequence of high genetic correlations between the sexes (Halliday and Arnold, 1987; Gromko, 1992).

Increasing genetic diversity among offspring may be favoured as a form of genetic 'bet-hedging' (for a review, see Yasui, 1998). The concept of bet-hedging is simple: when fitness varies through time, long-term average fitness is calculated as the *geometric* mean fitness across successive generations, rather than the arithmetic mean fitness within or across generations (Philippi and Seger, 1989; Hopper, 1999). Geometric means are sensitive to high variance among the values being averaged, whereas arithmetic means are not. At the extreme, a single generation in which fitness is zero results in the complete extinction of a lineage or genotype, even if the genotype was the best, most fit genotype in all previous generations. In general, for any fixed arithmetic mean fitness, increasing the variance in fitness across time results in a decrease in geometric mean fitness. Thus, selection favours the evolution of strategies that eliminate high variance in fitness (because of those occasional periods of especially low fitness), even for some degrees of cost in arithmetic mean fitness (the amount of cost required to counteract this selection depends on the magnitude of the variance being avoided by the bet-hedging strategy).

Two different, but related, bet-hedging hypotheses have been proposed to account for the evolution of multiple mating by females. The first examines fitness of females within a single type of environment; genetic bet-hedging can favour the evolution of multiple mating by reducing the probability that all of a female's eggs are fertilized by a poor-quality or incompatible male (Jennions and Petrie, 2000; Tregenza and Wedell, 2000; Zeh and Zeh, 2001; classified as a type of good genes hypothesis by Watson, 1998; Yasui, 1998, 2001). By mating with multiple males, a female does not increase her expected fitness during that generation (assuming random mating, the expected fitness is simply the arithmetic average of the fitness obtained from all possible matings) but does reduce the expected variance in fitness by a function of $\sqrt{n}$ (where $n$ is the number of matings) and, across multiple generations, the genotype with the lowest variance in fitness will have the highest geometric mean fitness.

The second type of bet-hedging hypothesis commonly discussed examines the fitness of multiple-mating females in variable environments (genetic diversity hypothesis; Watson, 1991; Yasui, 1998). It is generally observed that the effect of an individual's genotype on fitness varies among environments (a genotype × environment interaction; Via, 1994), with different genotypes performing best in different environments. If females are capable of assessing whether their mate has genes appropriate for the environment in which the offspring will develop, she should always mate with males of the correct genotype for the expected environment. However, when females are incapable of assessing the quality of their mate's genotype, or when mating is random, mating with a poor-quality male can have substantial fitness costs. Genetic bet-hedging can favour the evolution of multiple mating by reducing the probability that all of a female's eggs are fertilized by a male that is unsuited to the current environment (i.e. increasing the genetic diversity of her offspring; Watson, 1991; Yasui, 1998), even if that male would be the best of all possible males in a different environment. When the environment that the female encounters varies from generation to generation, due either to temporal variation in the environment or because females move among environments over time, the genotypes that are 'best' vary from generation to generation, and increasing genetic diversity among offspring can substantially reduce the variance in offspring fitness across generations and thus increase geometric mean fitness.

Despite good theoretical reasons to expect genetic bet-hedging to be a significant factor influencing the evolution of multiple mating (but see Yasui, 2001), there is little empirical evidence of its importance (Yasui, 1997, 1998). Some studies have shown that female multiple mating can serve to reduce the risk that females mate accidentally with a poor-quality male, thus reducing variance in reproductive success within a single environment (Watson, 1991). However, no studies have tested whether multiple mating can indeed serve as a genetic bet-hedging mechanism by which the long-term fitness of genotype is higher when exposed to a variable environment. Some authors, such as Yasui (1997, 1998), have argued that the amount of genetic diversity among offspring created during meiosis is so high that multiple mating is unlikely to have a significant influence on the genetic diversity of offspring. We disagree. Multiple mating can have a substantial effect on the amount of genetic diversity among offspring and can have significant influences on long-term fitness. We propose that multiple mating is favoured in nature at least in part because it results in decreased variance in fitness when offspring are raised in a variable environment. In most insects, when females are mating they do not yet know exactly what environment their progeny will develop within, the species of host upon which they will oviposit, the quality of that host, and so on. Even when females can assess the environment that their offspring will encounter (e.g. herbivorous insects that mate at their oviposition site), they may not be able to assess the quality of their mate with regard to genes that affect development in that environment. Thus, selection will favour maximizing genetic diversity among offspring to ensure that at least some offspring are of the 'right' genotype to develop in the chosen environment, minimizing the risk of having a period of low fitness.

## TESTING THE HYPOTHESIS

Previous attempts to test genetic bet-hedging hypotheses for the evolution of multiple mating have examined whether female mating decisions conform to predictions (e.g. Watson, 1991; Birkhead and Møller, 1992; Ligon and Zwartjes, 1995) rather than testing whether multiple mating actually provides the fitness benefits predicted by bet-hedging models. Genetic bet-hedging predicts that increasing genetic diversity within families will lead to a decrease in variance in fitness among generations (or among environments) and thus an increase in geometric mean fitness among generations. This does not require that the genetic diversity be created by multiple mating of females. In fact, the genetic advantages of multiple mating should apply equally to males and females; multiple mating by males should result in decreased variance in fitness and thus an increase in geometric mean fitness among generations (in addition to other benefits that males receive from multiple mating).

