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Variance-based selection may explain general mating patterns in social insects

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Female mating frequency is one of the key parameters of social insect evolution. Several hypotheses have been suggested to explain multiple mating and considerable empirical research has led to conflicting results. Building on several earlier analyses, we present a simple general model that links the number of queen matings to variance in colony performance and this variance to average colony fitness. The model predicts selection for multiple mating if the average colony succeeds in a focal task, and selection for single mating if the average colony fails, irrespective of the proximate mechanism that links genetic diversity to colony fitness. Empirical support comes from interspecific comparisons, e.g. between the bee genera *Apis* and *Bombus*, and from data on several ant species, but more comprehensive empirical tests are needed.

Keywords: polyandry; social evolution; division of labour; genetic diversity; disease resistance; social insects

1. INTRODUCTION

The mating behaviour of social Hymenoptera has attracted considerable scientific attention because it is highly variable and has profound consequences for social evolution (Crozier & Pamilo 1996; Oldroyd & Fewell 2007). Assuming that multiple mating must be costly and that the reproductive females control the number of copulations that they engage in (Strassmann 2001), several hypotheses have been suggested to explain the patterns of multiple mating. By contrast, the prevalence of single mating has not been explicitly addressed because single mating is presumably ancestral and leads to high intracolony relatedness that is essential to kin-selected evolution of sociality (Oldroyd & Fewell 2007).

Hypotheses to explain the evolution of multiple mating include sperm limitation (Kraus *et al.* 2004), genetic load at the complementary sex determination locus (Page 1980), enhanced division of labour

(Waibel *et al.* 2006) and disease resistance (Brown & Schmid-Hempel 2003), and decreased intracolony conflicts (Ratnieks & Boomsma 1995). These hypotheses of the benefits of multiple mating are distinct but not mutually exclusive. They have received variable experimental support and therefore the ultimate causation of female mating patterns in social Hymenoptera is still contentious, despite considerable research effort. Genetic load, division of labour and disease resistance mechanisms are all based on potential benefits of an increase in the intracolony genetic diversity. While recent accounts emphasize the direct benefits of genetic diversity *per se* (Brown & Schmid-Hempel 2003; Oldroyd & Fewell 2007), separate models have been suggested that explain the evolution of multiple mating with a decrease of intercolony variance in diploid drone production (Page 1980; Crozier & Page 1985), disease resistance (Sherman *et al.* 1988) and division of labour (Fuchs & Moritz 1999).

Based on these hypotheses, we derive a general model to argue that multiple mating can be regarded as a universal strategy to reduce the genetic sampling effect of mating, which may be selected for or against, depending on the average colony performance in the population. The increase of intracolony genetic variation by multiple mating may increase intracolony homeostasis (Oldroyd & Fewell 2007) but our analysis shows, in accordance with the earlier models (Page 1980; Crozier & Page 1985; Sherman *et al.* 1988; Fuchs & Moritz 1999), that it also leads to a reduction of intercolony fitness variance, regardless of the proximate mechanism. In contrast to former models, we emphasize that the actual mechanism may be of little relevance, and that the average success rate of colonies is critical to select for or against multiple mating.

2. MATERIAL AND METHODS

For a colony of social insects to survive and successfully reproduce, it needs to perform a series of tasks above a critical threshold value, θ . These tasks could be behavioural tasks in the classic sense, i.e. nectar and pollen foraging, brood care, nest construction or nest defence. For example, a certain number of workers may be needed to defend the nest against invaders. However, our argument extends to other colony functions, such as disease resistance or colony growth. For example, a critical colony size may be needed for successful overwintering. For simplicity, we consider the case of one task instead of a series of tasks and assume that the performance at or below θ leads to zero fitness (colony failure) and performance above θ leads to full ($=1$) fitness. This extreme case can be extended to other sigmoidal functions (Page 1980; Crozier & Page 1985; Sherman *et al.* 1988). Furthermore, we assume that there is a genetic basis for task performance, which seems justified by a genetic basis of division of labour among workers (Oldroyd & Fewell 2007), variable, gene-mediated disease resistance (Decanini *et al.* 2007) and the genetic determination of diploid drone production (Page 1980).

