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Female multiple mating as a genetic bet-hedging strategy when mate choice criteria are unreliable

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Female multiple mating (or polyandry) is considered to act as a genetic bet-hedging mechanism, by which females can reduce the assessment error in regard to mates' genetic quality when only uncertain information is available. In spite of frequent verbal arguments, no theoretical examination has been carried out to determine the effectiveness of bet-hedging by multiple mating. In the present paper, I show that three factors, female population size, remating costs and environmental fluctuation, all affect the effectiveness of bet-hedging. A mathematical model predicts that bet-hedging effectively works only in small populations, and computer simulations were used to confirm this prediction. The results of simulations differed according to the degree of environmental fluctuation. In relatively stable environments, if there is no remating cost, the fixation probability of a multiple mating strategy is slightly higher than that of a single mating strategy, independent of female population size. However, with very slight fitness costs, multiple mating drastically loses its advantage as population size increases, and almost always becomes extinct within large populations. This means that the evolution of polyandry solely by the mechanism of bet-hedging is unlikely in stable environments. However, in unpredictable environments, or when negative frequency-dependent selection on fitness-related loci is introduced, a multiple mating strategy is sometimes successful against a single mating strategy, even if it entails a small fitness cost. Therefore, female multiple mating may possibly evolve only in these limited conditions. In most cases, some deterministic mechanisms such as postcopulatory sperm selection by multiply mated females (or direct 'material' benefits) are more reasonable as the evolutionary causes of polyandry.

Key words: evolution; female multiple mating; genetic bet-hedging; polyandry.

INTRODUCTION

Female multiple mating (or polyandry) is one of the most intensively reviewed subjects in animal mating systems (Walker 1980; Thornhill & Alcock 1983; Knowlton & Greenwell 1984; Parker 1984, 1992; Halliday & Arnold 1987; Birkhead & Møller 1992; Keller & Reeve 1994; Reynolds 1996; Zeh & Zeh 1996, 1997; Yasui 1997, 1998; Arnqvist & Nilsson 2000; Jennions & Petrie 2000). Because the gamete production ability of males is far greater than that of females in many animals and parental investment by females is generally greater than that by males, the potential reproductive rate (PRR: Clutton-Brock & Vincent 1991) of males becomes greater than that of females. Thus, male fitness is limited by the number of mates, while female fitness is mainly limited by gamete pro-
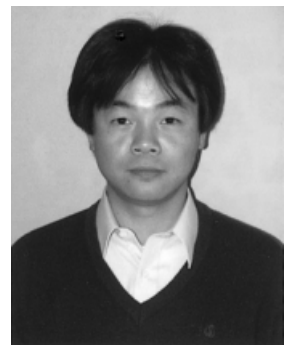
Fig. 1.   Dr Y. Yasui.

duction ability. Sexual selection theory predicts that males tend to mate promiscuously whereas females tend to mate with only one partner and invest in a limited number of offspring (Trivers 1985). In practice, however, females often mate with more than one male during a reproductive season in many species (Gwynne 1984; Birkhead & Møller 1992).

To settle this inconsistency, several categories of potential benefits of female multiple mating have been proposed (Thornhill & Alcock 1983; Halliday & Arnold 1987; Yasui 1997, 1998). The environmental (or direct) benefit hypothesis supposes that males replenish female's depleted sperm supplies, or provide females with food resources, defense against predators and sexual harassment, or parental care of offspring in reward for additional mating. On the other hand, a genetic (or indirect) benefit hypothesis supposes that females acquire genes which enhance the viability or competitiveness of their offspring (good genes hypothesis), or increase genetic diversity within their offspring, which may increase the possibility that some offspring within a clutch can survive in a fluctuating environment (genetic diversity hypothesis) (Watson 1991; Yasui 1998). Environmental benefits are easily understood and accepted by every researcher; however, genetic benefits have many theoretical difficulties and remain controversial (Yasui 1998; Jennions & Petrie 2000).

Since the 1990s the major interest of mating system researchers has shifted to the female role in sexual selection (Rosenqvist & Berglund 1992; Eberhard 1996). Nowadays, several researchers consider that the paternity distribution of eggs of multiply mated females might be determined not only by male–male sperm competition but also by postcopulatory sperm selection (or 'cryptic' choice) by females (Eberhard 1996; Telford & Jennions 1998; Stockley 1999; but see Simmons et al. 1996; Stockley 1997). Such a view presupposes that females have some criteria by which they discriminate sperm quality and then nonrandomly allocate fertilization toward sperm from favorable male genotypes. However, the information available to females on males and sperm quality is often unreliable (Watson 1991; Yasui 1998). In a changing environment, fit genotypes may be different between generations so that females cannot predict the genes that will be successful in the next generation. Even in relatively stable environments, fit genotypes may not change between generations but it is often difficult for females to discriminate which male individual has those genes (especially if genetic compatibility is important; Zeh & Zeh 1996). In either case, females have no reliable sire selection criteria for their eggs. A hypothetical female strategy to deal with such uncertainty is 'genetic bet-hedging' (Watson 1991; Parker 1992; Stockley et al. 1993; Schneider & Elgar 1998; Yasui 1998). By having eggs fertilized by more than one male, females may reduce assessment error in mate choice caused either by irregular environmental change (bet-hedging under the genetic diversity hypothesis) or by the female's imperfect ability to discriminate male genotypes (bet-hedging under the good genes hypothesis) (see Yasui 1998). Consequently, a 'bet-hedger' genotype is supposed to reduce the probability of extinction across the generations.

