

THE EVOLUTION OF MONANDRY AND QUEEN REPLACEMENT IN *Melipona* (HYMENOPTERA: APIDAE)

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ABSTRACT

Eight colonies of stingless bees (*Melipona compressipes*), were examined and the numbers of eggs, larvae, pupae, and adult workers were counted. A linear relationship was found between the number of workers present in the colony and the number of provisioned cells that contained eggs. All colonies were producing some reproductives suggesting that colonies of *M. compressipes* produce their reproductives during the rapid expansion phase of colony growth and, based on model 8 of Crozier and Page (Behav. Ecol. Sociobiol. 18: 105-115, 1985) should be monandrous. A model of the evolution of mating frequency and queen replacement is presented that predicts the co-occurrence of monandry and queen replacement that has been reported for *Melipona* spp.

INTRODUCTION

The genetic structure of *populations* is central to the evolution of insect sociality (Hamilton 1964a, 1964b, 1972) while *colony* genetic structure is important in explaining the evolution of social organization. Colony genetic structure results in differential social interactions among colony members. Recent studies have shown that individual members of insect societies are capable of recognizing and interacting differentially with nestmates of different genetic relationships in several social contexts (Getz and Smith, 1983; Page and Erickson, 1984, 1986, 1988; Breed *et al.*, 1985; Noonan, 1986; Evers and Seeley, 1986; Visscher, 1986; Frumhoff and Schneider, 1987; Frumhoff and Baker, 1988; Page *et al.*, 1989). In addition, the genetic structure of

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honey bee colonies has been shown to be a level of social organization that is important in the evolution of division of labor (Calderone and Page, 1988; Robinson and Page, 1988; Page *et al.*, 1989; Robinson and Page, 1989a,b; Robinson *et al.*, 1989). Colony genetic structure is strongly influenced by polyandry and polygyny, both of which are common phenomena in insect societies (Wilson, 1971; Page, 1986).

Recently, the evolution of polyandry has been the focus of much attention. Crozier and Page (1985) reviewed eight separate hypotheses for their generality in explaining the evolution of polyandry in social insects, their plausibility, and their ability to explain the observed trends that species with small-sized colonies tend to be monandrous while those with large colonies tend toward polyandry (see Cole, 1983). The hypothesis they considered the "current front-runner" (their hypothesis H8) was originally proposed for the special case of honey bees (Page, 1980), then generalized to the social Hymenoptera by Crozier (1980). This ecological-genetic hypothesis proposes that multiple mating by queens is selected when colonies produce their reproductives during the late stages of logistic colony growth (the concave, decreasing-returns-to-scale phase), while monandry is favored in species that produce them during the early, convex, increasing-returns-to-scale phase (see Oster and Wilson, 1978, pp. 47-50). The advantages or disadvantages of polyandry are a consequence of the effects of the proposed genic mechanism of sex determination of Hymenoptera on colony growth and development prior to and during the production of reproductives. In general, queens of species that have colonies with large numbers of workers produce reproductives during late stages of colony growth and should be polyandrous. Species with small numbers of workers produce reproductives during the early-buildup phase and should be monandrous. This comes from the assumption that the relationship of the fitness of a queen to the number of workers present in the colony is concave with populous colonies and convex with small ones (see Figure 1).

The model requires that the genic mechanism of sex determination result in the production of inviable or effectively sterile diploid males who negatively affect colony growth and development (see details of sex determination below). Diploid males have been identified in several species of social Hymenoptera including *Apis mellifera* (Mackensen, 1951, 1955; Woyke, 1965), *Apis cerana* (Woyke, 1979; Hoshiba *et al.*, 1981), *Melipona quinquefasciata* (Kerr and Silveira, 1972), *Melipona quadrfasciata* (Camargo, 1979), *Melipona compressipes* (Kerr, 1987a,b,c), *Bombus atratus* (Garofalo, 1973), *Scaptotrigona postica* (Kerr, 1987a), *Tetragona quadrangula* (Tarelho, 1973; Kerr, 1974, 1975), *Lasioglossum zephyrum* (Kukuk, 1988), *Formica presilabris* (Pamilo and Rosengren, 1984), a hybrid of *Lasius alienensis* and *Lasius niger* (Pearson, 1983), *Pseudolasius sp.* (Hung *et al.*, 1974), *Rhytidoponera chalybaea* and *Rhytidoponera confusa* (Ward, 1978), and *Solenopsis invicta* (Glancey *et al.*, 1976; Ross and Fletcher, 1985). *Melipona spp.* produce haploid males in proportions similar to *Apis spp.* (Laidlaw *et al.*, 1956; Woyke, 1976; Adams *et al.*, 1977; Silva, 1977; Camar-

go, 1979; Kerr, 1987a,b,c) and, because of similar life histories, would be expected to be polyandrous, as are the honey bees. Queens of *Apis mellifera* mate with an average of about 17 males (Adams *et al.*, 1977; Page, 1986) while queens of *A. cerana* mate with up to about 30 (Ruttner *et al.*, 1972; Woyke, 1973). However, based on observations (Kerr *et al.*, 1962; da Silva *et al.*, 1972), dissection (Kerr and Krause, 1950; Kerr *et al.*, 1962; Kerr, 1969), and gene segregation ratios from progeny analyses (Kerr, 1969; Contel and Kerr, 1976), *Melipona* queens are monandrous. Page (1986) suggested that, based on this apparent contradiction, *Melipona* could provide a test of the hypothesis.

