A Theoretical Analysis of Variation in Multiple Mating in Social Insects

by

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ABSTRACT

Many social insect females mate multiply (polyandry). However, little attention has been paid to the genetic basis of variation in female mate number within populations. In this study, analytical techniques and computer simulations were used to investigate the distribution of female mate number in populations. Simple genetic models were developed to illustrate how variation in rates of polyandry evolved and to determine if genetic loci associated with female mating behavior maintained variation over ecological timescales. The results of this study reveal that variability in female mate number may result from decision-making by females. In addition, genetic variation at loci associated with mating behavior can be maintained under some conditions. In conclusion, future investigations of polyandry in social insects may gain a greater understanding of factors promoting polyandry by studying the distribution of mate number within populations.

INTRODUCTION

Multiple mating by females (polyandry) occurs in a wide range of animal taxa (Arnqvist & Nilsson 2000, Jennions & Petrie 2000, Hosken & Stockley 2003). Polyandry in hymenopteran social insects is somewhat more restricted, but still takes place in several genera (Queller & Strassmann 1998, Crozier & Fjerdingstad 2001, Strassmann 2001). The occurrence of polyandry suggests that females obtain some fitness advantage by multiple matings. Indeed, several possible benefits to polyandry have been proposed. For example, females may gain from mating multiply if they receive direct material benefits from males. Direct benefits, such as sufficient sperm for reproduction or nuptial gifts, increase the viability or fecundity of the reproductive female. Alterna-

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tively, females may receive indirect, genetic benefits by mating with multiple males. Indirect benefits, such as the acquisition of good genes from males or the production of genetically diverse offspring, increase the fitness of a female's progeny (Vahed 1998, Arnqvist & Nilsson 2000, Jennions & Petrie 2000, Zeh & Zeh 2001).

Despite theoretical advances in understanding the evolution of variable mating strategies in males (Shuster & Wade 2003), little attention has been paid to the question of why females might show genetically-based variation in mating frequency. This question is particularly significant because evidence of variability in rates of polyandry is widespread (Avise *et al.* 2002, Griffith *et al.* 2002, Westneat & Stewart 2003, Torres-Vila *et al.* 2004). In addition, several studies have uncovered evidence of genetic variation associated with female mating frequency in natural populations (Solymar & Cade 1990, Torres-Vila *et al.* 2001, Torres-Vila *et al.* 2002, Wedell *et al.* 2002, Simmons 2003, Kraus *et al.* 2004). These results suggest that female mate number may be under selection to display variability within species.

The purpose of this study was to initiate an understanding of the factors affecting variation in female mate number. To address this issue, I used analytical techniques and computer simulations to explore if variability in genetically-influenced rates of polyandry could be maintained under equilibrium conditions. I conclude this study by suggesting future areas of research that may yield insights into the adaptive basis of polyandry in populations.

Model I: The problem of maintaining variation in female mate number

Description: I constructed a simple genetic model in which the number of times a female mated was determined by her genotype at a single, multiallelic locus, *M*. In the model, population size was assumed to be infinite, females and males were equally frequent, and generations were discrete and nonoverlapping. In addition, the effects of locus *M* were sex-limited to females. That is, males carried the alleles that influenced female mating behavior but males were not affected by their genotype at locus *M*.

A female of genotype M_xM_y, where x and y took on values from 1 to i, and i was the maximum number of alleles allowable at the locus, attempted to mate

$n = (x + y) / 2$ times. If $x + y$ was even, then a M_xM_y female mated exactly $n = (x + y) / 2$. If $x + y$ was odd, then 50% of M_xM_y females mated $(x + y) / 2 - 0.5$ times and 50% of M_xM_y females mated $(x + y) / 2 + 0.5$ times.

Females received direct benefits for mating multiply. Females that mated n times achieved absolute fitness of $an / (an + 1)$ where a (> 0) was a constant that determined the benefit of mating multiply. Under the specified function, the more often a female mated, the higher her fitness, although the benefits to mating multiply decreased as mate number increased. Mating multiply also carried a cost, because each mating attempt increased a female's susceptibility to predation and disease. Consequently, each time a female attempted to mate, there was a probability less than 1 ($0 < p < 1$) that she survived. Therefore, a female successfully survived mating n times with probability p^n.

