Review article

Evolution of multiple mating in the genus *Apis*

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(Invited paper)

Abstract – Multiple mating by social insect queens is a widespread phenomenon. Because of the apparent inclusive fitness benefits of monandry, and the potential costs of polyandry, explanations for the evolution of multiple mating have been frequently sought. Current leading explanations are collectively known as 'genetic variance' hypotheses which posit that both queen and colony fitness are increased by an increase in the intracolonial genetic diversity that accrues from multiple mating. However, the precise way in which genetic diversity acts to increase colony fitness is not clear. Furthermore, some of these hypotheses are probably insufficient to explain extreme levels of polyandry observed in the genus *Apis*.

Apis / genetic variance / polyandry / task specialization / parasite

1. INTRODUCTION

One of the more intriguing questions of evolutionary biology is a plausible adaptive explanation for the widespread incidence of multiple queens (polygyny) or multiple mating (polyandry) by queens in the eusocial Hymenoptera. The frequency of mating varies substantially among species. While many species are monandrous and monogynous (e.g., the majority of the stingless bees [39]), a few have evolved extremely high levels of polyandry or polygyny [55, 57, 81]. In particular, all species of the genus

Apis for which paternity frequency has been determined show high but extremely variable levels of polyandry [53].

Kin selection is especially appealing as a contributing factor to the evolution of eusociality in Hymenopteran species because the haplo-diploid reproductive system of this order generates extremely high levels of relatedness among the workers in colonies in which the queen is mated only once. Intuitively, multiple mating by social insect queens is unexpected because multiple mating reduces nestmate relatedness within a

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colony (Fig. 1a), and this presumably weakens the selective forces that maintain eusociality [22].

Concomitant with reduced intracolonial relatedness, additional copulations are speculated to be associated with increased risk to queens (Box 1). Thus explanations for the adaptive significance of multiple mating have been frequently sought [5, 11, 12, 31, 55].

This paper reviews explanations for the evolution of multiple mating in the genus *Apis*, re-examining the leading hypotheses for the adaptive significance of multiple mating, and then uses the techniques of comparative analysis to explore adaptive explanations for the unexpectedly high levels of polyandry found.

2. HYPOTHESES FOR THE EVOLUTION OF MULTIPLE MATING

In 1985 (and in the light of observations that polyandrous species tend to be more populous than monandrous ones), Crozier and Page [12] evaluated the plausibility of several hypotheses as explanations for the evolution of multiple mating in social insects (Box 2a). Since Crozier and Page's review, several additional hypotheses have been proposed (Box 2b).

Of the hypotheses thus far proposed, we regard only the 'genetic variance' (GV) hypotheses [31] as plausible explanations for the extreme levels of polyandry observed in *Apis*. These hypotheses propose that queen and colony fitness is increased by the increase in intracolonial genetic variance that results from multiple mating.

2.1. Classes of genetic variance hypotheses

Genetic variance hypotheses can be divided into two broad groups. The first set
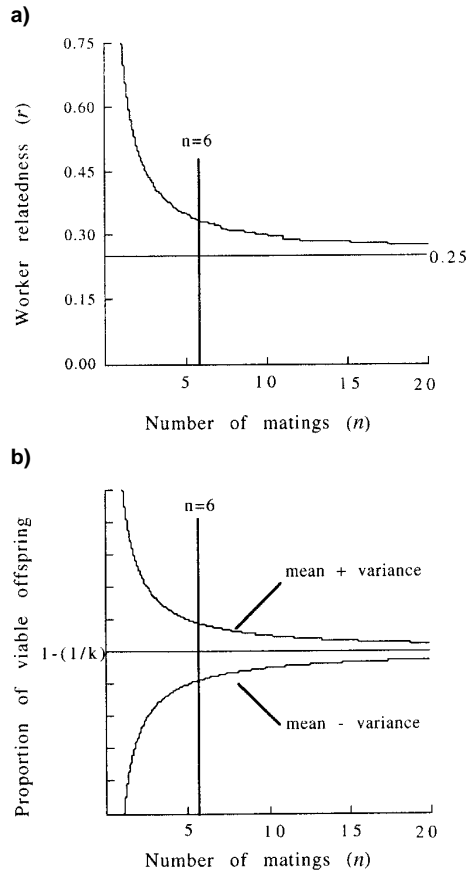

