

THE EVOLUTION OF MULTIPLE MATING BEHAVIOR BY HONEY BEE QUEENS (*APIS MELLIFERA* L.)

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ABSTRACT

A model is presented showing that natural selection operating at the individual level can adequately explain the evolution of multiple mating behavior by honey bee queens. Group selection need not be invoked. The fitness of a given female genotype is a function of the number of sex alleles in the population, the number of matings by an individual female and the specific parameters that determine the relationship of brood viability to individual fitness. Even though the exact relationship is not known, it is almost certainly not linear. A nonlinear relationship between worker brood viability and fitness and a significant genetic load associated with the sex-determination system in honey bees are the essential components of this model.

MULTIPLE mating by reproductive female honey bees (queens) has been well documented. However, a satisfactory explanation for the evolution of this behavior has never been presented. Group selection favoring the evolution of multiple mating for the maintenance of genetic variability in populations has been invoked (WILSON 1963; WOYKE 1973). In this paper, I will show how individual selection can account for the evolution of multiple mating when the genetic load associated with the sex determining system and colony population dynamics are considered.

MACKENSEN (1951) first advanced the hypothesis that sex in honey bees is determined by a single locus with multiple alleles. Estimations of the number of alleles in measured populations vary from six to 18 (MACKENSEN 1955; LAIDLAW, GOMES and KERR 1956; KERR 1967; WOYKE 1976; ADAMS et al. 1977). Individuals homozygous at this locus become diploid males. These male larvae are eaten within 72 hrs of eclosion (WOYKE 1963); therefore, they are effectively lethal. Normal males are haploid; therefore, hemizygous at this locus. A queen that mates one time with a male having a sex allele identical to one of hers will have a 50% mortality of her diploid offspring.

Mating in honey bees takes place at specific locations where drones and virgin queens from many colonies assemble (RUTTNER and RUTTNER 1966). Males in the area are attracted to flying queens and copulate with them in flight (GARY 1963). GARY (personal communication) estimated that 25,000 drones from more than 200 colonies attended one of these sites. PEER (1957) reported matings taking place between individuals from colonies more than 16.7 km apart.

Virgin queens mate with several drones while flying at these drone-congregating areas, while males mate just once and die. Estimations of the number of matings by a virgin queen on a single flight vary from one to 17 (TRIASKO 1951, 1956; TABER and WENDEL 1958; WOYKE 1960; KERR *et al.* 1962). Queens frequently make subsequent flights within several days of the first. On these flights, they may again mate with several drones (WOYKE 1960, 1964). ADAMS *et al.* (1977) estimated the total number of times a queen mates on all flights to be 17.25. Queens do not mate again after these initial flights; the sperm stored in the spermatheca will last her egg-laying life.

Honey bee colonies are comprised of one long-lived reproductive diploid female (queen), haploid males (drones) and diploid sterile workers (see WILSON 1971, pp. 94–98). The fitness of a queen is determined by her ability to reproduce by the production of reproductively successful males and the production of fertile daughters with subsequent colony division (swarming). The number of males produced by the queen is correlated with the colony worker population size (FREE and WILLIAMS 1975), which is a function of the viability of the diploid brood. Colonies with small populations rear very few or no drones. A positive correlation ($r = 0.54$; $P < 0.05$) exists between the amount of worker brood reared in a colony and the amount of drone brood produced (PAGE, unpublished).

When a colony swarms, a new queen is reared in the parent nest and the old queen leaves with approximately half of the adult workers and establishes a new nest. The success of the daughter colonies after division is a function of the number and age distribution of workers at the time of colony division. The relevant parameters affecting fitness as a result of swarming are: (1) the rate at which a colony can increase its worker population and divide, (2) the size of the colony at the time of the division, and (3) the timing of colony division to best exploit the seasonal resources for colony growth and maintenance. The effect of brood production on the relevant fitness parameters in honey bees does not suggest a linear relationship.

THE MODEL

This model consists of 2 parts: the first examines individual fitness as a function of diploid brood viability and the second looks at the probabilistic effects of mating behavior on individual fitness.