The average fitness for a certain colony type is then equivalent to its probability of performing the focal task above the threshold value, θ . This probability is given by the probability of having a critical number of workers that perform this task successfully (e.g. resisting disease, regulating temperature, growing because they are not diploid drones). Worker genotypes and hence task performance levels for any given task are binomially distributed in the population with an undetermined number of loci and alleles, which can be approximated by a normal distribution (Falconer & Mackay 1996). For any given colony, workers are drawn from this distribution according to their paternal and maternal genotypes. Thus, colony performance is also normally distributed. This is even true when considering traits that are determined by a single locus, such as diploid drone production, because truly continuous non-genetic variation adds to the actual task performance (i.e. successful larval development into an adult; Falconer & Mackay 1996).

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We further introduce Ψ , the average task performance of colonies in the population. The relationship of the average performance, Ψ , and the critical performance, Θ , determines whether the colonies on average fail ($\Theta > \Psi$) or succeed ($\Theta < \Psi$). Ψ is influenced by the adversity of the environment and the inherent biological risk/investment trade-off. For example, the colony foundation by an independent single female is inherently more risky but less costly than reproductive swarming. However, the average success of either strategy will also depend on environmental factors, such as climate, resources and habitat saturation (Rüppell & Heinze 1999).

3. RESULTS

For simplicity, the following argument is focused on the discussion of the additive genetic variance. A queen mates with n drones and produces a colony of k workers. The performance of the i th worker is the sum of the maternal (A_{mi}) and the paternal (A_{pi}) contributions. A_{mi} and A_{pi} are drawn from a normal distribution with a mean Ψ and variance σ_0^2 . The colony's performance, P_C , is then measured by the average performance of its workers. P_C is therefore given by

$$P_C = \frac{\sum_{i=1}^k (A_{mi} + A_{pi})}{k}. \quad (3.1)$$

Then

$$E(P_C) = E\left(\frac{1}{k} \sum_{i=1}^k (A_{mi} + A_{pi})\right) = \frac{1}{k} \sum_{i=1}^k E(A_{mi} + A_{pi}) = \Psi \quad (3.2)$$

and

$$\text{var}(P_C) = \text{var}\left(\frac{1}{k} \sum_{i=1}^k (A_{mi} + A_{pi})\right) \approx \frac{\sigma_0^2}{4} \left(1 + \frac{2}{n}\right). \quad (3.3)$$

Thus, the variance but not the mean of colony performance is a decreasing function of queen mating number (for a full derivation of equation (3.3), see the electronic supplementary material).

In our paradigm of selection (Haldane 1931), the probability of a colony failure depends on the variance of colony performance and thus the number of matings by the queen. However, the direction of this effect depends on the relationship between Ψ and Θ . When $\Theta < \Psi$, smaller variance leads to a lower probability of failure, while the opposite is true for $\Theta > \Psi$. Considering the first case, we calculate the probability of colony failure for the distribution $N(\Psi, \sigma^2)$ and show that it is larger than for $N(\Psi, \sigma'^2)$ when $\sigma > \sigma'$ (figure 1). Since the problem is symmetric, the opposite is true in the second case, and with $\Theta = \Psi$ the number of matings does not affect the probability of colony failure.

$P(\text{failure for } N(\Psi, \sigma^2))$

$$\begin{aligned} &= \frac{1}{2} \left[1 + \text{erf}\left(\frac{\Theta - \Psi}{\sigma\sqrt{2}}\right) \right] = \int_{-\infty}^{\Theta} \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(x-\Psi)^2}{2\sigma^2}\right) dx \\ &= \int_{-\infty}^{(\Theta - \Psi/\sigma')\sigma + \Psi} \frac{1}{\sigma'\sqrt{2\pi}} \exp\left(-\frac{(x-\Psi)^2}{2\sigma'^2}\right) dx \\ &> \int_{-\infty}^{\Theta} \frac{1}{\sigma'\sqrt{2\pi}} \exp\left(-\frac{(x-\Psi)^2}{2\sigma'^2}\right) dx \\ &= P(\text{failure for } N(\Psi, \sigma'^2)), \end{aligned} \quad (3.4)$$