Figure 1. a: Average worker relatedness as a function of mating frequency. Worker relatedness decreases as a function of number of effective matings (where $r = (1/2n) + 0.25$ [44]) to an asyntope of 0.25. Over 90% of the change in relatedness arises from the first 6 matings. **b:** The relationship between variance in brood viability and mating frequency. The proportion of viable offspring varies as a function of number of matings (n) and sex alleles (k). The expected proportion of viable offspring remains constant $(1-1/k)$. However, the variance reduces in proportion to $1/2n$. Once again, over 90% of the reduction in variance accrues from the first six matings.

arises from the Hymenopteran haplo-diploid reproductive system and relates to the effects of sex determination on brood viability [54, 57, 65], and to conflict between workers

and queens over optimal sex ratios [5, 42]. The second group relates to the postulated fitness benefits stemming from genetic diversity within the worker population.

2.1.1. The hypotheses relating to sex determination and sex ratios

1. Multiple mating has evolved because it reduces variance in the production of diploid males among colonies (Box 2, hypothesis 8 [13, 54, 65, 82, 91]).

In honeybees, sex is determined by a series of balanced lethal alleles at the sex locus. Individuals heterozygous at this locus are diploid females, hemizygous individuals are haploid males and homozygous individuals are diploid males which are functionally lethal [93]. Thus if a queen mates with a single drone carrying a sex allele identical to one of her own, 50% of her diploid eggs will be inviable. The occurrence of these inviable eggs at high frequency within a colony slows its growth and increases its probability of failure [95]. By mating with a large number of drones, a queen can reduce the probability that a large proportion of her progeny will be inviable diploid drones. Page's model [54] showed that alleles that cause multiple mating will spread as a consequence of the genetic load imposed by the sex locus. Ratnieks [65] extended this model, noting that the timing of removal of diploid males is the critical factor in determining whether multiple mating is selectively advantageous. This hypotheses is perhaps the leading explanation for the evolution of multiple mating in social insects, lacking only explanatory power for extremely high numbers of matings such as those exhibited by *Apis* queens. It seems a particularly compelling argument for the initial switch from monandry to polyandry (assuming monandry is the ancestral state).

2. Multiple mating reduces conflict between queens and workers over a preferred ratio of investment in the sexuals (Box 2, hypothesis 5 [40, 64, 66]).

The number of matings alters the adaptive ratio of investment in reproductives by workers. In a monandrous Hymenopteran colony, workers should 'prefer', in an evolutionary sense, to invest more in the production of queens than drones (because they are three times more related to female offspring than to male offspring), whereas queens are equally related to both male and female offspring therefore 'preferring' equal investment in each sex [40, 88]. Multiple mating can reduce worker-queen conflict over sex investment, equalizing the investment ratio of both workers and queens close to 1:1 as average colony relatedness decreases. The weakness of this argument is that it seems very unlikely that workers can accurately detect the number of times their queen has mated and make appropriate adjustments to the production of males [51, 64]. Therefore it seems unlikely that the effects of multiple mating on worker queen conflict provides a strong enough selective force for the evolution of extreme multiple mating.

The second set of hypotheses suggests that genetic diversity within the worker population leads to greater colony fitness because combinations of worker genotypes are fitter than colonies comprised of just one genotype.

2.1.2. The subset of hypotheses relating to worker diversity

1. Genetic variance allows an increased expression of caste [12] or task polymorphism (Box 2, 2(b) [7, 8, 10, 14, 17, 19, 21, 45–49, 58, 60] .