The similarities in colony life history of *Melipona* and *Apis* (see Michener, 1974, pp. 329-364) include a single (except for *M. bicolor* with multiple queens, see Kerr, 1949 and da Silva, 1977), long-lived reproductive queen and unmated workers. Both produce an excessive number of males seasonally (Kerr, 1969; Page and Metcalf, 1984) and undergo colony fission during female reproduction.

The number of *xo* sex alleles is estimated to be 18.9 in *Apis mellifera* (Adams *et al.*, 1972) and 20 in *Melipona compressipes* (Kerr, 1987c), while the number of lethal equivalents is about 1.3 in *Apis mellifera* and 1.1. in meliponid populations (Kerr and Almeida, 1981).

Dissimilarities also exist. *A. mellifera* colonies are very large with populations that may be in excess of 60,000 workers (although this is probably only under extraordinary conditions) while colonies of *Melipona* are much smaller, usually less than 2,000 individuals (see Tables 6.1 and 6.2, Michener, 1974, and see also Wille, 1983). In *Melipona*, the virgin queen leaves the hive to found a new colony, whereas in *Apis*, the old queen leaves with the swarm and the new queen remains. *Melipona* queens are produced in large numbers (up to about 1/4 of all diploid eggs laid) throughout the season and are discarded, representing a considerable energetic load on the colony (see Kerr, 1969, 1987b). In *Apis*, only a few queens are produced seasonally in response to swarm-producing stimuli, queenlessness, or in response to stimuli that result in replacement of the queen through supersedure (see Winston, 1987, pp. 123-126, 181-198 for a recent review). *Melipona* workers in queenright colonies lay many of the eggs that develop into males (Beig, 1972; Contel and Kerr, 1976) while in *A. mellifera*, worker reproduction is rare in queenright colonies (Page and Erickson, 1988).

Melipona mass provision cells before eggs are laid, therefore, the entire investment is made in an individual before the cell is sealed (see Kerr, 1969). As a consequence, diploid males are raised to the adult stage (Camargo, 1976, 1979; Kerr, 1987c), emerge, and "cost" the entire investment in a worker (diploid males arise from fertilized, female-destined eggs). Honey bees workers, however, progressively provision cells and have more contact with brood. Workers detect diploid male larvae soon after they eclose from the egg and consume them (Woyke, 1963), thus ending the wasted investment in them.

Only 18% of diploid drones produce semen. The number of spermatozoa in those drones is about 25% of that of normal haploid males. In addition, only about 25% of diploid drones return from their first flights (Chaud-Netto and Kerr, 1978).

Queens of *M. quadrifasciata* (Camargo, 1976, 1979) and *M. compressipes* (Kerr, 1987a,b) are replaced with a daughter queen within about 4 days of the emergence of their first brood, if the brood contains diploid males. Removing diploid male brood and replacing it with brood from a nondiploid-male producing queen results in the maintenance of the queen (Camargo, 1976). The production of diploid males appears to have no effect on the replacement of queens of *Apis mellifera* (personal observations).

Based on these elements of the life history of these two species we expected that because of monandry *Melipona* should produce reproductives during the rapid expansion phase of colony growth, or should never reach the later stages of logistic growth due to constraints on colony development. Furthermore, we expected that queen replacement and monandry should be functionally related through the genic mechanism of sex determination.

METHODS

In this section we present the methods used to estimate the relationship between the number of individual workers present in colonies and the rate of growth of a colony based on the number of newly provisioned cells that contain eggs. We then present a general model that investigates the coevolution of mating behavior and queen replacement in *Melipona*. The model is adapted directly from Page (1980). We also discuss some of the implicit assumptions of the model.

Colony Development

Eight colonies of *Melipona compressipes* were selected from apiaries established by W.E. Kerr in São Luis, Maranhão, Brazil. All colonies were originally obtained from natural nests and had occupied the experimental hives for at least 2 years. Entire colonies were anesthetized with CO₂ to facilitate counts of adult workers. All individuals within colonies were counted and all brood cells were opened and their individual contents recorded as egg, larva, or pupa. Eggs require about nine days to hatch (Kerr, 1987b), therefore, egg counts reflected the total brood investment of the colony over the previous nine day interval, and the expected rate of growth and/or replacement of the adult population over the nine day interval ending about 50 days later (brood development time for *M. compressipes* workers is about 50 days). A linear regression analysis was conducted on the data with the number of provisioned cells containing eggs dependent on the number of adult workers (Sokal and Rohlf, 1981).

The Model

The model is presented in two parts. The first part presents the effects of the sex determination system on the distribution of diploid males among colonies as a function of the mating behavior of queens. The second part presents two models of the relationships between the production of diploid males and fitness of queens. The first of these fitness models is for the case without queen replacement; the second is with queen replacement.

Sex Determination Sex in *Melipona* appears to be regulated in a way similar to that shown for the honey bees *Apis mellifera* and *Apis cerana* (Kerr, 1975; Woyke, 1979). A single locus (the x_0 locus) is hypothesized to play a major role in regulating the production of the male or female phenotype (Camargo, 1979; Kerr, 1987a,b,c). Individuals that are heterozygous at this locus develop into females; homozygous individuals, develop into males. Homozygous diploid males represent a waste of reproductive investment because they most likely produce diploid and aneuploid sperm (Woyke and Skowronek, 1974) and colonies with triploid workers (Chaud-Netto, 1972).