However, whether multiple mating really functions as genetic bet-hedging to reduce the probability of extinction of the controlling genotype has not been examined theoretically. In the standard agreements of life-history-evolution theory (Sterns 1992) for organisms in a changing environment, the proper indicator of the return expected from each strategy is the mean fitness of the individuals (genotype) adopting that strategy. When generations are discrete, the mean fitness of the genotype within generations (W_{WG}) and between generations (W_{BG}; i.e. mean of W_{WG} over generations) should be calculated as the arithmetic and geometric means, respectively. When comparing between strategies that have equal between-generation arithmetic mean fitness, the strategy with the smallest between-generation fitness variance (S_{BG}^2; i.e. variance of W_{WG} over generations) achieves the greatest W_{BG}. Therefore, bet-hedging theory predicts that the strategy with the smallest S_{BG}^2 is evolutionarily stable (Slatkin 1974; Philippi & Seger 1989). However, does multiple mating really reduce S_{BG}^2 compared to a single mating strategy and, if it does, to what extent does it do so (Yasui 1998)? In this paper, I use a mathematical model and computer simulations to show that the efficiency of bet-hedging by multiple mating depends on the number of females, the costs of additional mating and environmental stability.
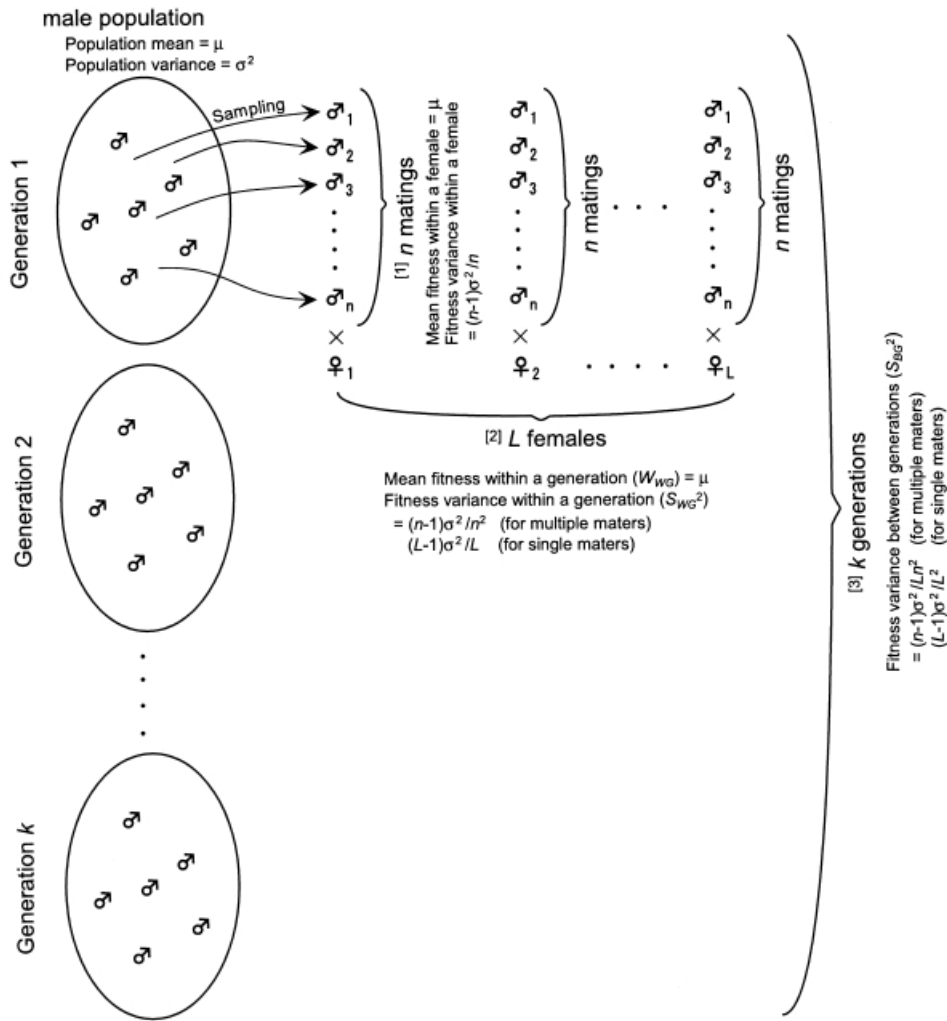
Fig. 2. The within-generation variance (S_{WG}^2) and between-generation variance (S_{BG}^2) of female fitness can be calculated from the formula of standard error of mean (SEM) when mating is statistically regarded as the sampling of mates by females from a male population (see text).

