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Multiple Mating and the Evolution of Social Behavior in the Hymenoptera

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Summary. The data on the frequency of mating by queens of eusocial Hymenoptera are reviewed.

It is pointed out that the issue of sperm clumping is probably irrelevant to the evolution of eusociality.

The hypothesis is presented that multiple mating is an adaptation for maintaining large colonies. In ants there is a significant relation between the size of the colony and the frequency of mating.

The effect of multiple mating on the spread of a gene for worker behavior is explored. If a female mates twice, the effective number of matings is less than two except in the case of identical sperm contribution by the males.

Sperm bias is defined as the contribution of unequal amounts of sperm by the males that mate with a queen. Sperm bias can be produced as a sampling phenomenon, by inter-male competition for females and by sperm competition.

The relation between the ergonomic efficiency of the workers at the production of reproductives and the number of matings that is consistent with the evolution of eusociality is derived. If workers are only about 10% more efficient at producing reproductives within a eusocial colony than they are solitarily, then two matings by the queen will still produce a selective advantage to eusocial behavior.

Introduction

It is generally assumed that if queens of social Hymenoptera mate more than once with unrelated males, then the genetic predisposition toward eusociality that is caused by haplodiploidy disappears (Charnov 1978a; Hamilton 1964, 1972; Lin and Michener 1972; Trivers and Hare 1976; West-Eberhard 1975). The evidence that most eusocial Hymenoptera are multiply inseminated has been interpreted as "not favorable to Hamilton's thesis", (Wilson 1971). In this paper, I shall first review current evidence on the number of matings by the social Hymenoptera. Second I shall suggest a reason for the evolution of multiple mating and finally I shall explore the consequences of multiple mating for the evolution of sterile castes.

The apparent widespread occurrence of multiple inseminations has been dealt with by proponents of the genetical theory of eusociality in two ways. The first is an evolutionary argument. The ancestors of eusocial species (for example the tiphiid wasps as ancestors of ants) may have been singly fertilized. Subsequent development of caste systems and division of labor has locked species into the eusocial lifestyle with multiple mating as a secondary phenomenon. Two important points may be raised here. The first is that the number of matings of solitary relatives of eusocial species need bear no relation to the number of matings of the solitary ancestors themselves. Even if contemporary tiphiid wasps are inseminated a single time, this may not be related to the number of times that the ancestors of tiphiid wasps mated approximately 100 million years ago (Carpenter and Hermann 1979). The second and more compelling argument is that the number of matings of non-social species has been used in two mutually exclusive ways. Some present-day wasps that have affinities to ants mate only a single time (e.g. Brothers 1972). This observation has been used (e.g. Hamilton 1972) to suggest that the forerunners of the ants were singly inseminated and could therefore develop into the eusocial ants.

A totally inverted and equally plausible argument has been made with respect to the solitary bees. Most solitary bees mate multiply (Kerr 1969). Kerr (1969) has made the suggestion that these solitary bees have not developed eusociality due to their habit of multiple mating. Because the number of matings of solitary species can be adapted to support the genetical theory of eusociality, no matter how many times they are mated, this is an exceedingly weak argument.

The second class of arguments designed to rescue the benefits of haplodiploidy from the difficulties of multiple insemination has been to suggest that multiple inseminations occur in such a way as to give a high degree of relatedness between successive sperm. This can be accomplished in two ways, by inbreeding or by sperm clumping. A high degree of relatedness between males may be attained by queens that mate with brothers from their own nest. However, as none of the known multiply mating social Hymenoptera mate with brothers within the nest (see below), and because most of them mate in large swarms, it is very improbable that the virgin queen will encounter a subset of males to whom she is highly related. Electrophoretic studies of multiply mated social Hymenoptera (Metcalf and Whitt 1977; Craig and Crozier 1979; Pamilo et al. 1978; Pamilo and Varvio-Aho 1979; Crozier 1977) have revealed no deviation of allele frequencies from Hardy-Weinberg equilibrium, a fact consistent with the hypothesis of random mating.

Sperm clumping is the tendency for the sperm of a male to be used as a unit. Sperm clumping has been postulated as a mechanism that increases the degree of relatedness among workers within a Hymenopteran insect colony (Alexander and Sherman 1977).

Taber (1955) claimed that the sperm of multiply inseminated honeybee queens exhibited sperm clumping. Page and Metcalf (1982) have shown that Taber's conclusions do not follow from his data. They present evidence that sperm of at least three males are used at any given time.

The issue of sperm clumping is, by itself, probably irrelevant to the evolution of eusocial behavior in the Hymenoptera. Sperm clumping can only be a mechanism that increases relatedness between workers and reproductives if the colony is iteroparous. If there is a single period of reproduction, as in annual species and in most primitively eusocial species, then it is not possible to devise a sperm clumping regime that increases the relatedness of workers to reproductives. In fact, sperm clumping in a multiply-mated, semelparous species creates problems for the evolution of eusocial behavior, it does not solve them.

Rather than attempt to explain away the effects of multiple mating, I propose to first examine the evidence for multiple mating in the social Hymenoptera, discuss the evolution of multiple mating and finally discuss the evolution of eusociality with multiple mating.

Effects of Multiple Mating

The data on the frequency of mating in the social Hymenoptera as well as in some non-eusocial aculeate Hymenoptera are shown together with certain characteristics of the species' life histories in Table 1. Page and Metcalf (1982) discuss differences in the quality of evidence for multiple mating by observation, dissection and by electrophoretic methods.

There is one glaring bias evident in all the scattered reports on the subject of mating in the social Hymenoptera. The vast majority of reports concern species with populous colonies. This is particularly true in the ants. Such species produce conspicuous swarms of males and females. This biases the reports toward multiple mating. In a larger mating swarm there is greater potential for a female to mate more than once; there are more males present. Seriously lacking is information about the mating habits of species that typically have small colonies. Many ponerine and myrmeciine ant species fall into this category and are additionally important in being primitive species. Except for *Rhytidoponera chalybea* and *R. confusa* (Ward 1978), that each mate once, data are lacking for these two subfamilies of ants.