In natural populations, the actual number and distribution of sex alleles is determined by the rate of mutation at the x_0 locus, selection intensity, and the effective size of the breeding population (Kimura and Crow, 1964; Yokoyama and Nei, 1979; Kerr and Vencovsky, 1982). If, however, we assume that all heteroallelic combinations have equal fitness, and make the usual Hardy-Weinberg population assumptions of infinite size, no migration or mutation, and panmixis, then at equilibrium all alleles are expected to be at equal frequency, $1/k$, where k is the number of alleles (Wright, 1939, 1965). With these assumptions, the probability for each mating that a queen will mate with a male that has an allele in common with one of her two alleles is $2/k$. If a queen mates with n males, the probability $P_{(y)}$ that she will mate with exactly y males with alleles matching one of hers is, from the binomial probability density function,

$$P_{(y)} = \frac{n!}{y!(n-y)!} (2/k)^y (1-2/k)^{n-y} \quad (1)$$

Assuming each male contributes equal numbers of spermatozoa to the queen's spermatheca, the expected proportion of diploid males produced by a colony as a consequence of mating with n males is $y/2n$, therefore, the expected production of functional females (workers and queens) is $1 - y/2n$. The expected proportion of functional females (F) in the population is determined only by the number of x_0 alleles that are segregating, $F = 1 - 1/k$ (Shaskol'skii, 1968, Woyke, 1976, Adams *et al.*, 1977, Page and Marks, 1982). The number of matings by individual queens affects the

distribution of female production among colonies (see Page and Metcalf, 1982, Page and Marks, 1982). Assuming that the sperm of different mates are used at random by queens and that each male contributes an equal number of spermatozoa, the variance in functional female production among colonies in a population with k alleles and n matings per queen is: $1/2n (1/k) (1-2/k)$ (Page and Marks, 1982).

Fitness relationships

The true relationship between the proportion of diploid males produced and the fitness of a queen (W) is not known, however, we can explore different plausible fitness relationships, W_{1-3} , of concave, sigmoidal, or convex by assuming the inflection point is 0.50, 0.75, or 1.00, respectively (see equations 2a-c below). For $F = F(y)$, the number of functional females,

$$W_1(F) = \frac{2}{1 + e^{-10(F-0.50)}} - 1; \quad (2a)$$

$$W_2(F) = \frac{1}{1 + e^{-20(F-0.75)}}; \quad (2b)$$

$$W_3(F) = \frac{2}{1 + e^{-10(F-1.00)}}. \quad (2c)$$

Fitness relationships W_1 and W_3 are mirror images, W_2 is symmetrical about the inflection point. Each covers the fitness range from 0 to 1.00 with a change in the proportion of functional females between 0.50 and 1.00. Given k sex alleles in a population, it follows from equations 1 and 2 that the expected fitness of a genotype that specifies mating with n males, $E(W)$, is

$$E(W) = \sum_{y=0}^n P(y) \cdot W(F). \quad (3)$$

When we interpret the results of this model, we assume that the production of diploid males has a direct effect on the number of workers in a colony. The number of workers then affects the fitness of queens (see Crozier and Page, 1985). We also assume that colonies with 50 percent diploid male production have a fitness of 0.00. The scaling of fitness does not change the relationships between the different

mating models examined. However, the conditions of equation 12 must be met for threshold selection (see below). This requires that colonies producing 50% diploid males must be less than half as fit as those that produce none.

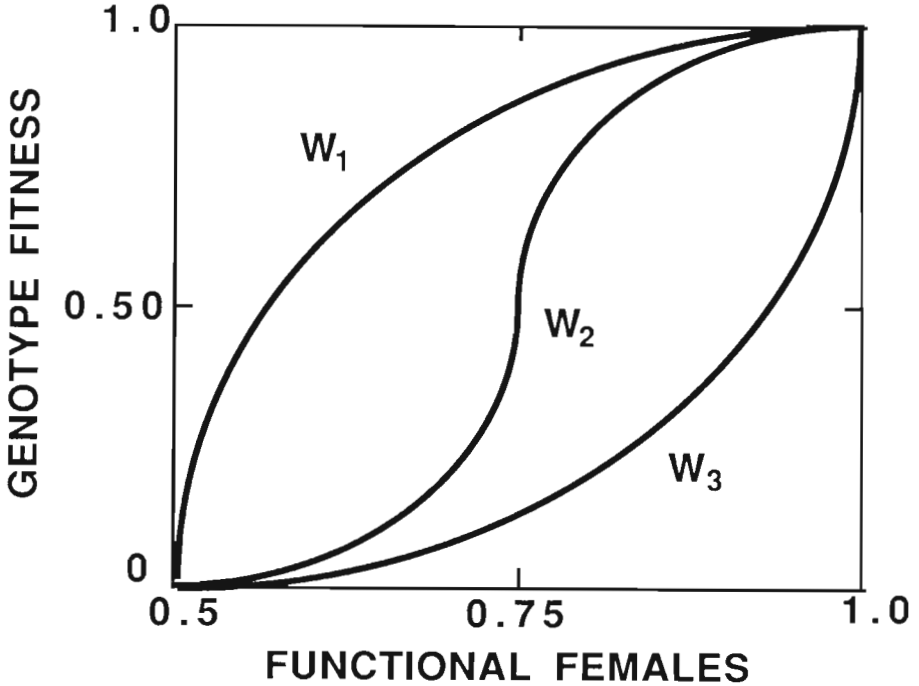


Figure 1 - Models of the relationship between genotype fitness and the production of functional females, F , in colonies.