MODEL

Fitness variances of females can be estimated by calculating the standard error (SE) of the mean fitness (Sokal & Rohlf 1995) if we consider mating as sampling of mates from a male 'population' (in the sense of statistics) (see the scheme in Fig. 2). There are three hierarchies in this model; [1] matings by each female; [2] females in each generation; and [3] discrete generations. In every generation, each of L females randomly samples n males from the male population ($n = 1$ for monandry and $n > 1$ for polyandry). Females cannot discriminate male or sperm quality because of the lack of reliable sire selection criteria. To exclusively test the effects of female mating frequency on female fitness, it is assumed that males vary only in genetic quality and females vary only in mating frequency. There are two types of males, good and bad, in the population (good : bad = $1 - p : p$ in genotypic frequencies). The survival rates of offspring fathered by good and bad males are 1 and $1 - c$, respectively. The fecundity of females is f and all males mated with the same female fertilize an equal portion (f/n) of their eggs. Thus, the mating-order does not affect the fitness (i.e. the 'fair raffle' model of sperm competition, Parker *et al.* 1990). Female fitness (= the number of survived offspring) is calculated as the product of male quality and female fecundity (f). The frequency distribution of male quality weighted by f constitutes the frequency distribution of female fitness. The popula-

tion mean (μ) and population variance (σ^2) of female fitness are as follows:

$$\mu = p \cdot f \cdot (1-c) + (1-p) \cdot f \cdot 1 = f(1-pc) \quad (1)$$

$$\sigma^2 = p \cdot \{f \cdot (1-c)\}^2 + (1-p) \cdot (f \cdot 1)^2 - \mu^2$$
$$= f^2 pc^2 (1-p). \quad (2)$$

In the hierarchy [1], the mean and variance of a female's fitness per mating (i.e. sample mean, m, and sample variance, s^2) can be estimated from the population parameters (μ and σ^2). The expected value of the sample mean ($m = \sum x_i$; x_i is the number of survived offspring fathered by male i) is equal to μ because the sample mean is the unbiased estimator of population mean. However, fitness variance (s^2) within a multiply mated female is less than σ^2 because sample variance is an underestimate of population variance when it is calculated from small samples (i.e. n matings). Then, the sample variance is calculated as

$$s^2 = \frac{(n-1)\sigma^2}{n} \text{ where } \sigma^2 = \frac{\sum (x_i - m)^2}{n-1}$$
$$\text{and } s^2 = \frac{\sum (x_i - m)^2}{n}. \quad (3)$$

There is no fitness variance within a singly mated female because $n = 1$.

In each generation (hierarchy [2] in Fig. 2), the mean fitness obtained from L females (W_{WG}) is expected as μ ($W_{WG} = \dfrac{\sum m_j}{L} = \dfrac{\sum \mu}{L} = \mu$; m_j is the fitness of female j). The within-generation fitness variance (S_{WG}^2) for single maters is

$$S_{WG}^2 = \frac{(L-1)\sigma^2}{L} \quad (4)$$

because this is equivalent to the sample variance among L females (substitute n in (3) with L). On the other hand, S_{WG}^2 for multiple maters is equivalent to the square of the standard error of L means, which is calculated by dividing the variance in hierarchy [1] (s^2) by the sample size in that level (n). Thus,

$$S_{WG}^2 = \frac{s^2}{n} = \frac{(n-1)\sigma^2}{n^2}. \quad (5)$$

In the same manner, between-generation fitness variance (S_{BG}^2) in hierarchy [3] can be calculated by dividing the variance in hierarchy [2] (S_{WG}^2) by the sample size in that level (L). Thus,

$$S_{BG}^2 = \frac{S_{WG}^2}{L} = \frac{(L-1)\sigma^2}{L^2} \text{ for single maters and} \quad (6)$$

$$S_{BG}^2 = \frac{S_{WG}^2}{L} = \frac{(n-1)\sigma^2}{Ln^2} \text{ for multiple maters.} \quad (7)$$

Substituting (2) into equations (6) and (7) gives between-generation fitness variance, S_{BG}^2 as

$$S_{BG}^2 = \frac{(L-1)f^2 pc^2 (1-p)}{L^2} \text{ for single maters and}$$
$$\quad (8)$$

$$S_{BG}^2 = \frac{(n-1)f^2 pc^2 (1-p)}{Ln^2} \text{ for multiple maters.} \quad (9)$$