Behavioral polymorphisms among subfamilies have been found for a wide variety of critical tasks [14, 17, 19, 34, 41, 45, 46, 48, 49, 62, 70, 71, 74, 75]. It has been often argued that this variation is adaptive and that task specialization allows individual bees to focus on particular tasks and become expert in them [8, 47, 75]. Recent work suggests that the basis of these polyethisms is variance in the level of a

stimulus required to elicit a behavior, and that this variance is genetically determined [73, 74]. Thus task specialization could be a selective force in the evolution of multiple mating by honeybee queens. However, direct empirical evidence is lacking.

2. Genetic variance increases the range of environments a colony can tolerate (Box 2, hypothesis 2(c) [10, 12, 46–48, 50, 51, 72]).

Polyandry may help buffer colonies against environmental variance [9, 12, 61] by producing a genetically diverse worker population which is more able to survive environmental extremes and reach a phenotypic norm even under varied conditions. Kolmes et al. [34] presented data suggesting genotypic variation is important when colonies are stressed. Page and Mitchell [59] and Robinson and Page [72] presented models demonstrating how genotypic variability for response thresholds may lead to a 'self-organized' allocation of workers to specific tasks under changing environmental conditions, postulating that this is an efficient mechanism by which optimal task allocation can be achieved by independently acting bees.

3. Increased genetic variance mitigates against the effects of parasitism by increasing intracolonial resistance (Box 2, hypothesis 9 [27, 78–81, 83–85]).

A monandrous social insect colony has a large number of genetically similar individuals living in close proximity. Thus a particularly virulent parasite or pathogen, adapted to like genotypes within a colony, should rapidly spread and thus have the potential to cause colony failure [78]. Multiple mating produces a more diverse range of genotypes, possibly reducing the rate of transmission of disease within a colony. This hypothesis is analogous to the 'red queen' hypothesis for the maintenance of sex, which proposes that rare host genotypes generated by sexual recombination will be more resistant to frequent pathogenic genotypes [15, 38].

In support of the 'red queen' hypothesis, it has been shown that in the facultatively sexual snail *Potamopyrgus antipodarum,* the frequency of sexual reproduction increases with parasite load [37]. Similarly, in social insects, those species with a greater exposure to parasites and pathogens are predicted to mate more often than other species, generating diverse worker genotypes which are less likely to catastrophically succumb to infection [78, 83]. Indeed, comparative studies show that species with low worker relatedness generally have lower parasite levels than species with higher worker relatedness [81].

Several studies have demonstrated an advantage of genotypic variability on reduced intracolonial parasite transmission [84, 85] and parasite load on colony performance in bumblebee colonies kept under natural conditions [4, 36]. However, there is no evidence supporting the notion that genotypic variability reduces parasite virulence in honeybees [61, 92]. Indeed, contrary to the predictions of this hypothesis, Harbo [28] found increased viability of the parasite *Varroa jacobsoni* in genetically diverse colonies relative to genetically uniform colonies. Furthermore, evidence of genetic diversity reducing parasitic load in *Bombus terrestris,* a species that is typically monandrous [16], may imply that parasite reduction via multiple mating is not sufficient to drive the evolution of polyandry. Thus while this hypothesis seems plausible, it remains controversial [35, 83] and requires evidence from naturally polyandrous species.

4. Multiple mating increases the frequency of favorable heterotic allelic interactions within individual workers (Box 2, hypothesis 11 [68]).

Rinderer et al. [68] have suggested that multiple mating may be selected in queens via fitness gains accrued by heterotic interactions in individual workers for those loci which are genetically variable and show non-additive gene action. Although intuitively plausible [6], this notion has not been

modelled and its significance, if any, is not understood.

Multiple mating arises from the need for low frequencies of task specialists.

Fuchs and Moritz [20] have recently extended hypothesis 2b of Crozier and Page [12], demonstrating an alternative way in which high mating frequency may facilitate a more efficient division of labor. They propose a frequency-dependent selection model under which multiple mating is favored by increasing expression of task polymorphism. The critical assumption of the model is that colony fitness is enhanced by low proportions of specialists relative to their absence, but is lowered by high frequencies of specialists. Thus, this model may be looked at as a kind of genetic variance hypothesis since increasing the diversity of a colony increases the probability that a specialist trait will be rare, and therefore valuable to the colony.