There are a number of other advanced genera of ants, e.g. *Leptothorax, Stenamma, Strumigenys,* which are widespread and frequently common, but rarely have more than several hundred workers in the colony, do not have conspicuous mating flights and about which nothing is known concerning the number of times they mate.

It must further be pointed out that multiple mating is easier to confirm than single mating. A single observation of multiple mating is more decisive than one observation of single mating. One observation of multiple mating tends to negate several observations of single mating. Thus what tends to be recorded is a consistent prediliction for single mating or a capability for multiple mating.

Multiple mating appears to be somewhat more frequent among ants (22 of 32 species – 69%) than among the social bees and wasps (7 or 8 of 17 species – 41–47%). This may be a real phenomenon, but is more likely due to the fact that those ant species studied form more populous colonies than the bees and wasps. I doubt that this generality will be sustained when studies of ants are extended to less populous colonies and studies of bees and wasps are extended to more populous colonies.

In the bees and waps there is not an obvious relationship between colony size and the frequency of mating. The species with the largest colonies (honeybees) are the preeminent multiple maters. *Lasioglossum marginatum*, while it does not form colonies of enormous absolute size, does form the largest colonies of any halictine bee and is multiply mating.

In hornets there seems to be a considerable variation in the frequency of mating from species to species with no relation to colony size. Since there is variability within the genus *Vespula* in the number of matings this genus would seem ideally suited for further study. The flexibility in the number of matings by a queen of *V. germanica* would seem to indicate that there is the possibility for experimental manipulation. It is interesting to note that the workerless social parasite *Dolichovespula arctica* mates multiply while its congener, *D. saxonica*, with a normal social system, mates a single time.

Only those non-eusocial aculeate Hymenoptera which are not treated by Page and Metcalf (1982) are shown in Table 1. In the non-eusocial species for which data are given Table 1 and by Page and Metcalf, little can be said outside of the fact that there seems to be no justification for assuming that solitary ancestors of social species mated only a single time.

Among the species of ants for which data are available, all are iteroparous. Among the bees and wasps there are both semelparous and iteroparous species. There is no relation between multiple mating and iteroparity. The important point is that for those multiple mating, semelparous species, *Vespula atripilosa, V. vulgaris, Polistes metricus, P. variatus, Bombus huntii, B. hypnorum, Lasioglossum marginatum* and possibly *Dialictus zephyrus* and *Vespula germanica*, sperm clumping cannot be posited as a mechanism to increase relatedness within a colony.

Why Mate More Than Once?

Having described the frequency of multiple mating in the social Hymenoptera, it is worthwhile to ask under what conditions a genetic prediliction for multiple mating will be favored.

In a eusocial species, the workers of which produce Y reproductives each, a gene arises that causes females to mate more than once. The workers in such colonies each produce RY reproductives. Not surprisingly the gene for multiple mating will spread if $R > 1$ (see Appendix A). This result is independent of who controls investment, or the sex ratio of the reproductives.

The advantage of multiple mating may rest on increased productivity of larger colonies. In some species, the longevity of the colony is apparently limited by the amount of sperm stored by the queen (e.g. Brian 1957). Very old colonies may produce nothing but males, indicating that sperm supply has been exhausted. If, by mating more than once, a queen is able to maintain a larger colony size, the gene for multiple mating may spread.

In such species there should be selection on males to produce larger packets of sperm. However, there are tradeoffs in a colony between the number and size of males that can be produced (Davidson 1982). There may also be physical constraints on the size of males that fly efficiently. It is unclear how these conflicts will be resolved, but it is clear that they must be.

In order for an increase in colony size to be reflected in an increased output of reproductives ($R > 1$), the colony must be in a region of increasing returns to scale (Oster and Wilson 1978). Increasing colony size causes a disproportionately large increase in colony productivity.

One would predict that multiple mating should predominate in species that maintain large colonies. A species that typically forms small colonies may do so for a number of reasons. There may be limitations of nest architecture; for example those species that nest in small preformed cavities, such as acorns or hollow grass stems. There may be limitations of food availability; for example specialized predators, such as *Strumigenys* ants whose diets consists largerly of entomobryid collembolans. Such species may reach a region of decreasing returns to scale at small colony size and there would be little use in multiple mating.

Species that do not have these severe limitations on colony size may reach a region of decreasing returns to scale at much larger colony sizes. They can profit by mating more than once if it ensures the ability to establish and maintain a large colony.

It is possible to test for a relation between large colony size and multiple mating in ants because of the large range of colony sizes. Those species that characteristically have of the order of 10^2 workers tend to mate a single time while those that have of the order of 10^4 or more workers

Table 1. Summary of mating habits of eusocial Hymenoptera. The number of matings, reproductive strategy (semelparous or iteroparous) and colony size, when known, are included. Several noneusocial Hymenoptera that are not treated by Page and Metcalf (1982) are also included