Therefore, the expected value of S_{BG}^2 is inversely proportional to the number of female individuals (L) (Fig. 3). The difference in S_{BG}^2 between single-mating and multiple-mating females (i.e. the advantage of multiple mating) is diminishing as L increases (Figs 3,4; see also Yasui 1998). The increase in mating frequency of over two times scarcely contributes to female fitness (Fig. 4). These predictions are very general and independent of fitness functions of both sexes because these predictions are obtained before the definition of fitness functions (from eqns (6) and (7), whatever the σ^2 is, the S_{BG}^2 is inversely proportional to the L). Even if the variances of female traits other than
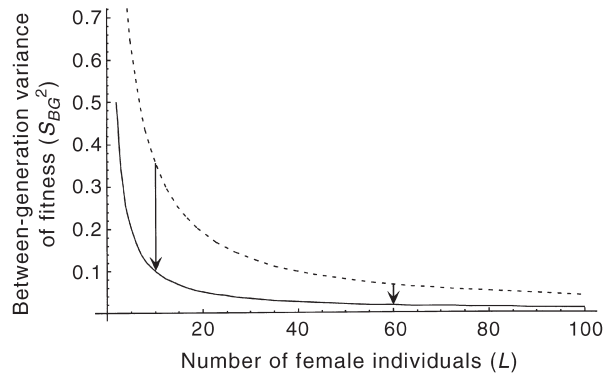

Fig. 3. When the number of the females (L) adopting the same strategy (single mating or double mating) is small (left arrow), double mating greatly reduces between-generation fitness variance (S_{BG}^2) but this effect diminishes as L increases (right arrow). Parameter values: $n = 2$, $f = 4$, $p = 0.5$ and $c = 1$. ----, Single mating; ——, double mating.
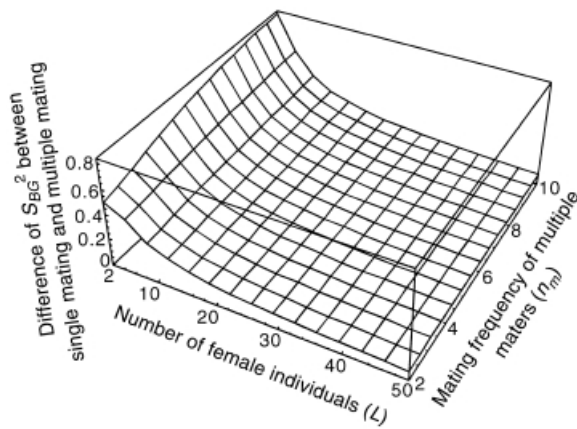
Fig. 4. The advantage of multiple mating over single mating depends on the number of female individuals (L) and mating frequency of multiple maters (n_m). The difference of between-generation variance of fitness S^2_{BG} (the right side of eqn (8) minus that of eqn (9)), revealing the effectiveness of bet-hedging, is visualized. The increase in n_m of over 2 scarcely contributes to female fitness when L is large. Parameter values: $f = 4$, $p = 0.5$ and $c = 1$.

mating frequency (n) (e.g. variances of fecundity and female's discrimination ability of male quality) are introduced into the model, these predictions cannot be affected unless these traits correlate with n. If multiple mating increases fecundity, it corresponds to a direct benefit and if multiply mated females more effectively choose favorable sperm, it is explained by the 'sexy sperm' (Harvey & May 1989; Curtsinger 1991) or 'good sperm' (Yasui 1997) hypotheses, not by genetic bet-hedging.

COMPUTER SIMULATION

This model predicts that the effectiveness of bet-hedging by polyandry diminishes in large female populations. However, it would be too hasty to conclude that from this simplified model. The population size at which the difference in S^2_{BG} between both strategies becomes negligible cannot be predicted by this model because the difference diminishes gradually but never disappears in any large population (Fig. 3). Moreover, within an actual evolutionary process, the number of both strategists dynamically changes from generation to generation in the same population. For instance, even if the number of individuals is equal in the initial generation (e.g. 20 single maters and 20 multiple

maters), once one genotype outnumbers the other by chance (e.g. 30 single maters and 10 multiple maters), the former would have greater probability of fixation. As the predictions of this model are based on the comparison of S^2_{BG} at the same numbers of individuals, the evolutionary outcome under this dynamic condition is difficult to predict analytically. Thus, computer simulations were carried out.

In the simulations, two female genotypes (single mating and multiple mating strategies) were allowed to compete in a population with a constant size. Females randomly mated with two male genotypes, good and bad, according to the male genotypic frequencies in the population. Generations were discrete and the frequency of the bad male genotypes was kept constant in each simulation over generations, as without this assumption of genetic equilibrium, the bad genes rapidly become extinct in the population and thereafter mate choice is unnecessary. This assumption is realistic with respect to current theory which suggests that genetic variance of fitness-related traits is maintained by several mechanisms such as mutation-selection balance (Iwasa *et al.* 1991; Andersson & Iwasa 1996; Maynard Smith 1998) and negative frequency-dependent selection due to environmental fluctuation, host–parasite coevolution (i.e. red queen hypothesis: Van Valen 1973) and so on. Such temporal fluctuation of selection pressures is introduced as three different levels of the equilibrium frequency of bad genotype ($p = 0.1$, 0.5 or 0.9). When the environment is relatively stable between generations, the correlation of relative fitness of a particular genotype between generations is expected to be positive (i.e. 'good genes' are advantageous in every generation), and then the equilibrium frequency of bad genes (p) is suppressed at low level by natural selection. On the other hand, when the environment is irregularly changing, such correlation is near zero or rather negative (i.e. successful genes in one generation will no longer be successful and sometimes may turn into 'bad genes' in the next generation) and, therefore, p is moderate or high.