Selection may occur for thresholds of acceptance of diploid males. If queens with functional female production below some threshold value are replaced, then the region of the fitness relationship that lies below that value is redistributed and devalued by $1/2$, a consequence of the decreased probability of gene transmission by descent, due to recombination. Assume $E(W_{NR})$ is the expected fitness of surviving queens with functional-female production above the threshold value T ; α is the difference in reproductive output of queens that produce proportions of functional females below the threshold value and their replacements (this could be due to the lag in worker brood production during queen replacement, risks of mating, etc.); and p_R is the probability of replacement. Then, under threshold selection, the expected fitness, $E(W_T)$ of a genotype that specifies mating n times is:

$$E(W_T) = E(W_{NR}) + 1/2 p_R E(W) - p_R \alpha. \quad (4)$$

$$p_R = \sum_{y=t+1}^n P(y), \quad (5)$$

where t is the number of matings by an individual queen with males that have an x_0 allele identical to one of hers that results in diploid male production in excess of the threshold value, T ;

$$t = 2n(1-T). \quad (6)$$

From equations 3 and 6 above,

$$E(W_{NR}) = \sum_{y=0}^t P(y) \cdot W(y). \quad (7)$$

The necessary condition for the increase in frequency of a genotype specifying a queen replacement threshold, given k alleles and n matings, is

$$E(W_T) > E(W). \quad (8)$$

The fitness probability distribution $E(W)$ can be partitioned into the expected fitness value of those queens at or below the threshold for replacement, $E(W_{NR})$, and those above the threshold, $E(W_R)$:

$$E(W) = E(W_{NR}) + E(W_R); \quad (9)$$

$$E(W_R) = \sum_{y=t+1}^n P(y) \cdot W(y). \quad (10)$$

Therefore, the condition for the spread of a genotype specifying a given threshold for queen replacement can be rewritten as

$$E(W_T) > E(W_{NR}) + E(W_R). \quad (11)$$

Substituting equation 4 into 11 and rearranging terms, the necessary condition for the evolution of a threshold is

$$E(W) > \frac{2E(W_R)}{PR} + 2\alpha. \quad (12)$$

Assuming that $\alpha = 0$, we investigate the effects of variable numbers of sex alleles (3 - 20), queen matings (1 - 20), and thresholds for queen replacement (0.50, 0.60, 0.75, and 0.90) on the fitness of queen genotypes. We examine three different models of the relationship between fitness and the production of functional females (concave, sigmoid, and convex)

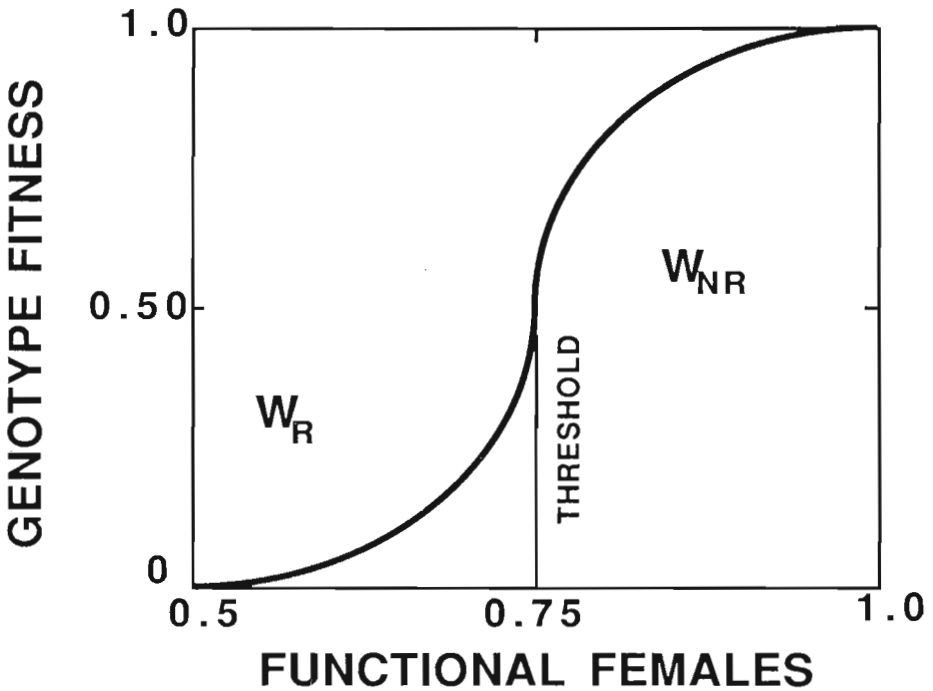


Figure 2 - Partitioning of the relationship of the proportion of functional females to genotype fitness into components of queens with functional female production above, W_{NR} , and below, W_R , the threshold for queen replacement. This curve assumes $c = 0.75$ and represents equation 2b.

Additional assumptions of the Model

Some assumptions are implicit in this model. We assume that replaced queens do not have any individual reproductive success other than the production of a single replacement daughter. This assumption may not hold in the strict sense because queens may lay some unfertilized eggs that develop into haploid males before

they are replaced. However, the number of sons produced (if any) would probably be very small compared to the number produced by a surviving queen.