Fortunately, it is common in genetic studies to perform experiments in which males are mated to multiple females. In animal quantitative genetics, the half-sib design, in which each male is mated to two or more females, is a common breeding design. Similarly, in plant quantitative genetics, the North Carolina II cross (Lynch and Walsh, 1998), in which all individuals are mated to multiple mates, is a standard design. In either plants or animals, whether a male is mated to three different females or a female is mated to three different males, the range of genotypes is the same, with the exception of sex-linked and non-nuclear genes, which account for only a small proportion of total genes. Many quantitative genetic designs examine genetic variances in multiple environments by splitting progeny among each of two or more environments. We take advantage of this type of design to test the hypothesis that multiple mating reduces the *variance* in offspring fitness among generations relative to offspring of once-mated parents. This approach has three advantages over a comparison of half-sibs created by multiple-mating females: (1) relatedness of offspring is obvious without the use of morphological or molecular markers; (2) variation in male fertility does not influence variances; and (3) maternal effects, in which offspring of a single mother tend to be phenotypically similar due to non-genetic similarities, does not confound the variance estimates.

To test the hypothesis, we examined the survivorship of milkweed bugs, *Lygaeus kalmii* (Hemiptera: Lygaeidae), raised on seeds of three different species of host plants (*Asclepias speciosa*, *A. fascicularis* and *Taraxacum officinale*). These three plants are quite different from each other, and the genotypes of milkweed bugs that perform best on one species are different from the genotypes of bugs that perform best on the other species (Fox and Caldwell, 1994). Because these host plants vary in availability across space and time, the species used by any particular generation of bugs varies as individuals move around and as the season progresses. Thus, any lineage of bugs can encounter each of these species in different generations such that selection favours high geometric mean fitness across multiple host species.

We examined whether geometric mean survivorship of nymphs is higher, and the variance in nymphal survivorship lower, for offspring of males that are mated to multiple females than for offspring of males mated to only a single female. We used data from a standard half-sib design in which males from two populations were each mated with up to four virgin females (16 sires and 36 dams in the Berkeley population, and 22 sires and 58 dams in the El Dorado population). In this type of design, both full-sib families (offspring sharing both parents) and half-sib families (those sharing only one father and having different mothers) are created. Offspring from these matings were randomly assigned to one of the three host plants described above, and raised to adults at 32°C (light : dark 14:10 h) in laboratory growth chambers. In total, survival data were collected on 4651 offspring. Details of the half-sib design are presented in Fox and Caldwell (1994).