In the context of honeybees, this model may be applicable to specialist traits such as the possession of resistance alleles or ability of workers to re-queen their colony when queenless [20]. The model has the advantage over other genetic variance hypotheses of having no upper limit to benefit obtained by additional matings. Therefore the frequency of matings is only limited by the cost of additional matings. However, it has limited explanatory power to explain the transition from monandry to mating with few males and is not easily testable [20]. Moreover, the means by which diversity for task thresholds is maintained in populations is not well understood.

3. EXPERIMENTAL SUPPORT OF GENETIC VARIANCE HYPOTHESES

Genetic variance hypotheses have empirical support from experiments comparing the performance of honeybee colonies with low and high genetic diversity. Traits asso-ciated with colony fitness such as brood area [21, 47] and honey production [20, 43] have been shown to be significantly greater in honeybee colonies with high rather than low genetic diversity, and tasks associated with colony establishment seem to be more buffered in colonies with high genetic diversity than in colonies with low genetic diversity [61]. Furthermore, non-additive effects of the number of subfamilies within colonies on colony performance have been shown [24, 25, 28, 47], possibly demonstrating a mechanism by which alleles favoring multiple mating can spread.

4. LIMITATIONS OF SOME GENETIC VARIANCE HYPOTHESES IN EXPLAINING EXTREME LEVELS OF MULTIPLE MATING

A number of the genetic variance hypotheses seem insufficient to explain the evolution of extreme polyandry as in *Apis*. This is because fitness benefits decline with each addition mating.

For example, reduction of intracolonial relatedness is a key aspect in reducing worker-queen conflict over sex investment ratios. However, while intracolonial genetic relatedness is substantially decreased by the first few matings, the rate of decrease becomes marginal with higher numbers (Fig. 1a) [20].

Similarly, a limitation of the sex allele hypotheses arises at high mating frequencies because when sex alleles are at equal frequency (as they are expected to be [94]); additional matings beyond 6–10 do not sub-stantially change the expected frequency of diploid males within colonies relative to the first few matings.

It can be shown [56, 57] that if k is the number of sex alleles in the population and n is the number of drones a queen mates with (assuming all males contribute equally to paternity, there is random mixing of the

sperm in the spermatheca of queens and sex alleles are at equal frequencies in the population), the expected proportion of viable brood is given by:

$$1 - 1/k \qquad (1)$$

a constant that depends only on the number of alleles in the population [56]. Thus additional matings do not increase mean brood viability.

The variance in brood viability is given by [56]:

$$1/2n(1/k)(1-2/k) \qquad (2)$$

which decreases with increasing n, as illustrated in Figure 1b. Although the variance continues to decrease as the number of matings increases, it is apparent from Figure 1b that the greatest decrease in variance occurs as the number of matings increases from 1 to 10. It is questionable whether the slight decrease in variance after this point would be reflected in a further increase in average fitness.

Similarly, other hypotheses that rest on the principle of reducing variance (Box 3, hypotheses 9 and 10), encounter similar constraints at high mating frequencies.

5. COMPARATIVE ANALYSIS

An alternative approach to understanding the evolution of extreme multiple mating is that of comparative analysis. If mating frequency is well correlated with a particular life history trait across a variety of species, the evolutionary antecedents of multiple mating may be suggested [50–53, 68]. The genus *Apis* is ideal for this kind of analysis because the species have very different ecological ranges and life history patterns [77]. Over the past few years, Oldroyd and colleagues have made a concerted effort to determine the mating frequency in queens of all *Apis* species, with the goal of explaining the evolution of polyandry using the comparative method [29]. These studies have demonstrated that all *Apis* species so far examined mate more than six to ten times, and all but *A. florea* have an effective paternity of greater than six, exhibiting extreme multiple mating (Tab. I).