We also assume that the male and female components of reproduction are equal and are affected in the same way by the production of diploid males. The change in fitness associated with male production, however, is not reduced by half immediately after queen replacement. In many species of *Melipona*, males are produced by both the queen and laying workers (Kerr, 1969; Beig, 1972; Contel and Kerr, 1976). The genetic relationship of a replaced queen to worker-produced males changes during the transition in composition of the colony from her sisters to her daughters, initially, and then granddaughters. The average life expectancy of workers is 51 days (Kerr, 1987b) while queens live approximately 2-7 years (L. Oliveira, unpublished data; W.E. Kerr, personal observations). Because workers live only a short time relative to queens, the transitional stage of potential simultaneous male production by sisters, daughters, and granddaughters of the replaced queen is probably short and the assumption that genotype fitness is reduced by half for replaced queens is a close approximation.

Finally, we assume that queen replacement is under control of the queen. Conflict between the interests of the workers (sisters of the queen) in terms of their inclusive fitness and those of the queen may exist in the context of some behavior (see Trivers and Hare, 1976). However, because workers in the colony at the time of queen replacement are sisters of the queen, they stand to gain or lose fitness in the same way as the queen because they have no asymmetries of relatedness to queen produced reproductives.

RESULTS

Colony development

The mean number of adults per colony was 607, range 85-1410, (see Table I) and is representative of the range of reported colony sizes for other species of *Melipona* (see Tables 6.1 and 6.2, Michener, 1974; Wille, 1983) including the range of 70-550 reported for nine colonies *M. compressipes* (formerly *M. interrupta triplarides*) in Panama (Roubik, 1983; Roubik and Buchmann, 1984). The relationship between the number of adult workers and the number of eggs in provisioned cells was linear over the range of colony sizes sampled ($R^2 = 0.89$; $F = 50$, $P < 0.01$).

Based on the number of eggs present and assuming a nine day egg maturation period (Kerr, 1987b), colonies were producing new individuals at a rate of 0.04 ± 0.017 standard deviation (S.D.) per day, per adult worker. (The same calculation using the total amount of brood present, eggs, larvae, and pupae, and assuming a 50 day brood maturation period (Kerr, 1987b), yields an estimate of 0.04 ± 0.020 S.D.). The observation that this is constant over the range of colony sizes suggests the ab-

sence of the negative feedback normally associated with later stages of colony growth that leads to the decreasing-return-to-scale phase (Oster and Wilson, 1978, pp. 47-50).

Table I - Composition of colonies of *Melipona compressipes*. The first 5 colonies were examined in early November 1986, the last 3 in late October, 1988.

Colony No.	Adult workers	Pupae	Larvae	Eggs
K41-2-86	1410	1256	739	596
R109-1-84	757	969	917	384
Q92	674	1102	866	272
K45-4-85	265	31	652	88
Q94-1-84	85	45	0	0
UEMA-11	642	417	224	230
UEMA-12	458	890	339	183
UEMA-37	819	665	364	195

Assuming an average life expectancy of about 50 days, each individual worker "produces" about two other individuals (including workers, virgin queens, and males) during her life. Colonies should grow geometrically provided that more than half of the eggs are destined to become viable workers. Differences in diploid male production result in differences in the mean number of new workers produced per day and, consequently, nonlinear differences in rates of colony growth. The relationship is convex between the proportion of eggs laid that develop into new viable workers and the number of workers in a colony at a given time during colony development.

All colonies were producing males while six of the eight colonies had newly-emerged virgin queens and queen pupae present. Combined, these observations suggest that colonies of *M. compressipes* produce reproductives before they reach the negative feedback phase of colony growth and, as a consequence, the relationships between functional female production and fitness is probably convex (Crozier and Page, 1985).

The Model

Convex relationships between colony size and fitness may lead to both monandry and queen replacement. This is illustrated by results of the model for the

case where the random variable for the inflection point of the curve, C , is set at 1.00 (equation 2c; see also Figure 3). Overall, queen fitness decreases with increasing numbers of matings and increases with an increase in the number of sex alleles assumed (K). The most fit queen genotype in all cases (Figure 3) mates with a single male and is replaced by her own daughter if she produces diploid male progeny. Queen replacement at some threshold level is favored relative to nonreplacement for most numbers of matings.

Under the special conditions that we tested, replacement of queens with 50% functional female brood should always be favored. This is demonstrated in each model for the case of a single mating where replacement at all threshold levels is favored over genotypes that do not replace ($T = 0.50$) queens. This is a consequence of the discretization occurring with monandry of the threshold fitness function to just two points where the proportion of viable brood is either 1.00 or 0.50. In this case all thresholds below 1.00 are functionally equal and should eliminate diploid-male producing queens.

Examining the other extreme case, where the relationship between colony size and fitness is concave, $C = 0.50$ (Equation 2a), yields a very different result (Figure 4). In this case, genotypes for polyandry without queen replacement always have the highest fitness. As discussed above, replacement of queens with $F = 0.50$ should always be favored. However, the occurrence of this class of queens becomes extremely unlikely with increasing numbers of sex alleles and matings, and, therefore, selection should be negligible. The expected frequency of 50% diploid-male producing queens, assuming 10 sex alleles, is about 1 in 10 million for queens that mate with 10 males and 1 in 5 for those that mate just once.