Species	Number of matings	Semel or iteroparous	Remarks
Non-Eusocial			
Mutillidae			
Pseudomethoca frigida	1	–	Brothers (1972)
Andrenidae			
Perdita texana	Multiple	–	Barrows et al. (1979). Communal
Anthoporidae			
Paratetrapedia oligotricha	Multiple	–	Michener and Lange (1958). Tendency to communal
Megachilidae			
Chalicodoma spissula	Multiple	–	Batra (1978)
Eusocial			
Vespidae			
Vespula germanica	1 in field Multiple in lab	S	Schulz-Langer (1954). 648–2,090 in colony Thomas (1960)
V. pennsylvanica	1	S	MacDonald et al. (1974). In flight cages. 400–1,000 workers at peak population
V. atripilosa	Multiple	S	MacDonald et al. (1974). 150–300 at peak population
V. vulgaris	Multiple	S	Marchal (1896), Kemper and Dohring (1967). About 1,000 at peak pool, Kemper and Dohring (1961)
Dolichovespula arctica	Multiple	S	Greene et al. (1978). Workerless social parasite
D. sexonica	1	S	Marchal (1896)
Polistes metricus	>1	S	Metcalf and Whitt (1977). Sperm used in ratio 9:1
P. variatus	>1	S	Metcalf (1980). Sperm used in ratio of 89:11 if two matings
Apidae			
Trigona jaty	1?	I	Kerr et al. (1962). Based low sperm count. 2,000–5,000 workers. Lindauer and Kerr (1960)
Melipona quadrifasciata	1	I	Kerr et al. (1962). Sperm counts from male and female. 300–400 workers, Lindauer and Kerr (1960)
M. marginata	1	I	Kerr (1969)
M. quinquefasciata	1	I	DaSilva et al. (1972)
Apis mellifera	About 12	I	Taber and Wendel (1958), Page and Metcalf (1982), 4,000–80,000 workers. Ribband (1953)
A. cerana	14–30	I	Woyke (1973)
Bombus bifarius	1	S	Hobbs (1967)
B. huntii	2–3	S	Hobbs (1967). About 3000 workers at peak popl
B. hypnorum	2–3	S	Hobbs (1967)
Halictidae			
Dialictus zephrus	Multiple Single	S	Batra (1966). Based on dissection. 4–45 workers. Barrows (1975). Based on observations
Lasioglossum marginatum	Multiple	S	Plateaux-Quenu (1962). 200–400 in colony. Lives 5–6 years. Largest haltictine colony
L. rohweri	1–4	S	Barrows (1975)
Formicidae			
Formica obscuripes	1 probably	I	Talbot (1959, 1972) 19,000 workers. Weber (1935). Females taken back into nest
F. sanguinea	1	I	Pamilo and Varvio-Aho (1979). Several queens per nest
F. dakotensis	1 usually	I	Talbot (1971)
Myrmica americana	1	I	Kannowski and Kannowski (1957). About 250 workers
Aphaenogaster rudis	1	I	Crozier (1973, 1977). About 300 workers, Headley (1949), Talbot (1951)
Iridomyrmex purpureus	1	I	Halliday (1975, 1979) 73 of 75 queens single mated
Rhytidoponera chalybea	1	I	Ward (1978). 147–271 workers, Ward (1981)
R. confusa	1	I	Ward (1978). 84–204 workers, Ward (1981)
S. invicta	1	I	Hung and Vinson (1976). 50,000–230,000 workers, Markin et al. (1973)
Pheidole sitarches	1	I	Wilson (1957) 200–300 workers
Myrmica ruginodis	Multiple	I	Forel (1928) 1,200 workers Brian (1950)
Solenopsis lou	Multiple	I	Forel (1928), F. Santschi personal communication

Table 1 (continued)

Species	Number of matings	Semel or iteroparous	Remarks
Monomorium salomonis	Multiple	I	Forel (1928), F. Santschi personal communication
Pogonomyrmex rugosus	Multiple	I	Hölldobler (1976). 7,700 workers, MacKay (1981)
P. occidentalis	Multiple	I	Nagel and Rettenmeyer (1973). 3,000 workers, Rogers et al. (1972), Lavigne (1969)
P. maricopa	Multiple	I	Hölldobler (1976)
P. desertorum	Multiple Once Usually	I	Hölldobler (1976). In arenas. 400–600 workers, Whitford and Bryant (1979). Davidson, personal communication observation of mating swarms
P. barbatus	Multiple	I	Hölldobler (1976). 12,350 workers, Wildermuth and Davis (1931)
Atta sexdens	3–8	I	Kerr (1961). About 10^6 workers. Weber (1972)
Mycocepurus goeldii	Up to 4	I	Kerr (1961)
Acromyrmex landolti	Multiple	I	Kerr and Bredaroli (unpublished). about 10^5 workers, Weber (1972)
Lasius niger	Multiple	I	Forel (1928), Donisthorpe (1915)
L. flavus	Multiple	I	Forel (1928). 19,000 workers, Pontin (1978)
Brachymyrmex depilis	2–3	I	Page (1982)
Eciton burchelli	1–5	I	Rettenmeyer (1963). 150,000–700,000 workers, Schnierla (1971)
Prenolepis imparis	Multiple	I	Talbot (1945). 1,600 workers, Talbot (1943)
Formica rufa	Multiple	I	Marikovsky (1961). Up to 10^5 workers Brian (1965)
F. opaciventris	Multiple	I	Scherba (1961). Females return to nest
F. subintegra	Multiple	I	Kannowski (1963)
F. montana	Multiple	I	Kannowski (1963)
F. yessensis	Multiple	I	Ito and Imamura (1974). Females taken back to nest. Highly polydomous
F. aquilonia	Multiple	I	Pamilo et al. (1978). Highly polydomous

Table 2. The relationship between colony size and number of matings in ants. Only those species for which reliable colony size estimates were available were used in the analysis. Also not included were those species in which the queen returns to the nest following mating or which are polygnous. In these species colony size is problematical. Ants with small colonies tend to mate once, those with very large colonies mate more than once ($P = 0.003$, Fisher's Exact Test)

	Of order of 10^2 workers	Of order of 10^4 or more workers
Single mating	5	1
Multiple mating	0	8

mate multiply (Table 2). This is especially significant in light of the bias toward studying species with large colonies.

Page and Metcalf (1982) propose that multiple mating arises as a consequence of the mechanism of sex-determination. Multiple mating reduces the variance in the number of diploid males produced and is at a selective advantage. The two explanations for the evolution of multiple mating are not in conflict with one another. However, if multiple mating is an adaptation that reduces the variance in diploid male production, then there is no predicted relation between the typical colony size of a species and the number of times the queen mates. That there is such a relationship, in ants, strongly argues that multiple mating is an adaptation that allows maintenance of a large colony size.