Estimation of fitness: SAKAGAMI and FUKUDA (1968) analyzed seasonal colony size increase based upon worker life-table studies and the worker brood-rearing data of NOLAN (1928). They found the growth curve for this colony to be similar to the logistic growth curve. Data points extracted from Figure 2 in SAKAGAMI and FUKUDA (1968) fit a logistic curve with parameters: $N_{\max} = 50,000$; $b = 0.068$; and $c = 85$ days (see equation 1 for explanation of symbols). Adult longevity estimates during colony expansion periods range from 28 to 32 days for temperate bees (SAKAGAMI and FUKUDA 1968) and 12.1 to 21.8 days for

tropical bees (WINSTON 1979). The size of a colony at the time of colony division can be estimated from the logistic growth equation:

$$N_{(t)} = \frac{N_{max}}{1 + \exp - b(t-c)} \tag{1}$$

where: $N_{(t)}$ = colony size at time t ; N_{max} = maximum population possible = maximum viable egg laying capacity of the queen times the average life expectancy of a worker; b = the rate of maximum potential increase in colony size; t = time; and c = the inflection point in units of time.

Brood production data are useful for determining both the rate of increase in individual numbers (dN/dt) and the total colony size. NOLAN (1925), ALLEN (1965), NELSON and JAY (1972), WINSTON (1979) and PAGE (1980) presented the seasonal brood-production data for Somerset, Maryland; Aberdeen, Scotland; Winnipeg, Manitoba, Canada; Kourou, French Guinana; and Davis, California, respectively. Colony size increase begins at different times of the year in these different areas, but the curves themselves are similar. In temperate regions, brood rearing is initiated following a winter lapse and undergoes a rapid expansion that peaks in about 100 days. In tropical areas, this peak occurs about 50 to 90 days after the initiation of brood expansion (WINSTON 1979).

Swarming is seasonal and occurs at or before the time peak worker brood production is reached. Consequently, colonies swarm during the period of rapid colony size increase, not at the peak colony size (see Figure 1). Differences in

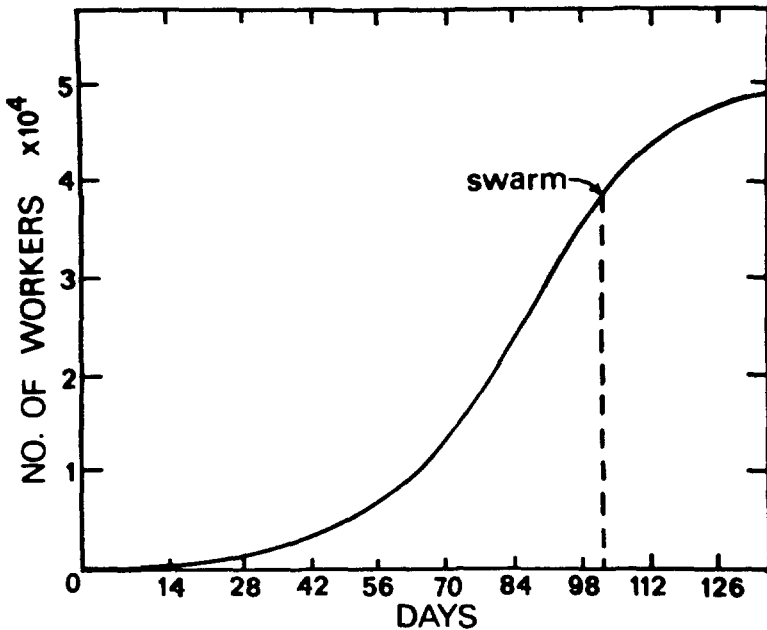


FIGURE 1.—The relationship between colony growth and swarming. Swarming occurs during the period of rapid colony growth; therefore, colonies that swarm do not reach N_{max} . (Modified from SAKAGAMI and FUKUDA 1968.)

the amount of brood reared through time as a result of homozygous lethal sex alleles can cause even greater differences in the number of adult workers at the time of colony division.