The intermediate case where the distribution of functional female production to fitness is assumed to be sigmoidal and symmetrical, $C = 0.75$, (figure 5) gives mixed results depending on the specific assumptions of the number of sex alleles. In some cases fitness "throughs" exist that must be crossed before polyandry can evolve. For instance, monandry with queen replacement is favored across the entire range of matings examined by the model for the case of 5 sex alleles even though polyandry is always favored over monandry, without queen replacement. A single mating with queen replacement thresholds is also favored over 2 matings for the cases of 10 and 20 sex alleles. All models presented show differential fitness among thresholds, suggesting the potential for differential selection.

Page (1980) showed that there was no selection on mating behavior when a linear relationship was assumed. In our model, however, replacement can still evolve under the assumptions of linearity. From equation 12, if we assume that $\alpha = 0$, the condition for evolving replacement queens requires that the mean fitness of queens under the conditions of no replacement, $E(W)$, be more than twice the average fitness of queens that have functional female production below the threshold level, $E(W_R)/p_R$.

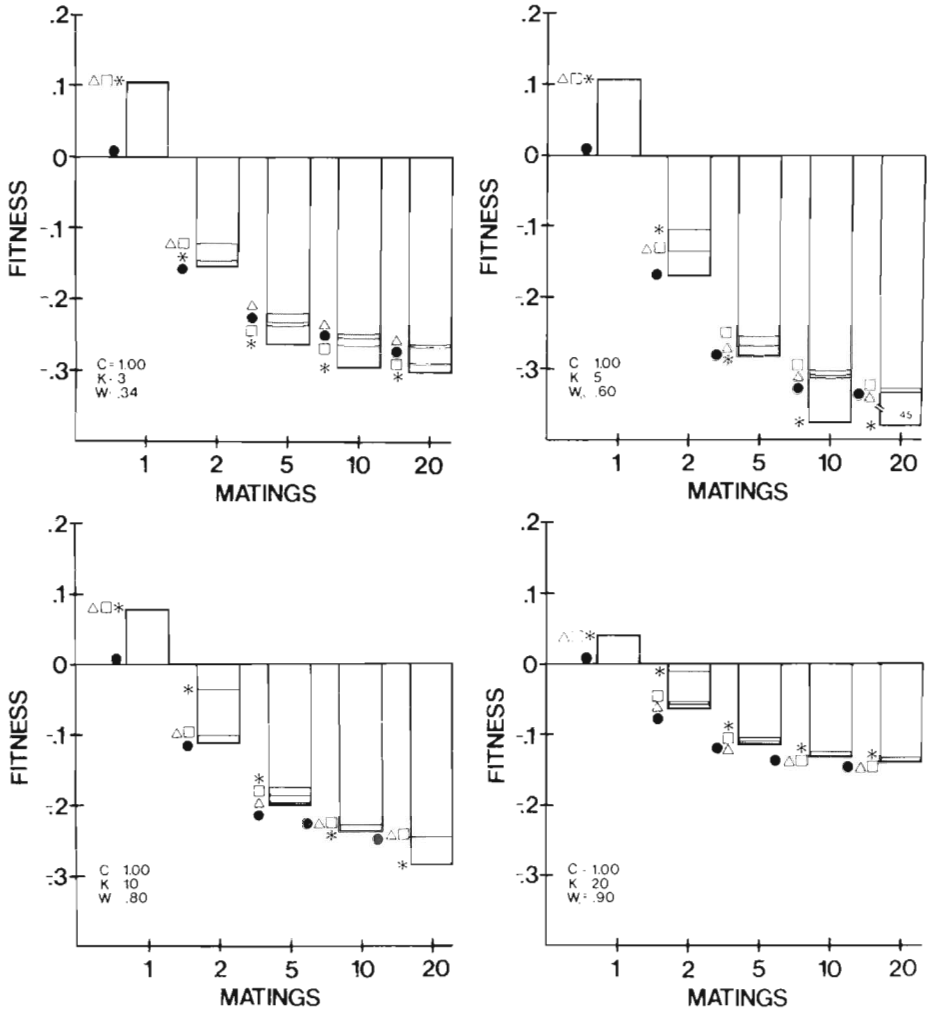


Figure 3 - Results of threshold selection model for the case $C = 1.00$ (assuming model 2c). Solid circles represent the fitness of queen genotypes that mate n times (Y-axis) without queen replacement $T = 0.50$; asterisks represent the fitness of genotypes that specify replacing all queens below the threshold value, $T = 0.90$; open squares, $T = 0.75$; open triangles $T = 0.60$. All fitness values are shown relative to the case of no queen replacement and monandry, W_0 . Shaded areas represent the increase in fitness for genotypes that replace queens at given thresholds relative to genotypes that do not replace queens.