Multiple Mating and the Evolution of Eusociality

Given that there are a number of eusocial species that mate more than once, it is worthwile to consider the conditions under which eusocial behavior can evolve if multiple matings occur. The mechanism that I consider below, sperm bias, is defined as contribution of unequal amunts of sperm by the males that mate with a female.

In Appendix B, I derive the conditions under which a gene that produces worker behavior will spread in a population of haplodiploids. If n is the number of times that a female mates and r is the fraction of females produced by workers in eusocial colonies, then the gene for eusocial behavior will increase in frequency if:

$$r > (1/2)n. \tag{1}$$

For a single mating, $n = 1$, any investment bias towards females ($r > 1/2$) will give an advantage to eusocial workers (Trivers and Hare 1976; Charnov 1978b). For as few as two matings, however, it is impossible to achieve an investment ratio that

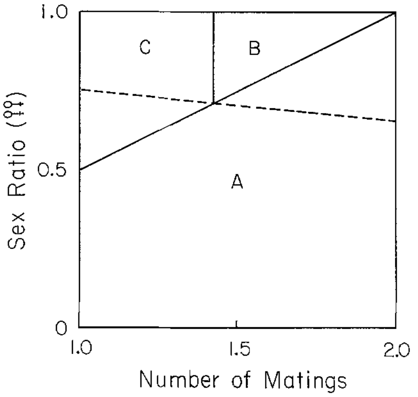

Fig. 1. The fraction of reproductive investment in female reproductives as a function of the number of matings by a queen. Above the *solid line* [Eq. (2)] there exists a genetical advantage to a worker in a eusocial colony. The *dotted line* in the ESS sex ratio (worker control of investment). In region C eusocial behavior has a selective advantage for workers and is consistent with further modification of the sex ratio

gives an advantage to the gene for eusocial behavior. This calculation is the motivation for the conclusion that multiple matings destroy to predisposition towards eusociality.

However, the number of matings can vary between one and two. Introducing the concept of fractional mating merely requires that one relax the unrealistic implicit assumption of equal sperm contribution by all males. 1.5 effective matings can be achieved by two matings, with one male contributing twice as many sperm as the other. Starr (1979) has suggested unequal sperm contribution by males and has developed a model to explore some effects of multiple matings. His model is developed on the assumption that one male contributes a fraction, s, of the sperm and each of the other n-1 males contribute $(1\text{-}s)/(n\text{-}1)$ of the total sperm. This assumption is not needed in order to arrive at some general conclusions.

Selection on the sexual investment ratio will modify it toward an evolutionary equilibrium. In an outbred, singly mating species, the optimal investment ratio is 3:1 biased towards females if workers control investment (Trivers and Hare 1976) and 1:1 if the queen controls investment (see Alexander and Sherman 1977). For multiply mating species, with workers controlling investment, the bias towards females should be:

$$\frac{1/4+1/(2n)}{1/4}:1=1+2/n:1$$

and thus the fraction of total investment devoted to females is:

$$\frac{1+(2/n)}{1+1+(2/n)}=\frac{n+2}{2n+2} \qquad (2)$$

and the fraction of total investment devoted to males is: $n/(2n+2)$. Charnov (1978a) has shown that the investment strategy described by 2 is an evolutinarily stable strategy (ESS).

Figure 1 shows the fraction of investment in females as a function of the effective number of matings. The dotted line shows how the ESS investment fraction in females, given by 2, varies with the number of fertilizations. The solid line shows the eusociality threshold, given by 1, or the extent of pre-existing investment bias towards females before haplodiploidy will produce any genetical advantage to eusociality. There are three regions labelled A, B and C. In region A, a gene for worker behavior would not be at a selective advantage because the investment ratios bias towards females is not great enough. In region B, eusociality could evolve, but it need not be a stable condition. If the number of matings did not change, a species should follow a vertical trajectory to come into line with the evolutionarily stable strategy. There would then be no advantage to eusociality due simply to haplodiploidy. In region C, eusociality could both evolve and the sexual investment ratio be an ESS. The maximum number of matings that is consistent with stable eusociality is given by:

$$\frac{n+2}{2n+2}>(1/2)n \quad \text{or} \quad n<\sqrt{2}=1.41. \qquad (3)$$

The condition required of expression 3 is that sperm be contributed in a ratio of approximately 5:2, or one male contributing 70% of the total and the remainder contributed by any number of other males. This result rests on the assumption, modified below, that workers and gynes are equally efficient at producing reproductives.

In *Polistes metricus* (Metcalf and Whitt 1977) and *P. variatus* (Metcalf 1980) the species for which data are available, the gynes are apparently mated twice. However, sperm from the two males are used in a 9:1 ratio. The effective number of matings is 1.1, which is well below the limiting number of matings required for stable eusociality.

Production of Sperm Bias

Sampling Effects. If a female mates with two males, it is highly unlikely that both will contribute exactly the same number of sperm. The effective number of matings will be less than two except in the single case of identical sperm contribution. If the size of the sperm contribution of males is a random variable with a known distribution, the ratio of the large to the smaller sperm contribution is the ratio of the second to the first order statistics of the distribution. A reasonable distribution for the size of sperm contribution of a given male is the Weibull distribution (Stauffer 1979). The Weibull distribution is only one of several possible distributions that could be used in such an analysis. It has the necessary property of being truncated at zero and the desirable properties of being unimodal with only a slight skewness and of having tractable order statistics. The ratio of the larger to the smaller of two numbers drawn at random from the Weibull distribution is:

$$f(x)=2\,\frac{c\,x^{c-1}}{(x^c+1)^2}$$

where c is the shape parameter of the Weibull distribution. The probability that this ratio takes on a value greater than or equal to k is:

$$2\int_k^\infty \frac{c\,x^{c-1}}{(x^c+1)^2}\,dx=\frac{2}{k^c+1}. \tag{4}$$

For $c=1$, the Weibull distribution is the negative exponential. With $c\geqq 2$, the distribution has a unimodal shape.