Results: The overall fitness of a M_xM_y female depended on the number of times she mated, which was directly associated with her genotype. Females that mated n times obtained composite absolute fitness of

$$w_n = \frac{anp^n}{an+1} \qquad (1)$$

In order to examine the distribution of mate number under Model I, I used computer simulations that followed the changes in allele frequencies at locus M over time, and ultimately provided a distribution of mate number under various combinations of mating constant, a, and survival probability, p. The initial genotype frequencies of females and males were randomly chosen from a uniform distribution. Results of repeated simulations demonstrated that the final genotype and mating frequencies depend on the model variables and not the initial conditions. Females then underwent selection based on their fitness as determined by (1). Since there was no assortative mating, the genotypes of males and females in the next generation resulted from random union of gametes. Mating, selection, and reproduction were allowed to continue until no male or female genotype frequency changed by more than 10^{-6}, at which time the population was considered to be at steady state.

Fig. 1A illustrates the association between the number of times a female mated and p. As expected, females mated more often when the costs of

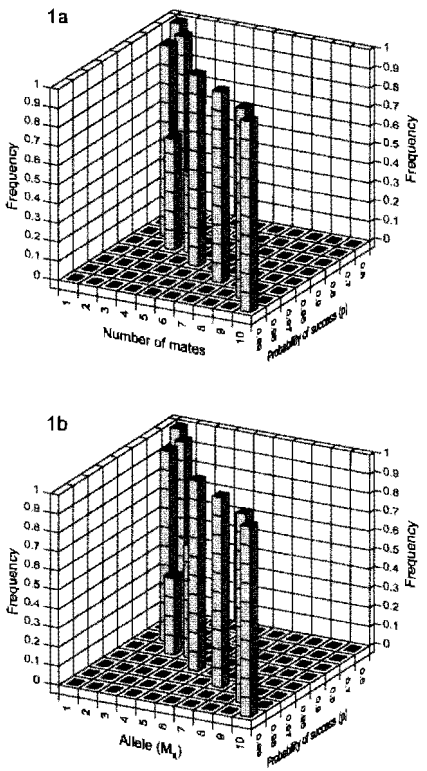

Fig. 1. Variation in number of mates (1a) and allele frequencies at mating locus M (1b) for females under Model I. The decay constant a is fixed at 0.5, the maximum number of female mates is set at ten, and the probability of a female successfully surviving mating, p, is allowed to vary.

mating were low. Of greater interest, however, was the fact that the equilibrium frequency distribution of female mate number rarely showed variation within populations. Rather, all females typically mated with the same number of males at equilibrium. For instance, with $p = 0.95$, all females in the population ultimately mated five times (Fig. 1A). Only one of the examples shown ($p = 0.9$) maintained any variation in female mating frequency. In this case, females that mated three or four times both enjoyed equal and maximum fitness. This led to the establishment of a balanced polymorphism. Nevertheless, this represented an exceptional case, and there was generally little variation in female mate number for a given set of variables.

The lack of variation in female mating frequency ultimately reflected a lack of variation at the genetic locus M (Fig. 1B). Typically, for a given value of p, females of only a single homozygous genotype achieved maximum fitness. Therefore, only a single allele ultimately remained at equilibrium. For instance, with $p = 0.95$, the frequency of the allele M_5 approached 1.0 at equilibrium and all females in the population mated five times (Fig. 1). The exception to this generality was the special case when females of distinct genotypes had equal fitness (i.e., when $p = 0.9$). In this case, genetic variation was maintained at an appreciable level.

To further investigate the conditions leading to the maintenance of phenotypic and genotypic variation under Model I, 10,000 values of p and a were randomly selected from a uniform distribution. For each of the selected

combinations, mating, selection, and reproduction were allowed to occur until equilibrium was reached. The equilibrium distribution of female mate number and frequency of alleles at locus *M* were then analyzed to establish if variability was maintained.

As expected, variation in phenotype or genotype was rarely maintained under Model I. Of the 10,000 sets of variables examined, only 12 resulted in the maintenance of appreciable variation in female mate number (defined as the frequency of at least two mating classes exceeding 0.05). Variation at locus *M* (defined as the maintenance of at least two alleles at a frequency of greater than 0.05) was also only present in these 12 cases. Of the remaining cases, 6570 and 234 ended in fixation of allele M_1 (frequency of $M_1 > 0.95$) and M_{10} (frequency of $M_{10} > 0.95$), respectively. The remaining 3184 cases resulted in fixation of an allele leading to an intermediate number of mates (frequency of $M_x > 0.95$ with $1 < x < 10$).

Conclusions: Model I represented a simple example of how polyandry may be associated with fitness and how a genetic locus may influence mating behavior. The results of analytical analysis and computer simulations arrived at the general conclusion that variation in mating frequency, in addition to genetic variation associated with mating behavior, was generally not maintained within populations.