## BET-HEDGING AND MULTIPLE MATING EFFECTS ON FITNESS WITHIN A CONSTANT ENVIRONMENT

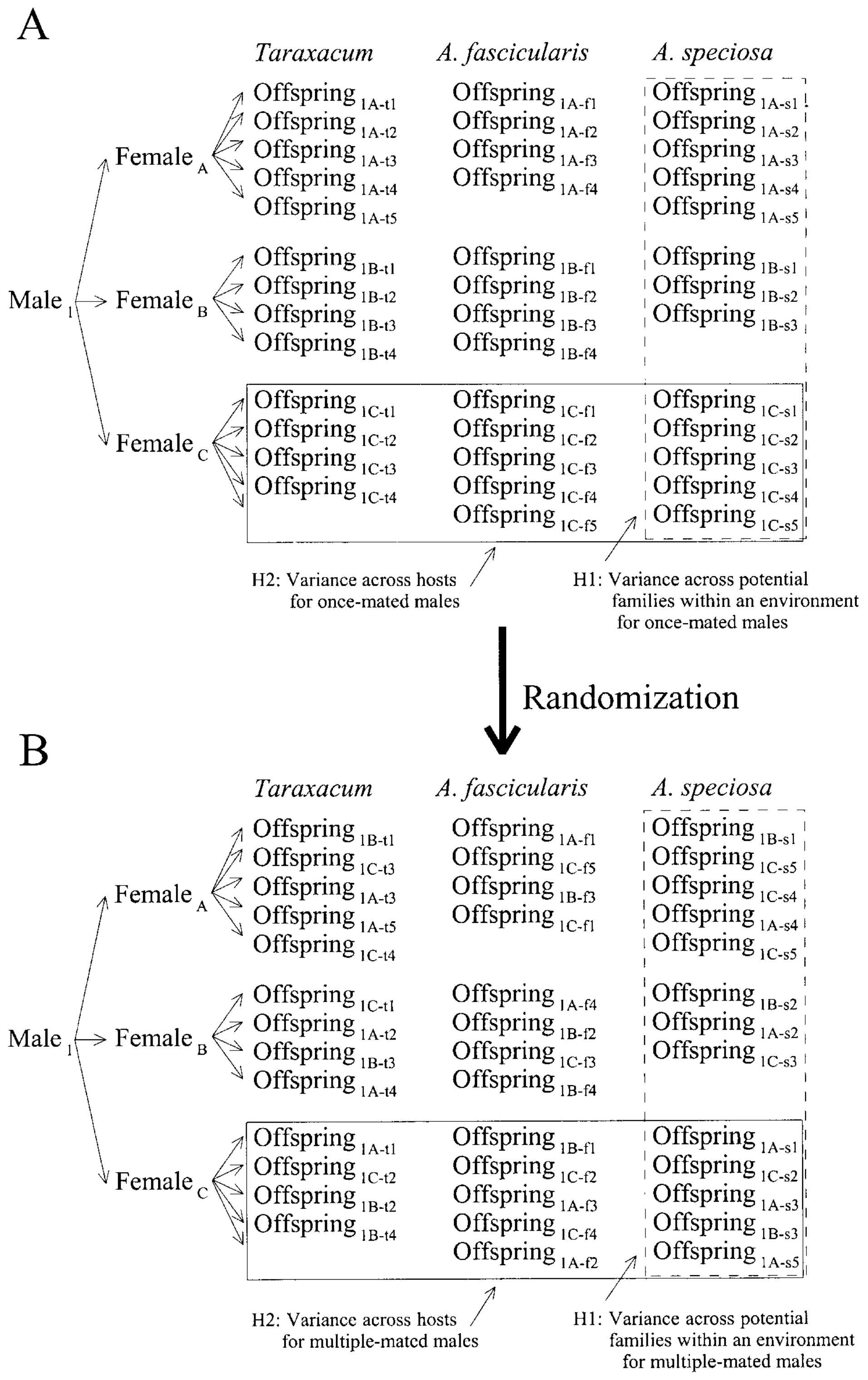
First, we examine the scenario in which a genotype of male could mate with one female in each generation (once-mating genotype), or mate with multiple females in each generation (multiple-mating genotype), with all offspring raised in a single environment. The genetic bet-hedging hypothesis predicts that the multiple-mating genotype will have lower variance in fitness, and thus higher geometric mean fitness, across generations. The half-sib data set provides a means to test this hypothesis by allowing us to compare half-sib offspring with full-sib offspring. Each full-sib family represents one potential family that a male could have produced had it mated with only a single female. Each half-sib family represents the offspring that a male would have produced if it had mated with multiple females. In the

*Lygaeus* experiment, each male was mated with *N* females and thus produced *N* families of size $n_i$. The variance in mean survival across these full-sib families (within each male) provides an estimate of the variance in offspring survival that a once-mated genotype would experience, across generations, had it mated with one female in each generation. We compare this with the variance in mean offspring survival that the male would experience, across generations, had it mated with multiple females in each generation. These families are represented in the experiment as the half-sib families. We ask: Provided that the individuals produced families of size $n_i$ each generation, would the variance in offspring survival across generations be lower, and the geometric mean of survival across generations be higher, for the multiple-mated genotype than for the once-mated genotype?

To estimate this variance and geometric mean fitness across families, we need to first define our half-sib families that we will compare to our full-sib families. The complete set of all offspring produced by a male (pooling offspring from all *N* matings) represents one large half-sib family. However, it contains substantially more offspring than each full-sib family that was produced by that male (Fig. 1A). We thus randomly subdivided this complete set of half-sib offspring into *N* smaller families, each with $n_i$ offspring, where *N* is the number of females mated to that specific male and $n_i$ is the size of each full-sib family (Fig. 1B) (randomization done using S-Plus; Venables and Ripley, 1997). Each half-sib family is thus matched for size with a full-sib family (*N* families of size $n_i$). This is important because the variance among families is a function of both the true variance among families and sampling error when estimating means of the families – the amount of sampling error decreases as the number of offspring per family increases. By standardizing family sizes, we remove the difference between treatments in sampling error and can compare variances and geometric means directly. Note that our method does *not* generate random data to use as a null hypothesis; we are only standardizing sample sizes to remove the sample size artifact intrinsic in comparing variances.

For each sire we then calculated (a) the arithmetic mean survival of offspring among families within each male, (b) the variance in mean survival among families and (c) the geometric mean survival across all families. We compared these estimates between families produced by once-mated males (full-sibs) and multiple-mated males (half-sibs). We treated each sire as a replicate experiment, and thus calculated the variance in mean survival and geometric mean survival across matings separately for each male (with 16 and 22 sires in the Berkeley and El Dorado populations, respectively). We performed a paired *t*-test (with each sire treated as an independent data point) to test for differences between once-mated and multiple-mated males. In this experiment, we raised offspring in three different environments (for details, see Fox and Caldwell, 1994). We treated each rearing environment as an independent data set (random re-assignment of offspring was done within each environment, and we compared geometric mean fitness between once- and multiple-mated males separately for each environment; we address the question of variance across environments below). Thus, in total we performed 18 comparisons – two populations of *L. kalmii* × three host plants × offspring survival measured at three time periods (survival to 5 days, 10 days and to adult moult).