For the maximum number of matings consistent with stable eusociality, the ratio of sperm contribution must be $1/(\sqrt{2}-1)=2.41$. The probability that two sperm packets drawn at random from a Weibull distribution ($c=2$) have this ratio or greater is 0.29. Approximately 30% of the matings taking place randomly will produce sufficient sperm bias to maintain a genetical advantage to eusociality.

Statistical production of sperm bias in this example is limited. The case considered above concerns only two matings. For three matings, one would have to consider the ratio of the third to the sum of the first and second order statistics.

Inter-Male Competition for Females. It is to the selective advantage of the male to employ mechanisms to monopolize sperm contribution (Parker 1970). This may be achieved by contests among males for females, postcopulatory guarding of females, prolonged copulation, or use of mechanisms that interfere with the frequency or efficiency of further mating. Contests among males for females are frequently observed in mating swarms (Kannowski 1963; Talbot 1971; Davidson personal communication). Hölldobler (1976) has described the fierce struggles among males in the mating aggregations of *Pogonomyrmex* ants. However, there is no evidence that contests among males reduce the number of copulations of females. Post-copulatory guarding of females has not been described in the social Hymenoptera (but see Greene et al. 1978). This is no doubt partly due to the fact that males are usually capable of mating more than once (Kannowski 1963; Pamilo et al. 1978).

Variability in the length of copulation has been observed in *Pogonomyrmex* ants (Hölldobler 1976). In an experimental study it was shown that the first of three copulations of *P. rugosus* lasts for about one-half of the total copulation time. The duration of copulations has not been measured in field observations.

The loss of genitalia has been described in the bees, *Melipona* (Kerr 1969; DaSilva et al. 1972) and *Apis mellifera* (see Michener 1974) and in the ant *Pogonomyrmex rugosus* (Hölldobler 1976). In honeybees this 'mating sign' may or may not prevent further, immediate mating. It is removed in grooming by the workers when the queen returns to the hive. It is not effective in preventing the honeybee queens from mating approximately twelve times (Taber and Wendel 1958). In *Melipona* the male genitalia act as an effective copulatory plug and limit the number of matings to one. Hölldobler ventured the opinion that the loss of genitalia by male *P. rugosus* may be a way of insuring a monopoly on mating.

Sperm Competiton. Sperm competition (Parker 1970) can take the form of preferential use of the sperm contributed by the last male to mate with a female, or preferential use of the sperm of the first male to mate with a female. Parker reports that sperm competition occurs in honeybees, taking the form of a weak sperm precedence (the first mating preferentially produces offspring). However experiments to disentangle the effects of unequal sperm contribution or sperm clumping from those of sperm competition have not been performed on honeybees, much less on other social Hymenoptera.

It is to the advantage of any male to employ mechanisms to monopolize sperm contribution. Selective pressures on males to adopt such mechanisms may undo entirely the effects of multiple mating.

Ergonomic Efficiency of Eusociality

The preceding discussion was based on the assumption that Hymenopteran 'workers' are equally efficient at raising brothers and sisters in a eusocial colony as they would be at raising sons and daughters solitarily. If this ergonomic conversion efficiency is greater or less than unity, one might imagine that the constraints placed upon the

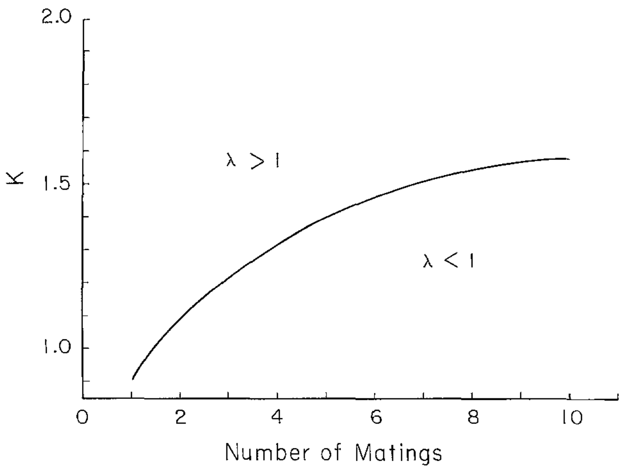

Fig. 2. The relationship between the relative reproductivity of a worker in a eusocial colony (K) and the maximum number of matings that are consistent with the spread of a gene for worker behavior (see Appendix 2). If the parameters of a species are *above the line,* the gene will spread; *below the line,* the gene will die out of the population

spread of a gene for eusocial behavior will be less or more stringent.

Thus, if a worker in a eusocial colony is able to contribute K reproductives to the colony output for each offspring produced solitarily, then requirements for the spread of a gene which produces worker behavior will be altered. Thus, K is the relative reproductive efficiency of workers in a eusocial colony. The relationship between the value of K and the number of matings of a 'queen' is shown in Fig. 2. The derivation of this relationship is shown in Appendix B.

If the value of K is as low as 1.25, more than 3 matings are 'permissible'. Since the number of matings here refers to the number of equivalent fertilizations, it is subject to upward revision unless all males contribute exactly identical numbers of sperm. Because of the increase in the 'allowable' number of matings, the potential for production of sufficient sperm bias by sampling variability is markedly enhanced. For example, if $K = 1.05$, that is workers are only 5% more efficient at reproduction in a eusocial colony than solitarily, (yielding $n_{\max} = 1.8$), and a female characteristically mates twice, approximately 78% of the females will have a sufficient sperm bias (Weibull distribution of sperm packet size, $c = 2$).

In primitively eusocial species in which there is only a marginal difference between the reproductives and the workers, there may be a crucial balance between the number of matings of the queen and the relative reproductive efficiency of members of the colony. However, in highly eusocial species the number of matings of the queen is effectively irrelevant. In certain species the ovaries of workers have disappeared (e.g. *Solenopsis*), rendering them sterile. In other highly eusocial species, (e.g. *Apis mellifera* or *Eciton burchelli*) that found colonies by haplometrosis, workers are again effectively incapable of reproduction. For these species K is much greater than one permitting any number of matings.