Oldroyd et al. [53], following Koeniger and Koeniger [33], used comparative analysis to infer the evolution of traits associated with mating behavior in *Apis*. Mating behavior is probably subject to divergent sexual selection based on the a priori notion that colony level selection is strongly in the direction of polyandry [33, 53]. In the cavity-nesting species (*A. mellifera, A. cerana, A. koschevnikovi* and presumably *A. nigrocincta* and *A.nuluensis*), drones are selected to produce large numbers of spermatozoa to increase their share of potential offspring, whereas queens are selected to mate many times and expel excess semen [53]. In the

Table I. Levels of polyandry and intracolonial genetic relationships in the genus *Apis* as determined by microsatellite analysis (modified from Tab. I in [53]).

Species	Paternity frequency, observed mean ($\pm$ SE)	Effective paternity frequency	Coefficient of relatedness	Author
A. mellifera	13.8 ± 2.5	12.4 ± 2.2	0.30 ± 0.009	Estoup et al. [16]
A. florea	8.0 ± 1.6	5.6 ± 1.0	0.35 ± 0.02	Oldroyd et al. [50]
A. dorsata	26.7 ± 6.6	20.0 ± 6.6	0.29 ± 0.007	Oldroyd et al. [51]
A. dorsata	18.0 ± 1.6	25.6 ± 1.05	0.27 ± 0.02	Moritz et al. [42]
A. andreniformis	13.5 ± 2.3	9.1 ± 0.83	0.30 ± 0.007	Oldroyd et al. [52]
A. cerana	18.0 ± 3.03	12.0 ± 1.6	0.29 ± 0.005	Oldroyd et al. [53]
A. koschevnikovi	16.3 ± 10.5	10.5 ± 8.4	0.31 ± 0.03	Rinderer et al. [68]

open-nesting species (*A. florea, A. andreni-formis, A. dorsata*), direct insertion of the penile bulb into the spermatheca appears to be an adaptation of males to increase paternity frequency while not requiring massive sperm production [53]. Figure 2 (adapted from [53] to include *A. koschevnikovi*) reveals that polyandry, excess semen production and excretion of excess semen are all pleisomorphic characters for the genus, whereas the enlarged penile bulb and clasping organs of the open-nesting species are derived.

The mating frequency of *A. dorsata* queens appears to be qualitatively different from other *Apis* species. Therefore it has been presumed that a satisfactory explanation of this difference may provide the key as to why queens of this genus mate so many times [42, 51]. Body size, colony size, migration, pathogen load and tendency to aggregate are all traits which might provide clues as to why *A. dorsata* mate so many more times than other *Apis* species. For example, it has been suggested that drone density at congregation areas or ecological conditions such as climate and landscape may be correlated with mating frequency [26]. However, because many life history traits covary it may be difficult if not impossible to determine which traits have the most effect on mating frequency. Furthermore, these traits vary within as well as among species. This complicates the possibility of making meaningful associations between mating frequency and life history traits across the genus. Therefore, if comparative analysis is to be of any value in finding explanations for mating frequency, experimental approaches may be necessary to tease apart the effects of the covarying traits.