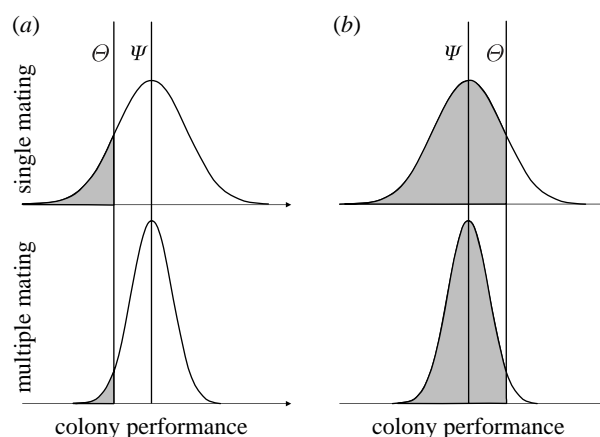


Figure 1. The average fitness return of female multiple mating depends on the relationship of the average colony performance (Ψ) to the critical performance (Θ) that ensures colony success. (a) $\Psi > \Theta$ selects for multiple mating and (b) $\Psi < \Theta$ selects for single mating, by minimizing the proportion of colonies falling below the critical performance level (shaded area).

where the inequality holds because

$$\frac{\Theta - \Psi}{\sigma'} \sigma + \Psi > \Theta,$$

whenever $\Theta < \Psi$, $\sigma < \sigma'$.

The colony fitness (= 1 - probability of colony failure) is a sigmoidal function of $\Psi - \Theta$ for all plausible mating numbers. The effect of $\Psi - \Theta$ is most pronounced with high mating numbers (= low variance), and the fitness effect of variance reduction is most pronounced at intermediate $|\Psi - \Theta|$. Furthermore, our model shows diminishing returns of mating number because the variance reduction, and thus the fitness impact, of each additional drone declines with n (figure 2).

4. DISCUSSION

Numerous hypotheses for multiple mating of social insect queens have been proposed and empirical data point to several benefits (Brown & Schmid-Hempel 2003; Oldroyd & Fewell 2007), while the widespread occurrence of single mating has been heuristically neglected because it is believed to be the ancestral condition in social insects. The presented model relies on few, biologically realistic assumptions and may provide a unifying explanation and extending previous variance-based models (Page 1980; Crozier & Page 1985, Sherman et al. 1988). The model operates in the context of division of labour, disease resistance, diploid drone production or any other colony performance-based mechanism. It emphasizes that the principle of variance reduction through multiple mating can have positive or negative fitness effects, depending on the average selective circumstances on colony performance.

Our genetically explicit model shows that multiple mating leads to reduced variance in colony performance, given that performance has a genetic basis that is bi-parentally inherited. This effect is the strongest for low numbers of matings and decreases