Appendix A

Evolution of Multiple Mating

A different type of life history is assumed in this appendix than in the following appendices. Here, I assume we are starting with a eusocial species. The wild type females (aa) mate once. Aa females mate more than once; the number of matings is irrelevant. The frequency of A is ε_1, and of Aa is ε_2. Workers in aa × a colonies produce Y total offspring with a fraction, r, of them females. aa × A colonies produce $\varepsilon_2 r R y/2$ Aa females and $\varepsilon_2 (1\text{-}r) R Y/2$ A males. Collecting like genotypes and putting new genotype frequencies in the form of matrix multiplication

$$\begin{pmatrix} 0 & R/2 \\ 1 & R/2 \end{pmatrix} \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix} = \begin{pmatrix} \varepsilon_1' \\ \varepsilon_2' \end{pmatrix}$$

the characteristic equation for which is:

$$\lambda^2 - \lambda R/2 - R/2 = 0.$$

If $R > 1$, then $\lambda > 1$.

Appendix B

Evolution of Worker Behavior with Multiple Mating

The discussion in Appendices B and C is similar to the discussion of eusocial evolution by Charnov (1978b). The following discussion is modified by introducing the complication of multiple mating.

The basic life history is the following. There is a species of solitary Hymenoptera that is homozygous at some locus (aa ♀, a ♂). Each female raises Y offspring. A mutant allele (A) arises which causes the females to remain in the nest and each rear Y siblings. The proportion of females that they raise is r. The mother of the colony (the queen) has mated n times. The frequency of the A genotype among the males in the population is ε_1 and of the Aa genotype in females is ε_2. While the mutant allele is rare, we can ignore events which take place with frequency of order ε^2 or less.

Thus there will be three types of mating.

(1) aa × $\{a\}_n$. This mating takes place with frequency 1, and yields $Y/4$ aa and $Y/4$ a.

(2) Aa × $\{a\}_n$. This mating takes place with frequency ε_2, and yields $\varepsilon_2 Y/4$ Aa and $\varepsilon_2 Y/4$ A.

(3) aa × A × $\{a\}_{n-1}$. This mating takes place with frequency $n\varepsilon_1$ and yields $\varepsilon_1 Y/2$ Aa.

The males produced in 2 mate with aa females yielding a total of $\varepsilon_2 Y^2 8$ Aa offspring. The aa females (there are $Y/2$ of them) each produce $Y/2$ aa and $Y/2$ a yielding a total of $Y^2/4$ aa and $Y^2/4$ a. The Aa females do not go off to mate, but remain at home and act as workers. The Aa workers from mating type 2, (there are $\varepsilon_2 Y/4$ of them) each produce $(1-\mathrm{r})Y/2$ A and yielding a total of $\varepsilon_2(1-r)Y^2/8$ A and $\varepsilon_2 r Y^2/8$ Aa. The Aa workers from mating type 3 (there are $\varepsilon_1 Y/2$ of them) each produce Yr/n Aa yielding a total of $\varepsilon_1 r Y^2/2n$ Aa.

Adding up all the offspring produced, one is left with the following quantities:

$$\begin{aligned} \mathrm{a} &= Y^2/4 \\ \mathrm{aa} &= Y^2/4 \\ \mathrm{A} &= \varepsilon_2(1\text{–}4)\,Y^2/8 \\ \mathrm{Aa} &= \varepsilon_1 r Y^2/2n + \varepsilon_2 Y^2/8 + \varepsilon_2 r Y^2/8. \end{aligned}$$

The new genotype frequencies ε_1' and ε_2' are the total mutant genotypes divided by the total wild type individuals. Thus:

$$\begin{aligned} \varepsilon_1' &= \varepsilon_2(1-r)/2 \\ \varepsilon_2' &= \varepsilon_1\, 2r/n + \varepsilon_2(1+r)/2. \end{aligned} \qquad \mathrm{A}(1)$$

Writting A(1) as matrix multiplication:

$$\begin{pmatrix} 0 & (1-r)/2 \\ 2r/n & (1+r)/2 \end{pmatrix} \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix} = \begin{pmatrix} \varepsilon_1' \\ \varepsilon_2' \end{pmatrix}. \qquad \mathrm{A}(2)$$

The characteristic equation for this system of equations is:

$$\lambda^2 - \lambda\left(\frac{1+r}{2}\right) - r(1-r)/n = 0. \qquad \mathrm{A}(3)$$

The mutant allele, A, will spread in the population if the dominant eigenvalue, λ, is greater than 1. Setting the condition $\lambda > 1$ and solving A(3) for r in terms of n:

$$r > n/2.$$

This is the condition obtained in (1). If $n=1$, r must be greater than 1/2, which is to say there must be a female biased sex ratio. For $n \geqq 2$, $r \geqq 1$, which is the motivation for saying that haplodiploidy is irrelevant to the evolution of eusociality in the case of multiple mating.

Appendix C

Ergonomic Efficiency of Eusociality

The situation in this appendix is identical to the situation described in Appendix B except that each female produces X offspring solitarily and Y siblings in eusocial colonies, $K = Y/X$.

Performing the same bookkeeping and writing the new genotype frequencies as matrix multiplication:

$$\begin{pmatrix} 0 & K(1-r)/2 \\ 2rK/n & (rK+1)/2 \end{pmatrix} \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \end{pmatrix} = \begin{pmatrix} \varepsilon_1' \\ \varepsilon_2' \end{pmatrix}.$$

The characteristic equation for this system of equations is:

$$\lambda^2 - \lambda\left(\frac{1+rK}{2}\right) - K^2(1-r)r/n = 0.$$

If one sets the condition $\lambda > 1$ in order to obtain the condition under which the mutant allele will spread one obtains:

$$r > (n+2K)/4K - 1/4K^2\sqrt{(Kn+2K^2)^2 - 8nK^2}.$$

Recalling that under worker control of investment, $\hat{r} = (n+2)/(2n+2)$, one can obtain the values of K above which the gene for eusocial behavior will spread and which are implicitly consistent with any subsequent sex ratio modification. The joint distribution of n and K which yield values of $\lambda > 1$ is shown in Fig. 2. As n becomes large, K approaches 2. This is consistent with intuition, because as n becomes large, the degree of relatedness to brothers and sisters becomes 1/4, while the degree of relatedness to offspring remains 1/2.