6. CONCLUSION

Despite many years of theoretical and empirical research, a decisive explanation for the evolution of extreme polyandry in *Apis* remains elusive. This is probably because no single factor is the sole selective force in the evolution of polyandry. While the sex allele hypothesis appears particularly compelling as the initial causative factor for the switch from monandry to polyandry, this explanation does not seem sufficient to explain extreme polyandry. We therefore suspect that a variety of forces select for high genetic diversity, and that
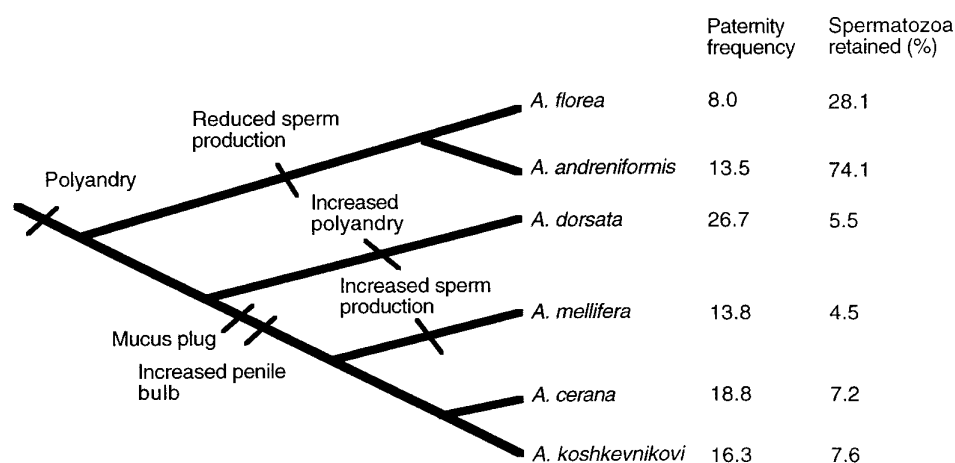

Figure 2. Cladogram of the genus *Apis* [3] with reconstructions of reproductive behavioral traits. The average paternity frequency and the proportion of injected spermatozoa retained are superimposed.
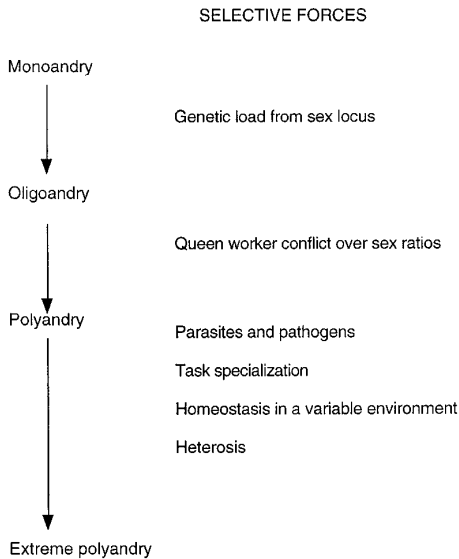
SELECTIVE FORCES

Monoandry

Genetic load from sex locus

Oligoandry

Queen worker conflict over sex ratios

Polyandry

Parasites and pathogens

Task specialization

Homeostasis in a variable environment

Heterosis

Extreme polyandry

Figure 3. A plausible evolutionary scenario for the evolution of extreme polyandry in the genus *Apis*.

these together maintain the high frequency of matings observed in *Apis* queens. Thus the effects of high rates of polyandry should not be attributed to any single GV hypothesis alone. A possible scenario for the evolution of polyandry in honeybees is given in Figure 3.

7. FUTURE RESEARCH

In order to determine the significance of extreme mating frequencies (beyond 6–10) the gain of fitness with each additional mating must be evaluated against the cost of mating. These costs have not been well quantified, and yet good estimates are critical to our understanding of the evolution of polyandry.

Comparative analysis has enabled the mapping of mating characteristics onto the phylogeny in *Apis*. However, for two reasons this has not yet led to useful insight into the evolution of high mating frequencies within the genus. First, although molecular techniques such as microsatellite analysis permit very accurate estimates of mating frequencies [5], most studies have involved only a few colonies from a particular area, and extrapolating these results may be ill advised. Furthermore, the low numbers of individuals analyzed, particularly in early studies, probably led to gross underestimates of mating frequencies. Secondly, because so many life-history and environmental traits covary, meaningful comparisons between species are difficult. As the body of estimates on mating frequency within the genus increases, so will the possibility of comparative analysis aiding the explanations for the levels of polyandry within the genus. However, experimental manipulation may also be necessary in order to determine the effect of only one variable on mating frequency at a time.