Which male genotype females mated with was simulated by drawing a random number (y) between 0 and 1. Mating frequency of multiple maters was n_m ($n_m \geq 2$). The females that drew $p < y \leq 1.0$ (or $0 \leq y \leq p$) were regarded as mating with a good (or bad) male. The mothers produced f daughters and f sons (i.e. the sex ratio is 0.5). However, as the male genotypic frequency is kept

constant ($p = 0.1$, 0.5 or 0.9) as mentioned above, the dynamics of the number of male offspring can be neglected in the simulation. Thus, the present study hereafter shows only the number of females. At each mating, multiple-mating females (imagine some prolific insects) that mated with good males produced 100 viable daughters and those that mated with bad males produced 100 non-viable daughters. The summed number of the survived offspring from n_m matings was the fitness of multiple maters. Single-mating females competing with the multiple maters (mating n_m times) always produced $100 * n_m$ daughters but the daughters sired by bad males cannot survive. Multiplying by n_m is just a measure to equalize single maters' mean fecundity to the multiple maters' mean in any mating frequency of the latter (it does not mean that the single mater's fecundity depends on mating frequency of the multiple maters). Thus, p, f and c in equations (1) and (2) were set as $0.1 \sim 0.9$, $100 * n_m$ and 1, respectively, in this simulation. Daughters adopt the same strategy as their mothers. Because the total number of offspring produced from all females is approximately $50 * n_m$ times as many as the constant population size $L_s + L_m$ (L_S and L_m are the number of individuals of single maters and multiple maters, respectively), offspring compete for survival with an equal chance irrespective of genotype.

Multiple mating often entails some fitness costs (e.g. time and energy for additional mating and increased risks of predation and infection during copulation; Arnqvist 1989; Chapman & Partridge 1996; Yasui 1997, 1998). In this study, the costs were simulated as a decrease of fecundity (f). For instance, say the doubly mated females with 1% costs (i.e. 1% decrease of mean fecundity) produced 99 daughters on average while singly mated females produced 100 daughters on average. Therefore, except for mating frequency and remating costs, all conditions were kept equal for the two female strategies. Consequently, the effects of multiple mating for a bet-hedging strategy can be exclusively estimated.

Two types of competition were simulated: one in which the number of both strategists in the initial generation was even (e.g. 100 single maters *vs* 100 double maters), and the other in which a female with one strategy invaded the population of the other strategy (e.g. 1 single mater *vs* 100
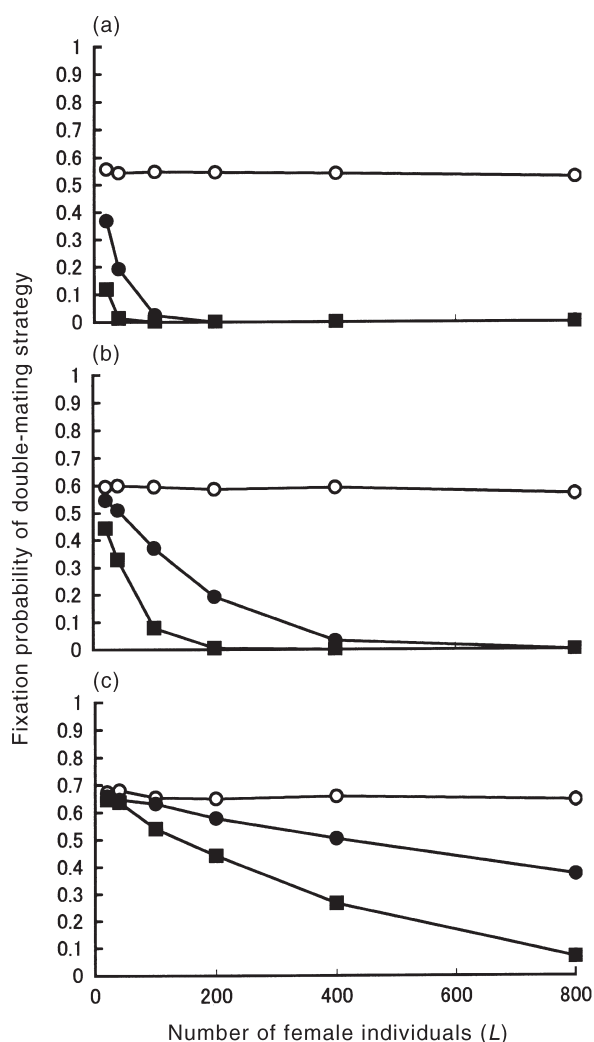

Fig. 5. The effects of female population size on the efficiency of bet-hedging. The double-mating strategy competed with the single-mating strategy. The initial number of individuals was equal between both strategies. The frequencies of bad genes were kept at (a) 10% (b) 50% and (c) 90% by the mutation–selection balance. ○, Multiple mating entailed no costs; ●, 1% costs (i.e. a 1% decrease of mean fitness): ■, 3% costs.

double maters). Each simulation included 5000 trials and each trial was continued until either strategy became extinct.