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References

Alexander RD, Sherman PW (1977) Local mate competition and parental investment in social insects. Science 196:494–500

Barrows EM (1975) Mating behavior in halictine bees (Hymen: Halictidae) III. Copulatory behavior and olfactory communication. Insectes Soc 22:307–331

Barrows EM, Chabot MR, Michener CD, Snyder TP (1979) Foraging and mating behavior in *Perdita texana.* J Kans Entomol Soc 49:275–179

Batra SWT (1966) Life cycle and behavior of the primitively social bee *Lasioglossum zephyrum.* Univ Kans Sci Bull 46:359–423

Batra SWT (1978) Aggression, territoriality, mating and nest aggregation of some solitary bees. J Kans Entomol Soc 51:547–559

Brian MV (1950) The stable winter population structure in species of *Myrmica.* J Anim Ecol 19:119–123

Brian MV (1957) The growth and development of colonies of the ant *Myrmica.* Insectes Soc 4:177–190

Brian MV (1965) Social insect populations. Academic Press, London

Brothers DJ (1972) Biology and immature stages of *Pseudomethoca f. frigida* with notes on other species (Hymenoptera: Mutillidae). Univ Kans Sci Bull 50:1–38

Carpenter FW, Hermann HR (1979) Antiquity of sociality in insects. In: Hermann HR (ed) Social insects, vol 1. Academic Press, New York, pp 81–89

Charnov EL (1978a) Sex ratio selection in eusocial hymenoptera. Am Nat 112:317–326

Charnov EL (1978b) Evolution of eusocial behavior: offspring choice or parental parasitism? J Theor Biol 75:451–465

Craig R, Crozier RH (1979) Relatedness in the polygynous ant *Myrmecia pilosula.* Evolution 33:335–341

Crozier RH (1973) Apparent differential selection at an isozyme locus between queens and workers of the ant *Aphaenogaster rudis.* Genetics 73:313–318

Crozier RH (1977) Genetic differentiation between populations of the ant *Aphaenogaster rudis* in the southeastern United States. Genetica 47:17–36

DaSilva DL, Zucchhi NR, Kerr WE (1972) Biological and behavioral aspects of reproduction in some species of *Melipona* (Hymenoptera, Apidae, Meliponinae). Anim Behav 20:123–132

Davidson DW (1982) Sexual selection in harvester ants [Hymenoptera: Formicidae: *Pogonomyrmex*]. Behav Ecol Sociobiol 10:245–250

Donisthorpe H St JK (1915) British ants. Brendon, Plymouth

Forel A (1928) The social world of ants, vol II (Translated by Ogden CK). Putnam, New York

Greene A, Akre RD, Landolt PJ (1978) Behavior of the yellowjacket social parasite *Dolichovespula arctica* (Rohmer). Melanderia 29:1–28

Halliday RB (1975) Electrophoretic variation of amylase in meat ants, *Irdomyrmex purpureus*, and its taxonomic significance. Aust J Zool 23:271–276

Halliday RB (1979) Esterase variation at three loci in meat ants. J Hered 70:57–61

Hamilton WD (1964) The genetical theory of social behavior. I, II. J Theor Biol 7:1–52

Hamilton WD (1972) Altruism and related phenomena, mostly in social insects. Annu Rev Syst Ecol 3:193–232

Headley AE (1949) A population study of the ant *Aphaenogster fulva* ssp. *aquia* Buckley (Hymenoptera, Formicidae). Ann Entomol Soc Am 42:265–272

Hobbs GA (1967) Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. VI. Subgenus *Pyrobombus*. Can Entomol 99:1271–1292

Hölldobler B (1976) The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). Behav Ecol and Sociobiol 1:405–423

Hung AC-F, Vinson SB (1976) Biochemical evidence for queen monogamy and sterile male diploidy in the fire ant, *Solenopsis invicta*. Isozyme Bull 4:55

Ito M, Imamura S (1974) Observations on the nuptial flight and internidal relationship in a polydomous ant, *Formica yessensis* Forel. J Fac Sci Hokkaido Univ Ser VI Zool 19:681–694

Kannowski PB (1963) The flight activities of formicine ants. Symp Genet Biol (Italica) 12:74–102

Kannowski PB, Kannowski P (1957) The mating activities of the ant *Myrmica americana* Weber. Ohio J Sci 57:371

Kemper H, Dohring E (1961) Zur Frage nach der Volksstärke und der Vermehrungspotenz bei den sozialen Faltenwespen Deutschlands. Z Angew Zool 48:163–197

Kemper H, Dohring E (1967) *Die Sozialen Faltenwespen Mitteleuropas*. Parey, Berlin Hamburg

Kerr W (1961) Acasalamento de rainhas com varios machos em duas especies da Tribu Attini (Hymenoptera, Formicidea). Rev Brasil Biol 21:45–48

Kerr WE (1969) Some aspects of the evolution of social bees. Evol Biol 3:119–175

Kerr W, Zucchi R, Nakadaira JT, Botolo JE (1962) Reproduction in the social bees. J NY Entomol Soc 70:265–76

Lavigne R (1969) Bionomics and nest structure of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). Ann Entomol Soc Am 62:1166–1175

Lin N, Michener CD (1972) Evolution and selection in social insects. Q Rev Biol 47:131–159

Lindauer M, Kerr W (1960) Communication between the workers of stingless bees. Bee World 41:29–41, 65–71

MacDonald JF, Akre RD, Hill WB (1974) Comparative biology and behavior of *Vespula atripilosa* and *V. pennsylvanica* (Hymenoptera: Vespidae). Melanderia 18:1–66