The size of the colony at the time of division is important in temperate areas with respect to the speed with which daughter colonies can increase and provision the nest for overwintering, and for expansion and subsequent colony division in the tropics. The size of a colony is dependent upon the viability of the brood produced by the queen. The time required for colony expansion to colony division is a function of the number of workers and their age composition (WINSTON 1979). Figure 2 shows the relationship between colony size at the beginning of the growth cycle and the colony size attainable in a given time period. By transforming equation (1), the equation relating $N_{(t)}$ to the initial starting colony size (N_0) is:

$$N_{(t)} = \frac{N_{\max}}{1 + \left[\left(\frac{N_{\max} - N_0}{N_0} \right) e^{-rt} \right]} \quad (2)$$

The size of the colony at time (t) is not linearly proportional to the initial population (N_0). Larger starting colonies have disproportionately more adult work-

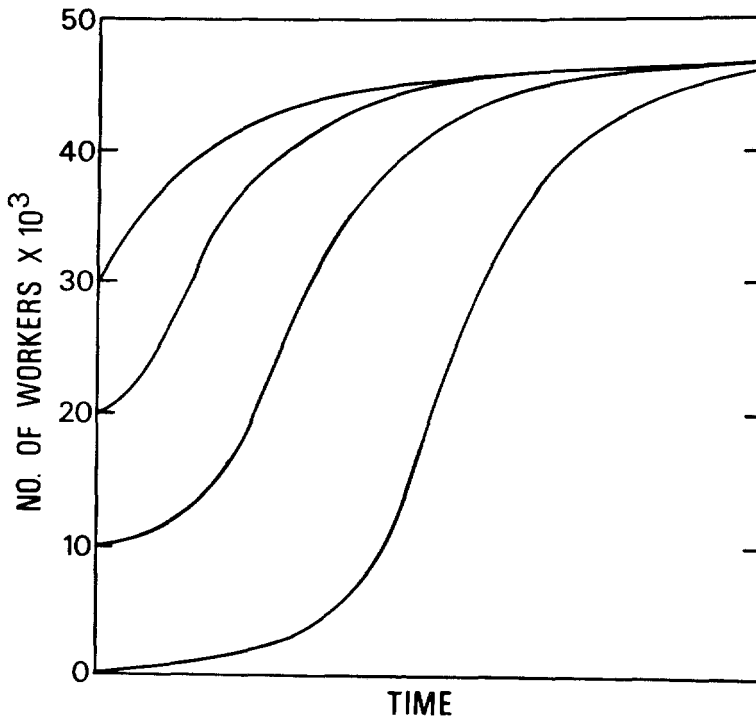


FIGURE 2.—The relationship between the initial number of workers in the colony (N_0) and the number of workers at time t ($N_{(t)}$) when $t > 0$ is not a simple linear function.

ers throughout their development to the time of colony division, can produce more males and yield larger daughter colonies.

The amount of brood present in a colony is a nonlinear function of the number of adult workers present to care for it (NELSON and JAY 1972; VILLUMSTAD 1977; GAROFALO 1977). Inviabile brood occupies needed brood nest area in rapidly expanding colonies. The net result of brood mortality due to homozygous sex alleles is a decrease in N_{\max} and a decrease in b . This will lead to a slower rate of colony expansion, with fewer colony divisions during a season in multivoltine populations, a lower production of reproductive males, a lower seasonal food productivity and decreased ability to survive unfavorable seasons.

Colony food-hoarding behavior increases the fitness of a queen by increasing colony survival during unfavorable seasons and by providing the nutritional requirements for larger populations of workers and drones. FARRAR (1937) showed that the average quantity of honey stored by an individual worker increases with an increase in colony size. FARRAR (1931) also showed an 8- to 20-fold increase in colony foraging activity with an increase in colony size of about 3-fold. Colonies with greater stores of honey and pollen have a larger number of workers in the spring (FARRAR 1936). NELSON and JAY (1972) showed that larger initial spring colonies build up faster than smaller ones and store more honey in seasonally marginal years.

Multiple mating model: Female honey bees are heterozygous at the sex-determining locus. In the population, there are 2 classes of sex-determining alleles with respect to an individual reproductive female: those that are identical and those that are nonidentical. If we assume that all alleles are at equal frequency in the population (WRIGHT 1939, 1965; ADAMS *et al.* 1977), then the proportion of alleles that are identical to an individual female (p) is:

$$p = 2/K \tag{3}$$

and the proportion that are nonidentical (q) is:

$$q = 1 - p \tag{4}$$

where K = the number of alleles in the population.