Regardless of the seed species upon which offspring were reared, there was no difference in arithmetic mean fitness across families (within each male) between full-sib and half-sib families (Fig. 2). However, as expected from the genetic bet-hedging hypothesis, the variance in nymphal survival across matings was substantially lower for families created by multiple-mating males than for families created by males mating only once (Fig. 3). This



H2: Variance across hosts for once-mated males

H1: Variance across potential families within an environment for once-mated males

H2: Variance across hosts for multiple-mated males

H1: Variance across potential families within an environment for multiple-mated males translated into higher geometric mean fitness for multiple-mated males for 15 of 18 comparisons ($P = 0.004$). The average increase in geometric mean fitness for multiple-mated males was 4.1% (mean fitness of multiple-mated males divided by mean fitness of once-mated males; Fig. 1). Because we generated our half-sib families by multiply-mating males instead of females, this result is not confounded by sperm competition within females, resulting in 'better' quality males obtaining fertilizations within multiple-mated females leading to the artifact of increased offspring performance in multiple-mated females (Curtsinger, 1991).

## BET-HEDGING AND MULTIPLE MATING EFFECTS ON FITNESS IN A VARIABLE ENVIRONMENT

Next, we examine the scenario in which the progeny of once-mated and multiple-mated males are reared in a different environment in each generation. In our experiment with *Lygaeus*, we split all of the families and raised bugs on each of three host species. We can thus compare the geometric mean survivorship and variance in mean survivorship across host species for full-sib versus half-sib families. To interpret the analysis, imagine that bugs experience a different seed species in each of three sequential generations (the order does not matter). At the end of three generations, the genotype that is most common will be the genotype that had the highest geometric mean fitness across these three environments. Is this the multiple-mating genotype?

Again, we tested this hypothesis by comparing the variance in mean survival, and the geometric mean survival, between half-sib and full-sib families. This analysis is identical to

**Fig. 1.** Example of the randomization procedure used to test whether multiple mating reduces variance among generations. The top panel (A) shows a single half-sib family (all offspring from one male) generated from the half-sib mating design, with offspring from each maternal family split among three host species (the total data set has 16 and 22 such data sets in the Berkeley and El Dorado populations, respectively). The subscripts identify the male (sire) number, female (dam) number, rearing host (t, f and s represent *Asclepias fascicularis*, *A. speciosa* and *Taraxacum officinale*, respectively) and offspring number within each family–host combination. The randomization procedure reassigns these offspring (*within* males and *within* host species) to three new families of the same size ($n_i$) as the original three families. The three families from this mating design (panel A) represent three potential families a male could have produced if he had mated only once, and are thus three replicate families for a once-mated male. The randomized families (panel B) represent three replicate families that a male would have sired had he mated with three different females. Note that the offspring in panel (B) are *exactly* the same as in panel (A) except that their familial relationships have been reassigned. To test whether multiple mating reduces the variance across generations when offspring are reared within a constant environment (H1), we compare the variance in mean survival among the three real full-sib families (three replicates of families produced by a once-mating genotype; solid box in panel A) with the variance in mean survival among the three randomized half-sib families (three replicate families produced by a multiple-mating genotype; solid box in panel B) within each of the three host species (there are thus three estimates of these variances for each male, one for each host). To test whether multiple mating reduces the variance across environments when offspring are reared in a complex environment (H2), we compare the variance in mean survival among the three rearing environments within each full-sib family (dashed box, panel A) with variance among the rearing environments within each randomized trio of half-sib families (dashed box, panel B). See text for more details.