MacKay WP (1981) A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Psyche 88:25–74

Marchal P (1896) La reproduction et l'evolution des guepes sociales. Arch Zool Exp 4:1–100

Marikovsky PI (1961) Material on sexual biology of the ant *Formica rufa* L. Insectes Soc 4:23–30

Markin GP, Dillier JH, Collins HL (1973) Growth and development of colonies of the red imported fire ant, *Solenopsis invicta*. Ann Entomol Soc Am 66:803–808

Metcalf RA (1980) Sex ratios, parent-offspring conflict and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. Am Nat 116:642–654

Metcalf RA, Whitt GS (1977) Intra-nest relatedness in the social wasp *Polistes metricus*. Behav Ecol Sociobiol 2:339–351

Michener CD (1974) *The social behavior of the bees: a comparative study*. Harvard/Belknap Press, Cambridge (Massachusetts)

Michener CD, Lange RB (1958) Observations on the ethology of neotropical anthophorine bees. Univ Kans Sci Bull 39:69–96

Nagel HG, Rettenmeyer CW (1973) Nuptial flights, reproductive behavior and colony founding of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). J Kans Entomol Soc 46:82–101

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Monographs in population biology, vol 12. Princeton University Press, Princeton (New Jersey)

Page RE (1982) Polyandry in *Brachymyremex depilis* Emery (Hymenoptera: Formicidae). Pan Pac Entomol (in press)

Page RE, Metcalf RA (1982) Multiple mating, sperm utilization and social evolution. Am Nat 119:263–281

Pamilo P, Rosengren R, Vepsalainen K, Varvio-Aho S-L, Pisarski B (1978) Population structure of *Formica* ants. I. Patterns of enzyme gene variation. Hereditas 89:233–248

Pamilo P, Varvio-Aho S-L (1979) Genetic structure of nests in the ant *Formica sanguinea*. Behav Ecol Sociobiol 6:91–98

Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. Biol Rev 45:525–568

Plateaux-Quenu C (1962) Biology of *Halictus marginatus* Brulle. J Apicult Res 1:44–51

Pontin AJ (1978) The numbers and distribution of subterranean aphids and their exploitation by the ant *Lasius flavus* (Fabr.). Ecol Entomol 3:203–207

Rettenmeyer CW (1963) Behavioral studies of army ants. Univ Kans Sci Bull 44:281–465

Ribband CR (1953) The behavior and social life of honeybees. Bee Research Association, London

Rogers L, Lavigne R, Miller JL (1972) Bioenergetics of the western harvester ant in the shortgrass plains ecosystem. Envrion Entomol 1:763–8

Scherba G (1961) Nest structure and reproduction in the mound-building ant *Formica opaciventris* Emery in Wyoming. J NY Entomol Soc 69:71–87

Schnierla TC (1971) Army ants: a study in social organization. Topoff HR (ed). Freeman, San Francisco (California)

Schulz-Langer E (1954) Beobachtungen zur Copulation gefangengehaltener Wespen. Zool Anz 152:39–42

Starr CK (1979) Origin and evolution of insect sociality: a review of modern theory. In: Hermann HR (ed) Social insects, vol I. Academic Press, New York, pp 35–79

Stauffer HB (1979) A derivation for the Weibull distribution. J Ther Biol 81:55–63

Taber S (1955) Sperm distribution in the spermathecae of multiplymated queen honeybees. J Econ Entomol 48:522–525

Taber S IV, Wendel J (1958) Concerning the number of times queen bees mate. J Econ Entomol 51:786–789

Talbot M (1943) Population studies of the ant, *Prenolepis imparis* Say. Ecology 24:31–44

Talbot M (1945) A comparison of flights of four species of ants. Am Midl Nat 34:504–510

Talbot M (1951) Populations and hibernating conditions of the ant *Aphaenogaster (Attomyrma) rudis* Emery (Hymenoptera: Formicidae). Ann Entomol Soc Am 44:302–307

Talbot M (1959) Flight activities of two species of ants of the genus *Formica*. Am Midl Nat 61:124–132

Talbot M (1971) Flights of the ant *Formica dakotensis* Emery. Psyche 78:169–179

Talbot M (1972) Flights and swarms of the ant *Formica obscuripes* Forel. J Kans Entomol Soc 45:254–258

Thomas CR (1960) The European Wasp (*Vespula germanica Fab.*) in New Zealand. Inf Ser Dept Sci Ind Res (New Zealand) 27:1–74

Trivers RL, Hare H (1976) Haplodiploidy and the evolution of social insects. Science 191:249–263

Ward PS (1978) Genetic variation, colony structure and social behavior in the *Rhytidoponera impressa* group, a species complex of ponerine ants. Ph D dissertation, University of Sydney (Australia)

Ward PS (1981) Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae) II. Colony origin, seasonal cycles and reproduction. Psyche 88:109–126

Weber NA (1935) The biology of the thatching ant, *Formica rufa obscuripes* Forel, in North Dakota. Ecol Monogr 5:165–206

Weber NA (1972) *Gardening Ants: The Attines.* American Philosophicl Society, Philadelphia (Pennsylvania)

West-Eberhard MJ (1975) The evolution of social behavior by kin selection. Q Rev Biol 50:1–33

Whitford WG, Bryant M (1979) Behavior of a predator and its prey: the horned lizard (*Phrynosoma cornutum*) and harvester ants (*Pogonomyrmex* spp.). Ecology 60:686–894

Wildermuth VL, Davis EG (1931) The red harvester ant and how to subdue it. Farmer's Bull US Dept Agricult 1668:1–12

Wilson EO (1957) The organization of a nuptial flight of the ant *Pheidole sitarches* Wheeler. Psyche 64:46–50

Wilson EO (1971) The insect societies. Harvard/Belknap Press, Cambridge (Massachusetts)

Woyke J (1973) Reproduction in *Apis cerana.* I. Mating behavior. J Apic Res 11:141–146