Box 1. Costs associated with mating behavior for A. mellifera queens

Virgin *A. mellifera* queens initiate mating behavior when they are about one week old by briefly leaving the colony and orienting to local landmarks [77]. After such orientation flights, queens fly to a drone congregation area (DCA), where they mate on the wing [33] with many drones. DCAs are rich in palatable stingless insects [67, 76, 89] and therefore mating at such leks presents a significant time-dependent predation risk to the queen. Mating risks include time and energy devoted to locating the DCA, copulation, risk of predation, exposure to disease and inclement weather [30, 32, 40, 52, 83, 87]. All of these risks are probably substantially increased with each additional mating flight.

In apiculture, a 20% loss of queens during mating flights is not uncommon and losses from wild colonies are also not expected to be uncommon [77]. Other *Apis* species can also be expected to encounter similar queen losses associated with mating behavior.

Box 2. The main arguments

The following arguments are as listed in Crozier and Page [12], with certain modifications:

1. Multiple mating increases effective population size and therefore is selected for, because it increases population longevity [11].

2. Multiple mating is favored because it increases the genetic variation within broods. This may be beneficial because: a) it increases genetic variation between founding queens and between workers; b) it forms a basis for caste differentiation; c) a mixture of genotypes is 'useful' in a variable environment.

3. Females mate a number of times because: a) of selection favoring sperm-competition within their spermathecae; b) competition between worker sib-groups favors a more rapid colony division rate, favoring multiple mating which intensifies such competition [23].

4. Multiple mating is favored by queens because it increases their genetic output relative to that of their worker progeny [40].

5. Multiple mating by queens is favored because it selects for worker adjustment of the sex ratio to be closer to that selected for at the queen level [40, 63, 66, 69, 86].

6. Multiple mating is easier for queens than resisting the mating attempts of males [1, 2].

7. Multiple mating by queens is favored because it enables queens to store sufficient sperm to build up large and long-lived colonies [11, 18, 88, 90].

8. Multiple mating by queens is selected under certain conditions of colony growth because, when accompanied by a sex determination system based on heterozygosity, it leads to higher colony reproductive success than single mating [54, 57, 65].

The following arguments have been put forward since Crozier and Page [12]:

9. Multiple mating is selected because it mitigates against the effects of parasitism [27, 78, 83–85].

10. Multiple mating is selected for because it increases the probability that an important specialist trait in a population is rare [20].

11. Polyandry increases the chance that the proportions of the paternity array will produce workers having increased fitness through heterosis [68].

ACKNOWLEDGMENTS

Résumé – Évolution de l'accouplement multiple chez le genre *Apis*. L'accouplement multiple chez les reines d'insectes sociaux est un phénomène largement répandu. À cause des bénéfices apparents de l'adéquation adaptative globale (« inclusive fitness ») dus à la monoandrie et aux coûts potentiels de la polyandrie, on a souvent recherché des explications à l'évolution de l'accouplement multiple. Les explications qui prévalent actuellement sont connues généralement comme hypothèses de « variance génétique ». Elles posent en principe l'hypothèse que la valeur adaptative de la reine et celle de la colonie sont accrues par un accroissement de la diversité génétique intracolonie qui dérive de l'accouplement multiple. On peut répartir ces hypothèses en deux grands groupes : 1) celles relatives aux effets du déterminisme du sexe sur la viabilité du couvain (hypothèses de l'allèle sexuel) et celles relatives au conflit entre ouvrières et reine concernant la répartition optimale des ressources allouées à chaque sexe ; et 2) celles relatives aux bénéfices postulés de la valeur adaptative provenant d'une diversité génétique accrue au sein de la population d'ouvrières. Tandis que