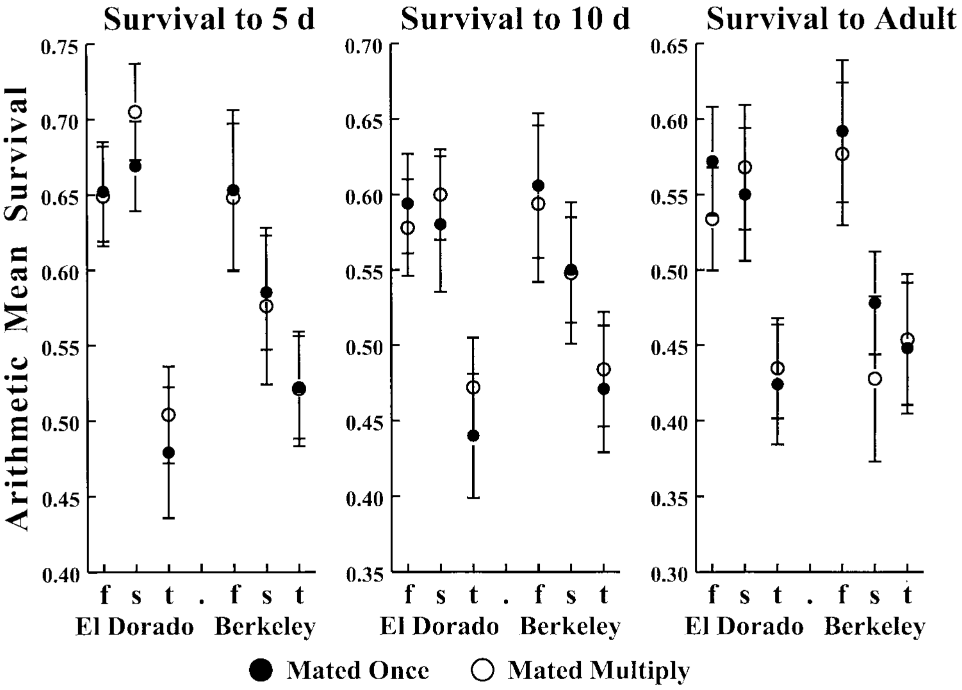


**Fig. 2.** Arithmetic mean (± standard error of the mean) of survival (across matings) for two populations of *Lygaeus kalmii* in which males are mated once or multiple times. The three environments (host species) are represented by f, s and t for *Asclepias fascicularis*, *A. speciosa* and *Taraxacum officinale*, respectively.

the previous analysis except that we now examine mean survival, and the variance in survival, across host species instead of within host species (solid boxes in Fig. 1). We calculated the arithmetic mean survivorship on each of the three host plants and then, using these means as our data, calculated the variance in survivorship across hosts and the mean survivorship across hosts. This was repeated for each set of paired families (those within the solid box in Fig. 1) within a male (sire), providing multiple mean and variance estimates per male. To test for differences between once-mated and multiple-mated males, we used an analysis of variance with population included as a fixed effect, male (nested within population) as a random effect and mating treatment as a fixed effect.

By far the largest effect on the arithmetic mean, geometric mean and variance in nymphal survivorship across hosts was the male (sire) effect within populations ($F > 2.3$ and $P < 0.001$ for all analyses). The genetic bet-hedging hypothesis predicts that the arithmetic mean survivorship across hosts will not differ between once-mated (full-sib families) and multiple-mated (half-sib families), but that the variance in survivorship across hosts will be lower, and the geometric mean survivorship higher, for offspring of multiple-mated males (i.e. half-sib families). Arithmetic mean survivorship across all three host species did not differ between males mated once and males mated multiple times, as expected (survivorship to 5 days, 10 days or adult; Fig. 4A; $P > 0.35$ for each). However, as predicted by the