If we assume random mating and a very large male population, then the probability distribution for a queen mating with y males having alleles identical to her will approximate the binomial:

$$P_{(x=y)} = \binom{n}{y} p^y \cdot q^{n-y} \quad y = 0, 1, \dots, n, \tag{5}$$

where n = the total number of matings by an individual queen and y = the number of males with which she mated that have sex alleles identical to hers.

The proportion of viable diploid brood produced by a queen is dependent upon the total number of matings and the number of matings with males having matching sex alleles. For n matings, individual diploid ($2N$) brood viability (V) is:

$$V = 1 - y/2n \tag{6}$$

It is interesting to note, however, that the mean viability of $2N$ brood (\bar{V}) for all reproductive females in the population is dependent only upon the number of alleles maintained:

$$\bar{V} = (K - 1)/K . \quad (7)$$

If we assume no inbreeding or migration, then the number of alleles maintained is dependent upon the effective population size and the rate of mutation (KIMURA and CROW 1964; YOKOYAMA and NEI 1979). The effect of multiple mating is to decrease the variance in $2N$ brood viability between colonies in the population (SKASKOL'SKII 1968; ADAMS *et al.* 1977).

The previous considerations strongly suggest that the fitness of the queen is not related in any simple way to the viability of diploid brood. Fitness increases as a function of increasing brood viability, and almost certainly this relationship is not linear. Since this relationship is not linear, let us use a function that is geometrically versatile where we can examine the effects of concave, convex and sigmoid relationships of viability to fitness. The logistic function where fitness (W) is a function of viability (V) has the desired characteristics when the inflection point is varied. This choice of the logistic function in no way implies that it was derived from the logistic growth of the colonies or that any apparent relationship exists between them. The form of the equation for this model is:

$$W = \frac{a}{1 + \exp - b(V-c)} , \quad (8)$$

where: W = the fitness of an individual reproductive female; $a = 1$, the upper asymptote for fitness; $b = 20$, the slope of the curve; c = the inflection point in units of viability; and V = the proportion of viable $2N$ brood (see equation 6 and Figure 3).

The fitness of an individual mating n times is considered to be zero when the $2N$ brood viability is 0.50. Colonies losing half of their brood do not build up sufficiently to swarm or to rear drones and are likely to replace the queen with a new one; therefore, that queen will have a net reproductive success of zero.

The average fitness of a genotype that specifies mating n times (\tilde{W}) is equal to:

$$\tilde{W} = \sum_{y=0}^n P_{(y=y)} \cdot W \quad y = 0, 1, \dots, n \quad (9)$$

$$\tilde{W} = \sum_{y=0}^n \frac{\binom{n}{y} p^y \cdot q^{n-y}}{1 + \exp - 20 \left[\left(1 - \frac{y}{2n} \right) - c \right]} . \quad (10)$$

RESULTS AND DISCUSSION

The exact relationship of brood viability to individual fitness is not known; however, the logistic growth function provides us with a versatile estimator. The

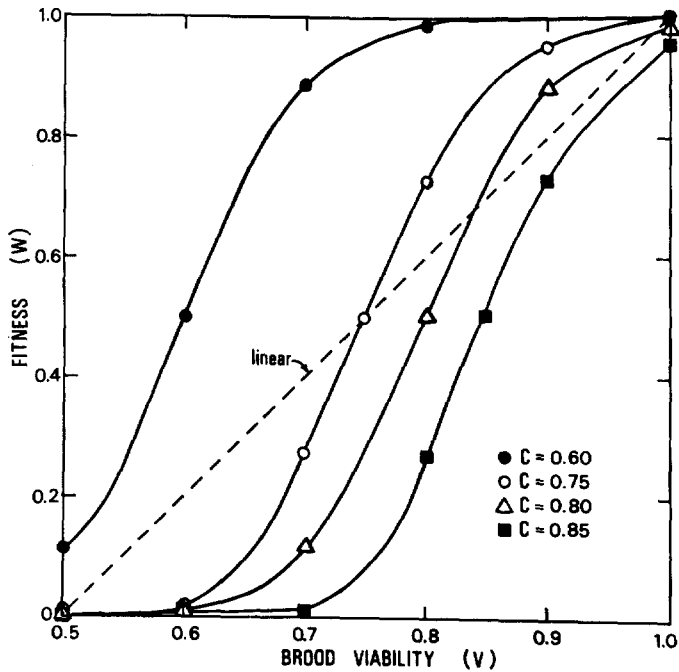


FIGURE 3.—The logistic growth function provides a geometrically versatile fitness estimator when the inflection point (c) is varied.

inflection point (c) for this function can be varied to investigate the effect of variations in the fitness estimator for this model (see Figure 3). Table 1 shows fitness estimations (\tilde{W}) for the case $c = 0.60$ with one, five, 10 and 20 matings for populations with three, five and 10 sex alleles. In all cases, selection will favor an increase in the number of matings.