RESULTS

Three factors, number of female individuals, equilibrium frequency of bad male genotype (p, a negative function of environmental stability) and costs of female multiple mating greatly influenced the results of the simulations.
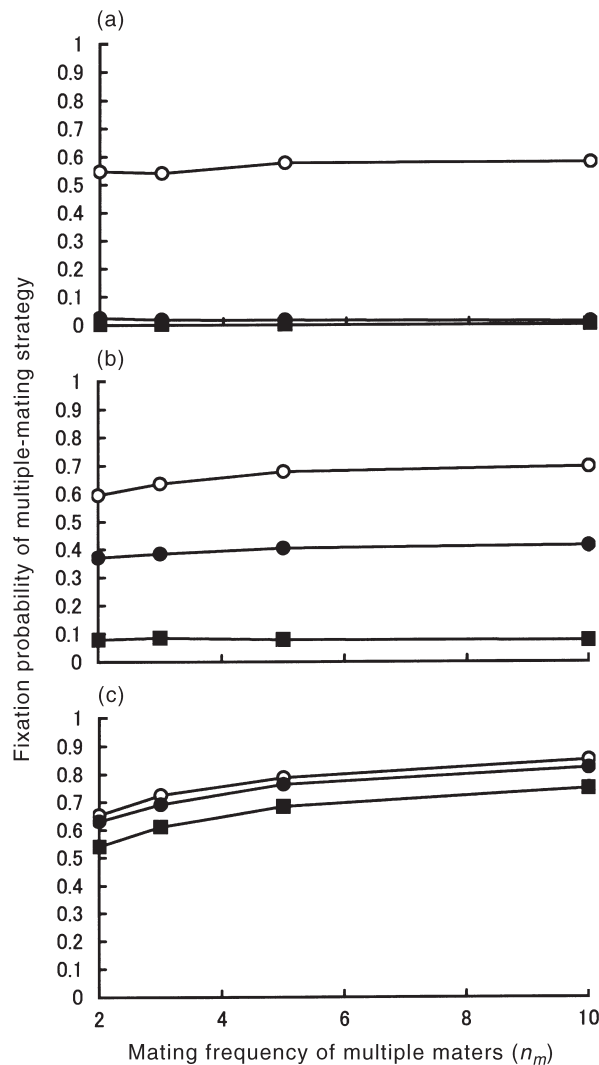
Fig. 6. The effects of the mating frequency of multiple-maters on the efficiency of bet-hedging (population size = 100). The relative advantage of multiple (2–10) mating against single mating is shown. The initial number of individuals was equal between both strategies. The other conditions are equal to Fig. 4.

Competition with the equal initial genetic frequencies of females

Each plot in Figs 5 and 6 represents the proportion of the trials in which the multiple-mating strategy became fixed when the initial genetic frequency of females was set as even between single and multiple mating. When multiple mating entailed no costs (open circles in Fig. 5), the fixation probability of multiple mating was slightly higher than that of single mating, almost inde-

pendent of environmental stability and female population size. However, with only 1% costs, multiple mating drastically lost its advantage in relatively stable environments ($p \le 0.5$; closed circles and closed squares in Fig. 5ab). Costly multiple mating almost always became extinct especially at high densities (≥ 400 individuals). However, in an unstable changing environment ($p = 0.9$; Fig. 5c), multiple mating often exterminated single mating even at high densities despite the slight fecundity costs. The increase in mating frequency (n_m) beyond two had less of an effect on the fixation probability (Fig. 6), as predicted by the model (Fig. 4).

The invadability of the strategies

Environmental stability had a strong effect on the invading ability of female strategies (Table 1). In relatively stable environments ($p = 0.1$), the single-mating strategy and the double-mating strategy never invaded each other except when the costs of double mating were extremely high ($\ge 30\%$ decrease of fecundity) and the population size was small (21 individuals: Table 1a).

In moderately stable environments ($p = 0.5$), when double mating entailed no fecundity costs, it was able to invade more frequently than single-mating strategy in small populations (21 individuals: Table 1b). However, in large populations (201 individuals), both strategies were unable to invade each other. When even 1% costs of multiple mating were included into the model, single mating was as competitive as multiple mating in both large and small populations. When costs were raised to 3% single-mating strategy was significantly more likely to invade.

However, in unstable environments ($p = 0.9$), except for the cases with high density (201 individuals) and high costs (3% costs), double mating invaded more frequently than single mating (Table 1c).