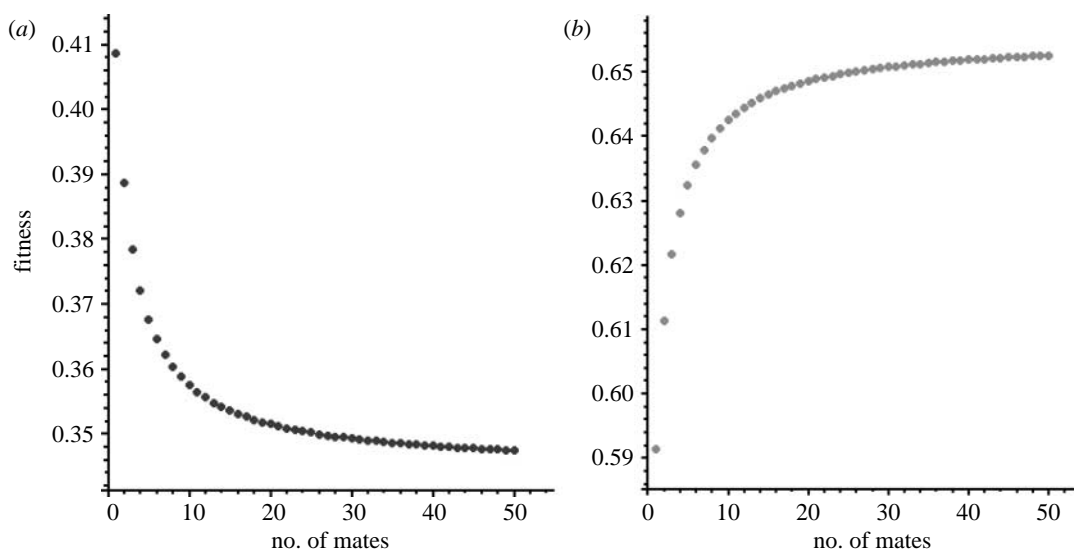


Figure 2. Average colony fitness as a function of the number of mates, with $\sigma^2 = 1/4$, and (a) $\Psi - \Theta = -0.1$ and (b) $\Psi - \Theta = 0.1$.

with higher mating numbers, similar to some earlier models (Page 1980; Sherman *et al.* 1988) but not others (Fuchs & Moritz 1999). The reduced variance, and thus multiple mating, can be selected for or against, dependent on the average colony success rate of the population. Generally, the model predicts that (i) multiple mating is more common under benign conditions and (ii) it is selected for by life-history strategies that minimize risk by maximizing investment in individual units of selection.

Population comparisons of the ant *Lasius niger* that show lower mating frequencies at higher latitude (Fjerdingstad *et al.* 2003) are in accordance with our first prediction, and more such population comparative data are urgently needed. The second prediction is in agreement with the general association of multiple mating with large colony size (Oldroyd & Fewell 2007), because large social insect colonies require more somatic investment and are generally less likely to fail than small ones (Kaspari & Vargo 1995). A detailed evaluation of the second prediction would compare mating numbers with risk/investment ratios in the colony tasks with the highest fitness impact. The empirical basis for this is lacking but it may be exemplified by considering colony foundation as one focal task that has a high fitness impact. Dependent colony foundation by swarming or budding is generally more costly but less risky than independent colony foundation (Rüppell & Heinze 1999). Hence our model could explain why the swarming honeybees (genus *Apis*) mate multiply in contrast to the independently founding bumble-bees (genus *Bombus*). Furthermore, the high mating frequency of army ants (Kronauer *et al.* 2004, 2007) and the intra- and interspecific associations between dependent colony founding and multiple mating in the ant genus *Myrmica* (Pedersen & Boomsma 1999) support this prediction. However, other multiple mating social insects, such as harvester ants (Wiernasz *et al.* 2004) and leaf-cutter ants, (Boomsma *et al.* 1999) found their colonies independently and some swarm-founding bees and wasps show low mating frequencies (Palmer *et al.* 2002; but see Kronauer & Boomsma (2007) for a

potential explanation). For a specific empirical evaluation of our model, it will be essential to determine the strength of natural selection and $\Psi - \Theta$ for various tasks and life-history stages in social insects.

In conclusion, our model shows that irrespective of the specific mechanism, the colony variance is reduced by multiple mating and that this reduction could be selected for or against, depending on whether the average colony performance is above or below (respectively) the critical performance that results in colony success. This conclusion is not significantly affected by the reality that colonies have to master a series of tasks and by possible deviations from normality of the performance distribution, as long as the latter is continuous. Our analysis is in agreement with the earlier analyses of specific mechanisms that have employed a similar reasoning (Page 1980; Crozier & Page 1985; Sherman *et al.* 1988) but combines, generalizes and extends these models. It emphasizes the importance of ecology and life history and that variance reduction may also select against multiple mating, possibly explaining the maintenance of single mating in many social insects (Strassmann 2001).

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