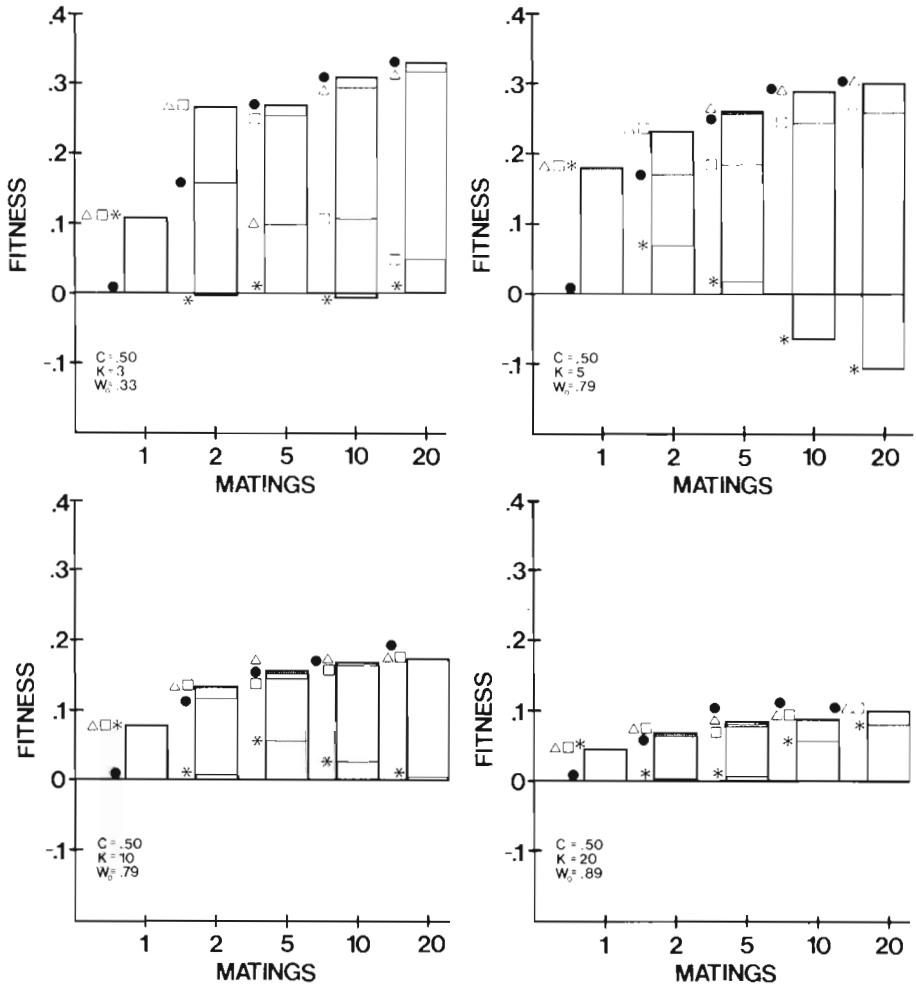


Figure 4 - Results for the model where the inflection point, $C = 0.50$ (from equation 2b). See caption, Figure 3.

DISCUSSION

Results of our model suggest that the genic mechanism of sex determination may have been important in both the evolution of mating behavior and replacement of queens in the social Hymenoptera. In general, queen replacement is favored with monandry, as in *Melipona*; queen retention with polyandry. Honey bee colonies (*Apis spp.*) produce reproductives in the later stages of logistic growth; the relationship be-

tween the number of functional workers and fitness is probably concave (Page, 1980; Page and Metcalf, 1982; Crozier and Page, 1985). Under the assumptions of our model, polyandry without queen replacement should be favored. Queens of *Apis mellifera* have been shown to be extremely polyandrous, mating with about 17 different males (see Page, 1986 for review), while queens of *Apis cerana* mate with more than 30 (Woyke, 1973). Queen replacement has not been linked to diploid male production in either species.

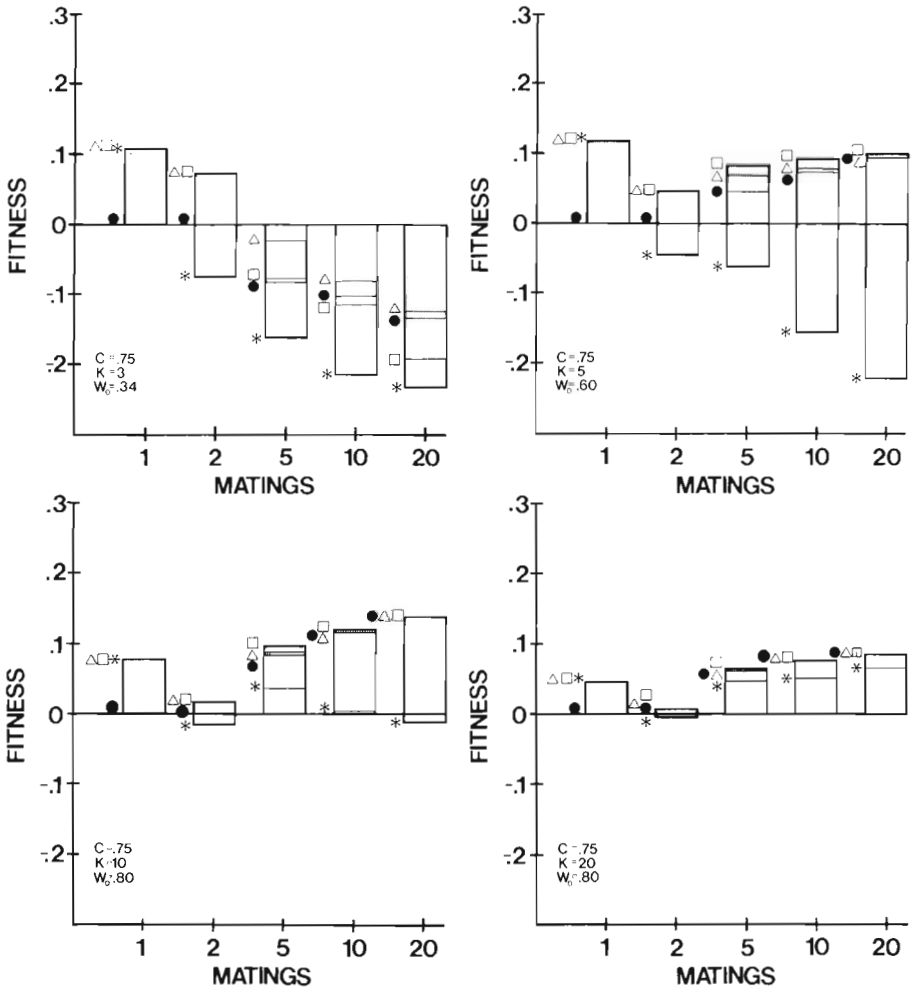


Figure 5 - Results for the model where the inflection point, $C = 0.75$ (from equation 2a). See caption, Figure 3.