DISCUSSION

The present study tests whether female multiple mating really functions as genetic bet-hedging (Watson 1991; Yasui 1998) when females cannot discriminate male genetic qualities. From the

Table 1 The intruding ability of one strategy (single mating, SM and double mating, DM) into the population occupied by the other strategy[a]

a. Stable environment (equilibrium frequency of bad male genotype = 0.1)

Composition of initial population (SM : DM)	With no cost for DM		With 10% cost for DM		With 30% cost for DM	
	SM fixed	DM fixed	SM fixed	DM fixed	SM fixed	DM fixed
1 : 20	0	5000	0	5000	24	4976[b]
20 : 1	5000	0	5000	0	5000	0
1 : 200	0	5000	0	5000	0	5000
200 : 1	5000	0	5000	0	5000	0

(b) Moderately stable environment (equilibrium frequency of bad male genotype = 0.5)

Composition of initial population (SM : DM)	With no cost for DM		With 1% cost for DM		With 3% cost for DM	
	SM fixed	DM fixed	SM fixed	DM fixed	SM fixed	DM fixed
1 : 20	35	4965[c]	50	4950[d]	79	4291[e]
20 : 1	4935	65	4955	45	4979	21
1 : 200	0	5000	3	4997[f]	49	4951[g]
200 : 1	5000	0	5000	0	5000	0

(c) Unstable environment (equilibrium frequency of bad male genotype = 0.9)[n]

Composition of initial population (SM : DM)	With no cost for DM		With 1% cost for DM		With 3% cost for DM	
	SM fixed	DM fixed	SM fixed	DM fixed	SM fixed	DM fixed
1 : 20	84	4810[h]	108	4760[i]	118	4757[j]
20 : 1	4035	376	4075	340	4095	311
1 : 200	8	4992[k]	14	4986[l]	25	4975[m]
200 : 1	4971	29	4972	28	4988	12

[a]The frequencies of fixation of the single-mating and double-mating in the 5000 trials of the simulation.
[b,e,g~m]Fisher's exact probability test; $P < 0.0001$; [c]$P = 0.0034$; [d]$P = 0.6802$; [f]$P = 0.2499$.
[n]Remains of the trials (5000—SM fixed—DM fixed) were the cases in which both genotypes became extinct at the same generation.

results of computer simulations, even if females entirely lack precise mate choice criteria, random multiple mating may sometimes be more competitive than random single mating when good male frequency, female population size and remating costs are small. What are the reasons for such parameter dependence of genetic bet-hedging?

Why does female population size influence the efficiency of bet-hedging?

The first important result of this study is that female population size affects the effectiveness of bet-hedging by multiple mating. In a relatively stable environment, the large number of single-mating females can compete with the same

number of multiple-mating females. If multiple mating entails very slight costs, a single-mating strategy can exclude a multiple-mating strategy from the population (Figs 5a,6a). Why are the effects of multiple mating so limited? The reason is understandable if we replace multiple mating with, say, seed dormancy within annual flowering plants; the typical example of evolutionary bet-hedging (Philippi & Seger 1989; Sterns 1992). There are two genotypes, the bet-hedger producing both dormant and non-dormant seeds and the non-bet-hedger producing only non-dormant seeds. The fitness, W_{WG}, of all individuals of the non-bet-hedger synchronously fluctuates between generations (i.e. all germinating seedlings are disadvantageous in a bad year whereas they achieve higher reproduction than the bet-hedger's mean in a good year), while the W_{WG} of the bet-hedgers does not fluctuate much, because every individual achieves an intermediate fitness in every year. Thus, partial dormancy as bet-hedging can be significantly more adaptive than a non-dormant strategy. However, this synchrony, that increases between-generation fitness variance S_{BG}^2 does not exist in the single-mating strategy. The fitness of single-mating individuals varies randomly depending on which male they mate with: good or bad. The low fitness of single-mating females that mate with bad males is offset by the high fitness of single-mating females that mate with good males in the same generation, if there are a sufficient number of individuals of the same monandry genotype. Consequently, although the fitness (m) of single-mating females varies among individuals, the within-generation mean (W_{WG}) of this genotype does not greatly fluctuate between generations (so S_{BG}^2 is small). Thus, multiple mating as bet-hedging cannot be effective in a large population. On the other hand, when the number of single-mating females L (thus equaling the total number of matings by all females) is small, they will mate with only a small fraction of the male population. This small sample (L) often contains more or less bad males than the true genotypic frequency (p) simply by chance. This sampling error causes the fluctuation of W_{WG} of the single-mating genotype through generations (so S_{BG}^2 increases). In contrast, for multiple-mating females, the sampling error is relatively small

even in a small population because their total number of matings (Ln_m) is n_m times greater than for single-mating females. As the female population size (L) increases, such a sampling error and thus the S_{BG}^2 is diminished even for single-mated females.

The effect of fitness costs was more prominent in a large population (Table 1; Fig. 5). Cost is a deterministic process that constantly works to reduce the fitness (independent of population size) whereas sampling error is a stochastic process that often disturbs the progress of the deterministic process (especially in small populations). Figure 5 shows that the relative intensity of the stochastic process decreases in large populations as theoretically predicted.