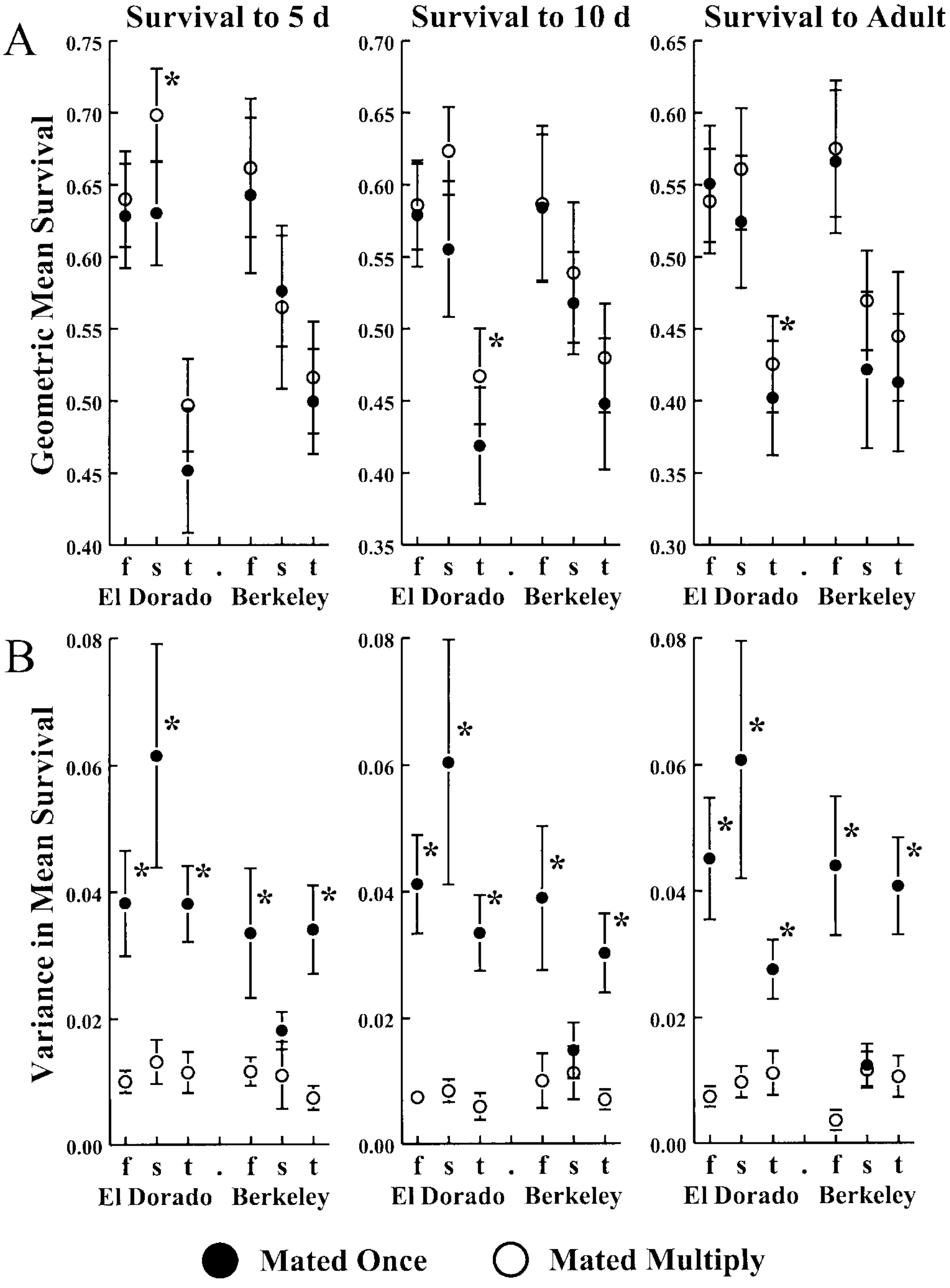


**Fig. 3.** Geometric mean and variance (± standard error of the mean) in survival (across matings) for two populations of *Lygaeus kalmii* in which males are mated once or multiple times. The three environments (host species) are represented by f, s and t for *Asclepias fascicularis*, *A. speciosa* and *Taraxacum officinale*, respectively. Note the large increase in variance, and consistent decrease in geometric mean survival, for offspring of once-mated parents.

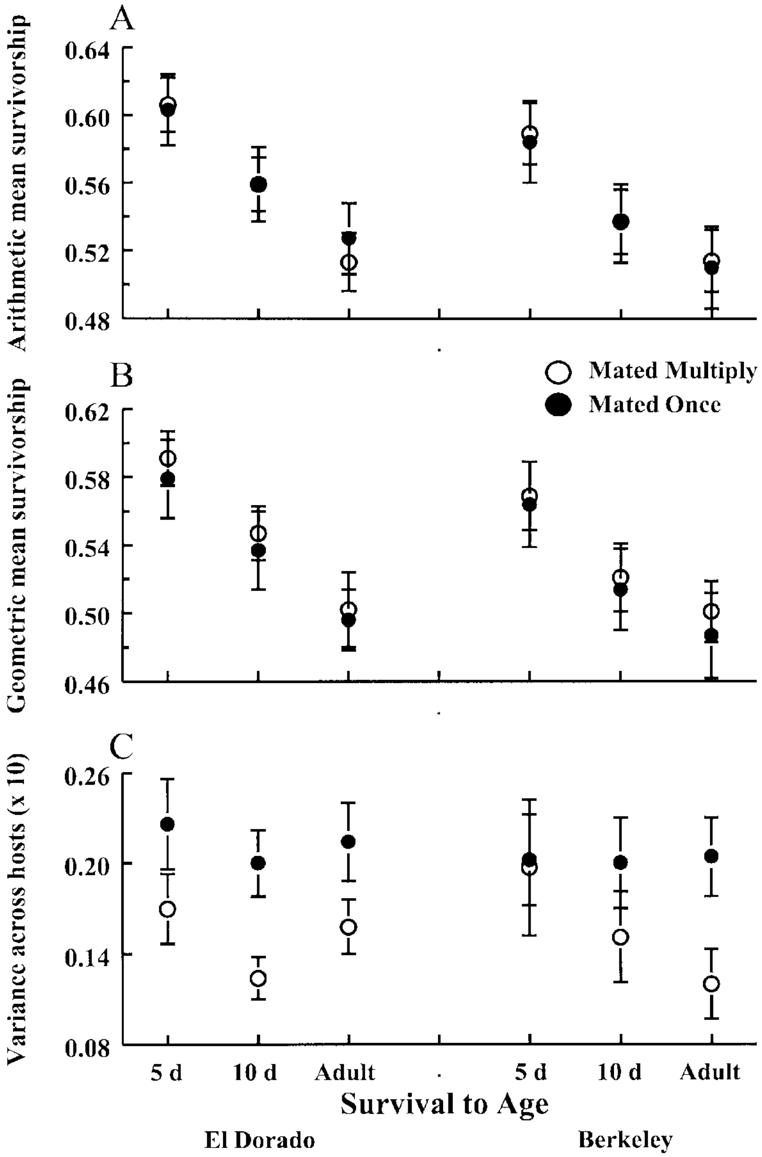


**Fig. 4.** Average and variance (± standard error of the mean) in survival (across three host species) for two populations of *Lygaeus kalmii* in which males are mated once or multiple times. Note the large increase in variance, and consistent decrease in geometric mean survival, for offspring of once-mated parents.

bet-hedging hypothesis, the variance in offspring survival among host species was lower for multiple-mated males (Fig. 4B; $P < 0.01$ for survival to 10 days and survival to adult, but non-significant for survival to 5 days; in separate analyses per population, this was significant for the El Dorado population but not for the Berkeley population). This translated into a consistently small increase in the geometric mean of survival across hosts (Fig. 4C). On average, the difference between the geometric means of half-sib versus full-sib families was 0.7%, which equals a 1.3% higher relative geometric mean survivorship for families of multiple-mated males. This observed increase in the geometric mean was not significant for any single comparison, but was highly significant when all six comparisons were considered simultaneously (sign test, probability of six out of six increases in mean fitness $< 0.02$).