nombre de ces hypothèses semble correcte pour expliquer les faibles niveaux d'accouplement multiple, il est plus difficile d'expliquer le grand nombre d'accouplements chez les reines d'*Apis*. Les effets de l'accouplement multiple sur les variables telles que la parenté des ouvrières et la proportion de mâles diploïdes au sein d'une colonie sont grandement modifiés par les quelques premiers accouplements. Par contre, aux fréquences d'accouplement plus élevées, le bénéfice apporté par chaque accouplement supplémentaire décroît selon une asymptote. Les explications les plus courantes concernant l'évolution de la polyandrie extrême incluent le gain de valeur adaptative par la spécialisation des tâches et la résistance aux parasites et aux agents pathogènes. Nous émettons l'hypothèse que la voie évolutive de la monoandrie à la polyandrie extrême s'est faite en plusieurs étapes. Initialement le coût génétique imposé par le locus sexuel provoquait un passage de la monoandrie à l'oligoandrie. Le conflit reine/ouvrières concernant les sex ratio a renforcé les pressions de sélection vers l'évolution de la polyandrie. Finalement, les pressions des agents pathogènes et des parasites, et le besoins d'une population d'ouvrières aux comportement variés ont pu être la cause première du développement de la polyandrie extrême chez le genre *Apis*.

Apis / variance génétique / polyandrie / spécialisation des tâches / parasite

Zusammenfassung – Evolution der Mehrfachpaarung in der Gattung *Apis*. Die Mehrfachpaarung von Königinnen der sozialen Insekten ist ein weit verbreitetes Phänomen. Wegen der offensichtlichen inklusiven Fitness der Einfachpaarung und der möglichen Kosten der Mehrfachpaarung wurde bereits häufig nach Erklärungen für die Evolution der Mehrfachpaarung gesucht. Die zur Zeit vorherrschenden Erklärungen sind allgemein als "genetische Varianz" Hypothesen bekannt. Diese postulieren, dass sowohl die Königinnen – als auch die Volksfitness durch eine Zunahme der genetischen Varianz durch Mehrfachpaarungen innerhalb des Volkes erhöht wird. Die Hypothesen können in zwei groβe Gruppen unterteilt werden: solche, die mit der Geschlechtsbestimmung auf die Lebensfähigkeit der Brut (Sexallel Hypothesen) bzw. mit dem Konflikt zwischen Arbeiterinnen und Königinnen über die optimale Geschlechtsverteilung zusammenhängen und solche, die mit einem postulierten Vorteil der Fitness zusammenhängen, der durch die genetische Vielfalt in der Arbeiterinnennenpopulation entsteht.

Viele dieser Hypothesen scheinen durchaus geeignet, eine niedriges Niveau an Mehrfachpaarung zu erklären. Dagegen ist die Ableitung von Vorteilen durch die extrem hohe Zahl von Paarungen der *Apis* Königinnen schwieriger. Die Effekte der Mehrfachpaarung auf Variable wie Verwandtschaft der Arbeiterinnen und das Verhältnis von diploiden Drohnen innerhalb eines Volkes verändern sich bei den ersten Paarungen sehr deutlich. Dagegen ist der Gewinn bei höherer Paarungsfrequenz, der durch zusätzliche Paarungen erreicht wird, asymptotisch kleiner. Die höchste Akzeptanz haben Erklärungen der extremen Polyandrie erhalten, die den Fitnessgewinn durch Spezialisierung in der Arbeitsteilung und Resistenz gegen Parasiten und Krankheitserreger (Pathogene) einschlieβen.

Wir nehmen an, dass sich der Weg der Evolution von der Einfachpaarung zu extrem vielen Paarungen über verschiedene Stufen entwickelte. Ursprünglich war der genetische Nachteil, der durch den Sex Locus verursacht wurde, ein Schalter für eine Entwicklung von der Paarung mit einem Drohn (Monandrie) zu einigen Zusatzpaarungen (Oligoandrie). Der Königinnen / Arbeiterinnen Konflikt über die Geschlechtsverteilung erhöht den Selektionsdruck in Richtung der Mehrfachpaarung (Polyandrie). Schlieβlich könnte der Druck durch Pathogene und Parasiten und die Notwendigkeit einer im Verhalten unterschiedlichen

Arbeiterinnenpopulation der ausschlagge-
bende Grund für die Entwicklung der extrem
hohen Polyandrie bei *Apis* gewesen sein.

Apis / **genetische Varianz / Polyandrie /
Arbeitsspezialisierung / Parasit**

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