Fluctuating environments favor genetic bet-hedging by female multiple mating

The second important result is that environmental fluctuation alters the effectiveness of bet-hedging. As mentioned above, in relatively stable environments costly multiple mating is overwhelmed by single mating because it cannot offset very slight remating costs even in small populations (Figs 5a,6a). In such stable environments, every female can confidently expect to meet a good male at their first mating because of the high frequency of good genes. Thus, multiple mating is unnecessary, in particular, if it entails costs. On the other hand, when environments fluctuate unpredictably, any single genotype cannot increase to high frequency because of the lack of continuous positive selection on it, thus 'good-gene' frequency is low. In such a situation, indiscriminate multiple mating can compete with single mating even with remating costs (Fig. 5c). The reason for this is that the single-mating strategy is more strongly influenced by the stochastic error in mate sampling when good males are rare. For example, when the good male frequency is as high as 0.9, the double-mating genotype needs only one individual to produce offspring, on average, while there must be two individuals of the single-mating genotype to expect successful reproduction. However, in the population where good male frequency is 0.1, the single-mating strategy needs 10 individuals (the double-mating strategy needs 5 individuals).

If the number of individuals decreases to less than 10 by chance, the single-mating strategy cannot recover but the double-mating strategy is still able to. Hence, the advantage of multiple mating in a small population (Fig. 3) becomes more conspicuous in a fluctuating environment. In the analyses of invadability (Table 1), when the environment is stable, both strategies never invade the population occupied by the opponent except for the case of very high remating costs (30% fecundity loss; Table 1a). This is because when 'good-gene' frequency is high, the situation where most individuals of the majority genotype fail in reproduction (the necessary condition for the invasion by minority genotype) seldom or never occurs. For example, when the good male frequency is 0.9, the probability that 20 single-mating females fail to reproduce while one double- mating female (without costs) successfully reproduces in a population including 21 females is only just $0.1^{20} * 0.9^1 = 9 * 10^{-21}$. When the single-mating strategy tries to invade in the same situation, this probability is $0.1^{40} * 0.9^1 = 9 * 10^{-41}$. The former is relatively larger, but still extremely improbable that it will occur in finite populations (Table 1a).

In addition to the stochastic sampling error by females, two other factors, inbreeding depression and genetic drift, may favor multiple mating in a small population. Inbreeding has the same effect as the increase of bad genes as it increases one's probability to mate with the individuals carrying common deleterious recessive alleles (Charlesworth & Charlesworth 1987). Random genetic drift also causes the increase of bad genes by chance, which are likely to be deleted by natural selection if these are in large population (Gabriel & Bürger 1994).

Re-examination of empirical data that overestimate the bet-hedging effects

Some empirical studies have tried to confirm the bet-hedging effects of female multiple mating in nature (e.g. on the sierra dome spider by Watson 1991; the European shrew by Stockley et al. 1993); however, these studies did not compare the geometric mean fitness (W_{BG}) between polyandrous genotype and monandrous genotype across more than one generation. Thus, the benefits of the variance reduction due to genetic bet-hedging may

have been overestimated (Jennions & Petrie 2000). This may be due to the long-term absence of a theoretical framework for genetic bet-hedging by female multiple mating. The present study and Yasui (1998) provide such a framework for future empirical studies of genetic bet-hedging. On the basis of this framework, empirical data should be re-examined with particular regard to the necessary prerequisites of effective bet-hedging (i.e. small population size, very slight fitness costs to multiple mating and great environmental fluctuation (or high genetic load in a population)). If genetic bet-hedging is as important as previously believed, comparative analyses among populations or among species should detect: (i) a negative relationship between population size and female mating frequency; and (ii) a positive relationship between the degree of temporal environmental change (genetic load in a population) and mating frequency.

Good genes or genetic diversity: Which is the situation where bet-hedging is more likely to work?

Bet-hedging by multiple mating is a strategy for dealing with the inaccurate information on mate quality (Watson 1991; Jennions & Petrie 2000). This inaccuracy is attributable either to a female's imperfect ability of mate discrimination (good genes hypothesis) or frequent shift of 'good genes' caused by irregular environmental change (genetic diversity hypothesis) (Yasui 1998; Jennions & Petrie 2000). The computer simulations in this study suggest that the latter may be a more plausible scenario for the evolution of female multiple mating by genetic bet-hedging as bet-hedging needs high bad-gene frequencies in a population. Even if the female's discrimination ability is imperfect and thus intersexual selection on male genotypic frequency does not work adequately, as supposed by the good gene hypothesis, the frequency of good males eventually increases to a high level in a stable environment as a result of natural selection. In such populations bet-hedging no longer works effectively (Figs 5a,6a).

The relationship between female mating frequency, genetic diversity in a clutch, and the dependence of mother's fitness on offspring genetic diversity still remain hypothetical with few

empirical data available (but see Schmid-Hempel 1994; Liersch & Schmid-Hempel 1998). Recently, however, Hosken and Blanckenhorn (1999) suggested that if fitness is non-linearly (for instance sigmoidally) related to diversity, female multiple mating may not be more adaptive than single mating in a highly diversified population but in a less diversified population. Such non-linear fitness functions should be considered to test the genetic diversity hypothesis of female multiple mating. Some competitive or cooperative (compensatory) interactions among sibs ('full-sib competition' and 'half-sib cooperation' by Yasui 1998) can produce non-linear fitness function. Accumulating the empirical data on these factors will enable a more comprehensive review of the genetic benefits of female multiple mating in the future.

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