## DISCUSSION

Multiple mating substantially reduced the variance in offspring survivorship relative to families of once-mated parents. Mathematically, when comparing two sets of values that have the same arithmetic mean, the set of values that exhibits the largest variance must necessarily have the smallest geometric mean. Thus, if the arithmetic mean across hosts does not differ between once- and multiple-mated males, then the geometric means must necessarily differ in the direction predicted by the hypothesis. Our results are qualitatively consistent with the hypothesis – the geometric mean of survivorship was higher for multiple-mated males than for once-mated males for both the within-environment and between-environment analyses.

However, the observed increases in geometric mean fitness were very small (1.3–4.1% higher relative geometric mean survivorship for families of multiple-mated males). Are such small differences in fitness large enough to be evolutionarily significant? If we assume for simplicity that (1) the estimated geometric means were calculated over three generations (one on each of the three host species, or across three matings within a single environment), (2) the mating types represent genotypes and that (3) there is no mixing of genotypes, then, if a population begins with 1% multiple-mating genotypes (and 99% once-mating genotypes), with only a 1.3% difference in geometric mean survival the multiple-mating genotype will reach a frequency of 50% after just 357 generations, and reach > 99% after just 712 generations. At a 4.1% advantage, the multiple-mating genotype will reach a frequency of 50% after just 115 generations, 90% at 170 generations and > 99.9% after just 287 generations. We thus conclude that the large differences in the variance in survival across hosts between once- and multiple-mated bugs is exactly as predicted by the genetic bet-hedging hypothesis, and that the resulting differences in geometric means are large enough to be evolutionarily significant and thus warrant further experimental exploration.

The main criticism of this analysis is likely to be that we did not examine multiple mating by females. Instead, we tested the genetic bet-hedging hypothesis by multiply mating males to generate genetic variation equivalent to that which would be generated by multiply mating females. We used a paternal half-sib analysis to test the genetic bet-hedging hypothesis primarily because of the substantial experimental difficulty of executing genetic experiments using multiple-mated females. In most animals, and especially insects, fertilization is internal and the only way to identify which father fertilized eggs is to use visible or molecular markers (which can be very expensive to score). However, there is one other source of data readily available which would provide a better test – the North Carolina II design in plants (Roff, 1997; Lynch and Walsh, 1998). Nothing about bet-hedging limits its applicability to insects or even animals. In plants, females (or the female part of flowers) can be mated to multiple males and the father of each offspring can be identified correctly – something that is very difficult to do with most animals. Thus, fertilizing a single plant with multiple pollen donors is easy to do without losing track of the parentage of the progeny. Because there is a vast literature in plant quantitative genetics, we suggest that other authors should examine results from their North Carolina II designs to determine whether the contribution of pollen from multiple donors (resulting in half-sib progeny within a family) results in decreased variance in fitness within families, especially when offspring are raised across multiple environments.

We conclude that multiple mating by parents substantially reduces the variation in offspring fitness across generations and across environments. This reduction in variance translates into a small, but potentially evolutionarily significant, increase in geometric mean fitness across generations. We thus suggest that bet-hedging hypotheses are viable explanations for at least some of the variation in mating frequency observed in insects. However, we emphasize that bet-hedging is only one of many factors contributing to the selective advantage to females of mating multiple times. Also, we ignored costs of multiple mating in this analysis; for example, females mating with multiple males may experience increased mortality (e.g. Partridge *et al.*, 1986; Kawagoe *et al.*, 2001), which may offset the bet-hedging benefits of multiple mating (Yasui, 1998). In other insects, the costs of multiple mating may be offset by direct nutritional benefits that females receive from males (e.g. Fox, 1993; Wagner *et al.*, 2001). Quantifying the relative importance of bet-hedging as an evolutionary explanation for multiple mating thus requires more extensive examination of the effects of multiple mating on geometric mean fitness relative to the potential fecundity costs associated with multiple mating.

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## REFERENCES

Arnqvist, G. and Nilsson, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.*, **60**: 145–164.

Baer, B. and Schmid-Hempel, P. 2001. Unexpected consequences of polyandry for parasitism and fitness in the bumblebee, *Bombus terrestris. Evolution*, **55**: 1639–1643.

Birkhead, T. and Møller, A.P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. New York: Academic Press.

Curtsinger, J.W. 1991. Sperm competition and the evolution of multiple mating. *Am. Nat.*, **138**: 93–102.

Evans, J.P. and Magurran, A.E. 2000. Multiple benefits to multiple mating in guppies. *Proc. Natl. Acad. Sci. USA*, **97**: 10074–10076.

Fox, C.W. 1993. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Oecologia*, **96**: 139–146.

Fox, C.W. and Caldwell, R.L. 1994. Host-associated fitness trade-offs do not limit the evolution of diet breadth in the small milkweed bug *Lygaeus kalmii* (Hemiptera: Lygaeidae). *Oecologia*, **97**: 382–389.