Model II: A solution to maintaining variation in female mate number

Description: Model II represented a more sophisticated framework than that developed in Model I. Specifically, two types of males, high-quality males (HQMs) and low-quality males (LQMs), now existed within populations. HQMs were present in the population at frequency v, while LQMs were present at frequency $1 - v$. The distinction between HQMs and LQMs was not genetically based. Rather males of distinct phenotype arose through environmental variation. HQMs possessed a resource that was passed to females during mating, which enhanced female survival. Females that mated with HQMs received direct fitness benefits and obtained maximum fitness of 1. In contrast, females that failed to mate with a HQM obtained lower

fitness of $1 - s$ ($0 < s < 1$). These females received low fitness regardless of the number of LQMs with which they mated.

As in Model I, female mating behavior was controlled by a sex-limited genetic locus M. Specifically, a M_xM_y female, where x and y took on values from 1 to i, mated a maximum of $n = (x + y) / 2$ times. If $x + y$ was even, then the female mated with as many as $n = (x + y) / 2$ males. If $x + y$ was odd, then 50% of M_xM_y females mated with as many as $(x + y) / 2 - 0.5$ males and 50% of M_xM_y females mated with as many as $(x + y) / 2 + 0.5$ males. In addition, as in Model I, each time a female attempted to mate, there was a probably less than 1 ($0 < p < 1$) that she survived.

In contrast to Model I, females continued to mate until one of two events occurred. First, females ceased mating if they successfully mated with a HQM on any mating attempt. Second, females stopped mating if they reached the maximum number of mates allowable given their genotype before successfully mating with a HQM. Consequently, females were able to 'choose' to stop mating under the assumptions of Model II.

Results: The expected absolute fitness of a female capable of mating a maximum of n times as determined by her genotype M_xM_y was

$$w_n = (1 - v)^n (1 - s) p^n + \sum_{i=1}^{n} v(1 - v)^{(i-1)} p^i \quad (2)$$

The first term defined the fitness of a female that failed to mate with a HQM. In this case, the female survived to mate n times with LQMs and ultimately obtained fitness $1 - s$. The second term (sum of terms) in (2) incorporated information on females that successfully mated with a HQM. Here, a 'fortunate' female may have mated with a HQM on any of her $i = 1$ to n mating attempts. If she mated with a HQM, she did not engage in any further matings. Consequently, the expected fitness of a female whose genotype dictated a maximum of n matings was given by (2), which represented a weighted average of all possible mating scenarios.

As with Model I, numerical methods were used to examine the distribution of female mate number. The initial genotype frequencies of females

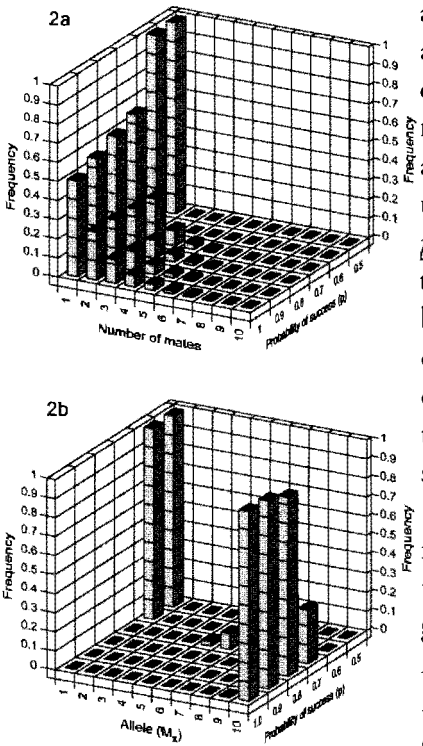

Fig . 2. Variation in number of mates (2a) and allele frequencies at mating locus M (2b) for females under Model II. The frequency of high-quality males, v, is fixed at 0.5, the selection coefficient against low-quality males, s, is equal to 0.5, the maximum number of female mates is set at ten, and the probability of a female successfully surviving mating, p, is allowed to vary.

and males were chosen at random from a uniform distribution; initial conditions did not affect the final genotype and mating frequencies. Mating, selection, and reproduction were allowed to occur under various combinations of v, s, and p. The genotypes of males and females in the next generation were then determined by random union of gametes. This cycle continued until no genotype frequency changed by more than 10^{-6}, at which time the population was considered to be at steady-state.