Table 2 shows \tilde{W} for the case $c = 0.75$. In this case, selection will favor genotypes that specify mating more times in populations with five or more alleles,

TABLE 1
Fitness estimations for $c = 0.60$

	n				
	1	5	10	20	
3	0.413	0.677	0.719	0.748	
K 5	0.648	0.918	0.953	0.969	
10	0.824	0.986	0.994	0.996	
					\tilde{W}

n = the number of matings, K = the number of sex alleles in the population and \tilde{W} = the corresponding fitness estimation. Rows (K) or columns (n) may be read. Selection on n and K will be in the direction of higher \tilde{W} values. For given K values, the direction of selection for the number of matings is determined by the direction of increasing \tilde{W} values in that row.

TABLE 2

Fitness estimations for $c = 0.75$

K	n				
	1	5	10	20	
3	0.335	0.266	0.229	0.200	
5	0.599	0.641	0.661	0.776	
10	0.795	0.879	0.914	0.934	

\tilde{W}

but will select for fewer matings in those populations with three or fewer sex alleles.

Table 3 shows \tilde{W} for $c = 0.80$. If we assume this estimator, then a population with five or fewer alleles will select for genotypes mating fewer times, while populations with ten or more sex alleles will be selected for more matings. Calculations with $c \geq 0.85$ show that selection will always favor fewer matings (with a limit of one) regardless of the number of alleles in the population. For $c \leq 0.60$ selection always favors more matings for $K \geq 3$.

If we assume that the relationship of V to W is a linear function, there is no change in fitness with changes in the number of matings (Table 4). This shows the lack of robustness of the linear model since any departure from linearity will result in selection favoring more or fewer matings per female.

This model shows that natural selection operating at the level of the individual can adequately explain the evolution of multiple mating behavior by queen honey bees. Group selection need not be invoked. The fitness (\tilde{W}) of a given genotype is a function of the number of alleles in the population, the number of matings by an individual female and the specific parameters that determine the relationship of brood viability to individual fitness. Knowledge of the exact parameters determining this relationship is not necessary to show the potential for selection. All nonlinear relationships result in selection for either fewer or more matings.

This individual selection model may also be useful in explaining the widespread occurrence of multiple insemination in other social Hymenoptera. If we assume a multiple-locus model for sex determination (CROZIER 1977), then the

TABLE 3

Fitness estimations for $c = 0.80$

K	n				
	1	5	10	20	
3	0.329	0.180	0.124	0.096	
5	0.590	0.506	0.503	0.501	
10	0.786	0.791	0.826	0.851	

 \tilde{W}

TABLE 4

Fitness estimations for the linear model

	n			
	1	5	10	20
3	0.667	0.667	0.667	0.667
K 5	0.800	0.800	0.800	0.800
10	0.900	0.900	0.900	0.900

 \tilde{W}

case for the honey bee is simply a variation where there is only one locus with multiple alleles segregating in the population. When two or more loci are segregating, an individual must be heterozygous at one or more of them to be a female. Selection will still favor multiple alleles at each locus and multiple mating; however, the associated genetic load will be reduced. In those cases where diploid males are very rare, one expects fewer matings by females. Single and multiple mating behaviors are common in females of different groups of Hymenoptera (WILSON 1971). Diploid males have been found in nine different genera of Hymenoptera, six of them social, of which only two clearly fit a single-locus sex determination model (CROZIER 1977). With variation in mating behavior and in the number of sex-determining loci segregating, it should be possible to test this hypothesis.

This model provides an evolutionary explanation for the mating behavior of queen honey bees that may be generalizable to other social Hymenoptera. A nonlinear relationship between worker brood viability and fitness, and a significant genetic load associated with the sex-determining system are the essential components of this model.

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