Galimberti, F., Boitani, L. and Marzetti, I. 2000. The frequency and costs of harassment in southern elephant seals. *Ethol. Ecol. Evol.*, **12**: 345–365.

Gromko, M.H. 1992. Genetic correlation of male and female mating frequency – evidence from *Drosophila melanogaster*. *Anim. Behav.*, **43**: 176–177.

Halliday, T.R. and Arnold, S.J. 1987. Multiple mating by females: a perspective from quantitative genetics. *Anim. Behav.*, **35**: 939–941.

Hopper, K.R. 1999. Risk-spreading and bet-hedging in insect population biology. *Annu. Rev. Entomol.*, **44**: 535–560.

Hosken, D.J. and Blanckenhorn, W.U. 1999. Female multiple mating, inbreeding avoidance, and fitness: it is not only the magnitude of costs and benefits that counts. *Behav. Ecol.*, **10**: 462–464.

Jennions, M.D. and Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biol. Rev. Camb. Phil. Soc.*, **75**: 21–64.

Jones, T.M. 2001. A potential cost of monandry in the lekking sandfly *Lutzomyia longipalpis. J. Insect Behav.*, **14**: 385–399.

Kawagoe, T., Suzuki, N. and Matsumoto, K. 2001. Multiple mating reduces longevity of females of the windmill butterfly *Atrophaneura alcinous. Ecol. Entomol.*, **26**: 258–262.

Lauer, M.J., Sih, A. and Krupa, J.J. 1996. Male density, female density and inter-sexual conflict in a stream-dwelling insect. *Anim. Behav.*, **52**: 929–939.

Ligon, J.D. and Zwartjes, P.W. 1995. Female red jungle fowl choose to mate with multiple males. *Anim. Behav.*, **49**: 127–135.

Loman, J., Madsen, T. and Hakansson, T. 1988. Increased fitness from multiple matings and genetic heterogeneity – a model. *Oikos*, **52**: 69–72.

Lynch, M. and Walsh, B. 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland, MA: Sinauer Associates.

Madsen, T., Shine, R., Loman, J. and Hakansson, T. 1992. Why do female adders copulate so frequently? *Nature*, **355**: 440–441.

Newcomer, S.D., Zeh, J.A. and Zeh, D.W. 1999. Genetic benefits enhance the reproductive success of polyandrous females. *Proc. Natl. Acad. Sci. USA*, **96**: 10236–10241.

Partridge, L., Fowler, K., Trevitt, S. and Sharp, W. 1986. An examination of the effects of males on the survival and egg-production rates of female *Drosophila melanogaster. J. Insect Physiol.*, **32**: 925–929.

Philippi, T. and Seger, J. 1989. Hedging one's evolutionary bets, revisited. *TREE*, **4**: 41–44.

Ridley, M. 1993. Clutch size and mating frequency in parasitic Hymenoptera. *Am. Nat.*, **142**: 892–910.

Roff, D.A. 1997. *Evolutionary Quantitative Genetics*. New York: Chapman & Hall.

Savalli, U.M. and Fox, C.W. 1998. Sexual selection and the fitness consequences of male body size in the seed beetle, *Stator limbatus. Anim. Behav.*, **55**: 473–483.

Tregenza, T. and Wedell, N. 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. *Mol. Ecol.*, **9**: 1013–1027.

Venables, W.N. and Ripley, B.D. 1997. *Modern Applied Statistics with S-Plus*. New York: Springer-Verlag.

Via, S. 1994. The evolution of phenotypic plasticity: what do we really know? In *Ecological Genetics* (L.A. Real, ed.), pp. 35–57. Princeton, NJ: Princeton University Press.

Wagner, W.E., Kelley, R.J., Tucket, K.R. and Harper, C.J. 2001. Females receive a lifespan benefit from male ejaculates in a field cricket. *Evolution*, **55**: 994–1001.

Walker, W.F. 1980. Sperm utilization strategies in nonsocial insects. *Am. Nat.*, **115**: 780–799.

Watson, P.J. 1991. Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). *Anim. Behav.*, **41**: 343–360.

Watson, P.J. 1998. Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Anim. Behav.*, **55**: 387–403.

Wiklund, C., Karlsson, B. and Leimar, O. 2001. Sexual conflict and cooperation in butterfly reproduction: a comparative study of polyandry and female fitness. *Proc. R. Soc. Lond. B*, **268**: 1661–1667.

Yasui, Y. 1997. A ‘good-sperm’ model can explain the evolution of costly multiple-mating by females. *Am. Nat.*, **149**: 573–584.

Yasui, Y. 1998. The ‘genetic benefits’ of multiple mating reconsidered. *TREE*, **13**: 246–250.

Yasui, Y. 2001. Female multiple mating as a genetic bet-hedging strategy when mate choice criteria are unreliable. *Ecol. Res.*, **16**: 605–616.

Zeh, J.A. and Zeh, D.W. 2001. Reproductive mode and the genetic benefits of polyandry. *Anim. Behav.*, **61**: 1051–1063.