Fig. 2 illustrates how the change in female mating strategy in Model II led to the maintenance of phenotypic and genotypic variation in some populations. As was the case with Model I, female mating frequency increased when p increased. However, in contrast to Model I, several cases arose where females displayed variation in the number of times that they mated (Fig. 2A). In particular, female mate number sometimes showed a geometric distribution within populations. For instance, when $p = 0.9$, an appreciable frequency of females (> 0.05) mated one, two, three, and four times. Note that variation in female mating frequency was only maintained when p was relatively high. Otherwise, with $p \leq 0.6$, all females in the population reverted to single mating.

The distribution of female mate number within populations sometimes reflected the maintenance of variation at the mating locus, M. For example, after 40,000 generations of mating, reproduction, and selection, genetic variation still existed when $p \cong 0.7$ (Fig. 2B). Moreover, variation in female mating

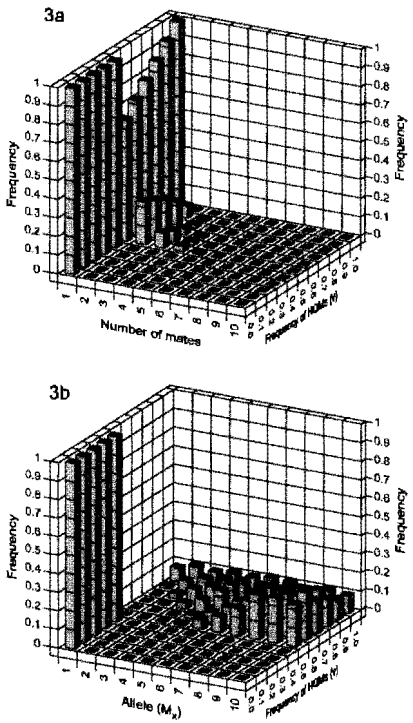

Fig. 3. Variation in number of mates (3a) and allele frequencies at mating locus M (3b) for females under Model II. The selection coefficient against low-quality males, s, is fixed at 0.5, the probability of a female successfully surviving mating, p, is equal to 0.7, the maximum number of female mates is set at ten, and the frequency of high-quality males, v, is allowed to vary.

frequency was sometimes maintained even when the population was fixed for a single allele. For the values of v and s used in the illustrated simulations, variation in mating frequency occurred without genetic variation if $p \geq 0.9$.

The frequency of multiple mating and maintenance of genetic variation were highly dependent on the proportion of HQMs in the population. In the example illustrated in Figure 3a, appreciable variation in female mate number resulted if $0.5 \leq v \leq 0.9$. Interestingly, the population of females reverted exclusively to single mating if v was either high or low. If $v > 0.9$, then most females needed to mate only once to obtain maximum fitness. In contrast, if $v < 0.5$, then the cost of remating for a female outweighed the benefits of trying to mate with a HQM in the population.

The frequency distribution of female mate number sometimes reflected the maintenance of genetic variation (Fig. 3b). Indeed, when $v \geq 0.5$, many alleles were maintained over ecologically relevant timescales. Only with $v < 0.5$ did the entire population become monomorphic. The distribution of alleles within the polymorphic populations was relatively flat in several of the illustrated examples, because the female mating strategies mandated by several of the genotypes resulted in approximately equal fitness.

I next tested the ability of Model II to maintain variation in female mating frequency and genotype under different combinations of variables. To investigate how often variation was maintained under this framework, 10,000

sets of v, p, and s were randomly selected from a uniform distribution. Mating, selection, and reproduction were allowed to take place for each case as described above. The final phenotypic and genotypic distributions were subsequently evaluated to determine if variation was maintained.

The results of the repeated simulations revealed that Model II was able to maintain substantial variation in female mate number and allele frequency within populations relatively often. In total, females showed variation in mating frequency 3050 times. In addition, multiple alleles were maintained at locus M in 2475 cases. In only 6429 and 1094 instances, did females fix for alleles M_1 and M_{10}, respectively (frequency of alleles greater 0.95). In two cases the population fixed for an allele governing intermediate numbers of mates (frequency of $M_x > 0.95$ with $1 < x < 10$).

Conclusions: Model II explored complex mating scenarios incorporating decision making by females in order to determine if phenotypic variation in mating frequency and genetic variation at loci related to mating behavior could be maintained. Simulations conducted under this model led to the maintenance of variation in mating frequency as well as the maintenance of variation in genotype under some conditions.

DISCUSSION

The purpose of this study was to initiate an understanding of factors leading to the maintenance of *variation* in mating frequency of females within populations. Explicit genetic models were used to examine the evolution of polyandry and the final distribution of female mate number under simple scenarios. I was particularly interested in studying variation in mating frequency that had a genetic basis and determining if genetic variation at loci associated with mating behavior could be maintained under ecological timescales.