The constraints that keep *Melipona* in the rapid growth phase of colony development are unknown to us. The production of males and virgin queens during colony development may diminish the potential worker population and keep the rate of growth below the intrinsic capacity and below that level at which negative feedback occurs. Virgin queens are produced in great excess in colonies, particularly during times of plentiful resources, the likely time of rapid colony expansion. These virgin queens are cast out of the colony and represent a significant resource that could have been directed toward the production of workers.

Nonlinear fitness relationships result in two potential levels of selection against common sex alleles: individual and colony. Homozygous *individuals* do not have any reproductive success (a fitness of zero) due to either the production of diploid or aneuploid sperm (Woyke and Skowronek, 1974) or because they are consumed by workers before they develop into adults (Woyke, 1963). Heterozygous queens that have common sex alleles have a lower average expected fitness because they are more likely to mate with males with matching alleles. With nonlinear fitness relationships, *colonies* resulting from mating-type combinations with more common alleles will be selected against because they are more likely to result in queen replacement and/or disproportionately lower reproductive output. This resulting selection against mating types (Owen, 1989) involving common alleles should result in the maintenance of more alleles at equilibrium than expected based on the results of linear, individual selection models (Wright, 1939, 1965; Kimura and Crow, 1964; Yokoyama and Nei, 1979).

Sherman *et al.* (1988) proposed that polyandry evolved in the social Hymenoptera in response to the occurrence of colony epidemics of pathogens and parasites. In their model, they hypothesize that colonies need genotypic diversity to provide a level of genetic resistance. Colonies that are genotypically narrow are more likely to be decimated by the plethora of pathogens and parasites while those that are more genotypically diverse, due to polyandry, are more likely to have some individuals that are resistant and survive, thus resulting in the survival of the colony. Species with large worker populations are assumed to be more likely to contract diseases and parasites and, therefore, more likely to be polyandrous.

The genetic load resulting from the production of diploid males has apparently been more important than the disease load in the evolution of the genetic and social structure of *Melipona*. Overall, the disease load of *Melipona* is significant, however, *Melipona* apparently have not evolved polyandry or queen replacement, in response to disease. Four of the eight colonies in our study (K45-5-85, Q94-1-84, UEMA-11 and UEMA-37) had significant levels of disease that resulted in brood death. Colony K45-1-84 had been diseased for at least five months; Q94-1-84 for at least four months. Neither colony had replaced its queen. Records of 164 colonies maintained by W.E. Kerr showed that ten (6.1%) had diseased brood at a serious level. This frequency of diseased colonies is comparable to frequencies of colonies of

honey bees in North America that are infected with the serious honey bee disease American foulbrood (Bailey, 1981).

Diploid males are very difficult to observe. Behavioral mechanisms exist in *Apis* and *Melipona* that make adult diploid males very rare even though they are relatively common at the time of zygote formation. Honey bee workers consume the diploid male larvae within a few hours of eclosion (Woyke, 1963) while diploid-male producing *Melipona* queens are replaced. It is likely that diploid males will be found to be common throughout the social Hymenoptera as more manipulative studies are conducted that circumvent the behavioral mechanisms that eliminate them from populations and further demonstrate the significance of the genic mechanism of sex determination on the genetic and social structure of insect societies.

ACKNOWLEDGMENTS

We thank the Tinker Foundation Foreign Research Travel Grant Program and the Ohio State University Office of Research and Graduate Studies for support to R.E. Page Jr. that enabled us to work together. Research was funded in part by grants from the National Science Foundation to R.E.P. and the Banco do Brasil Fundo de Incentivo a Pesquisa Técnico Científica (FIPEC) and the Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq) to W.E.K. Wayne Getz and Francis Ratnieks made valuable suggestions for improving this paper.

RESUMO

Oito colônias de tiuba (*Melipona compressipes*, Meliponinae, Apidae) foram anestesiadas com CO₂, e a seguir contou-se o número total de ovos, larvas, pupas e adultas de cada colméia. Todas as colônias estavam produzindo rainhas e machos e foi encontrada uma correlação linear entre o número de operárias adultas presentes na colônia e o número de células provisionadas que contém ovos. Essa correlação linear sugere que as colônias de *Melipona compressipes* produzem seus reprodutores durante a fase de rápida expansão do crescimento da colônia e, de acordo com o modelo 8 de Crozier e Page (Behav. Ecol. Sociobiol. 18: 105-115, 1985), deveriam ser monandras. Apresenta-se um modelo da evolução da frequência de acasalamento e da substituição da rainha, que prediz a ocorrência conjunta de monandria e substituição de rainha como relatado para todas as espécies de *Melipona* estudadas.

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(Received February 14, 1989)