The first framework developed (Model I) incorporated very simple elements of a polyandrous mating system. Polyandry was beneficial to females because females obtained direct fitness benefits by mating multiply. However, mating multiply carried a cost for females because they risked death through predation or disease each time they attempted to mate.

The results of computer simulations under Model I led to predictable results. Increasing the benefits or decreasing the costs of mating led to higher rates of polyandry within populations. However, females of only one genotype

typically enjoyed maximum fitness. Consequently, females almost always displayed identical mating behaviors at steady state, because selection generally led to the fixation of a single allele. Rare exceptions to this trend resulted from balanced polymorphisms, where females of two genotypes possessed the same fitness.

The second framework considered (Model II) was more complex than Model I. Under Model II, females received relatively high fitness by mating with a high-quality male (HQM) and relatively low fitness by mating with a low-quality male (LQM). Females were also penalized for each mating attempt. In addition, females mated until they successfully mated with a HQM or until they reached their genetically determined maximum number of mates. Consequently, Model II allowed for decision-making by females.

Analysis of Model II led to further insight into the causes of variation in female mating frequency. For example, high mating costs tended to depress rates of polyandry. The mating frequency of females was also affected by the presence of variation in male quality. When the frequency of HQMs was relatively low, females tended to mate few times at equilibrium, because it became costly for females to find and mate with a HQM. In addition, when the difference between the fitness benefits to a female of mating with a HQM and LQM was relatively small, then females also mated relatively few times at equilibrium, because the benefits of seeking out a HQM did not outweigh the costs. Consequently, monandry evolved when costs of remating were high or benefits to remating were low.

Of greater interest to the topic of this study, however, was the observation that Model II successfully uncovered cases where variation in female mating frequency was maintained for long periods of time. In particular, the distribution of female mate number often displayed a geometric distribution when variation in mating frequency was observed. This distribution reflected the probability of a female finding a HQM after successive mating attempts.

The pattern of variation in female mating frequency discovered through analysis of Model II may have practical implications. The observation of a geometric distribution of female mate number in natural populations may reflect the underlying cause of multiple mating by females. Specifically, females may be attempting to collect some type of direct or indirect benefit from mating that is possessed by only a proportion of males in the population.

In addition to revealing cases where phenotypic variation in mate number was maintained, Model II also successfully discovered situations where genetic variation at the mating locus was present for extended times. In these cases, the fitness of females of several distinct genotypes was approximately equal. This resulted in a balanced polymorphism over the timeframe considered. Of further interest, the presence of genetic variation at the mating locus did not always result in phenotypic variation in female mating frequency. Likewise, variation in female mate number did not necessarily reflect underlying variation in genotype, because females of any particular genotype were able to display multiple mating phenotypes. Consequently, empirical studies should not necessarily view the presence (or absence) of variation in female mate number as indicating that rates of polyandry will (or will not) be able to evolve.

The results of this investigation explicitly demonstrated that variation in female mate number could be maintained in populations. Relatively few previous studies have examined the maintenance of variation in female mating frequency. However some investigations have tangentially discovered that variation in rates of polyandry may be present at equilibrium under alternate mating scenarios. For example, Kokko *et al.* (2002) and Brown & Schmid-Hempel (2003) found that stable variation in female mating frequency arose in the presence of disease within populations. Shellman-Reeve & Reeve (2000), Ihara (2002), and Wakano & Ihara (2005) also demonstrated that variation in rates of polyandry may be maintained in cases where males varied in quality or provided parental care. Finally, Zonneveld (1992) discovered that variability in female remating rates could be present in populations at equilibrium as a function of rates of protandry.

One of the principle reasons this study was conducted was to generate interest in the genetic and adaptive basis of *variation* in rates of polyandry. Future theoretical studies on the subject should investigate cases where variability in female mate number is maintained at equilibrium. Moreover, such studies would be particularly helpful if they were explicitly genetic in nature. The genetic framework used in this study (a single gene with multiple alleles) was deliberately elementary. However, future studies may wish to incorporate quantitative genetic models, as mating behavior in natural populations is likely to be under control of multiple genetic loci.

In addition to promoting future theoretical studies, this investigation also points to areas of empirical research that may lead to a greater understanding of polyandry. Specifically, more investigations should consider the importance of natural variation in mating frequency to determine why females mate multiply. In particular, the distribution of female mate number may be informative in determining the factors promoting polyandry within populations.

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