I. INTRODUCTION

A. The Central Question of Altruism

Social insects are of special interest to biologists for three reasons:
1. Ecological

Insects in colonies often have dramatically different ecological impact than comparable numbers of closely related solitary insects. Army ants, for example, can prey on much larger animals than solitary hymenoptera of the same size. Mounds of ants and termites are a conspicuous feature of some landscapes. The concentrated brood and foodstores of some insect colonies may affect the foraging patterns of other animals and may even alter the array of organisms which can survive in the habitat.

2. Behavioral

The distinct polyethism within highly developed insect colonies and the spectacular cooperative foraging of certain insects, e.g., army ants and *Apis mellifera*, are well known.

3. Evolutionary

The altruism of some members of an insect colony raises the question of how it is possible for traits to be retained and passed on which decrease the probability that their bearers will leave progeny. As indicated by the following famous quotation, Darwin was aware of this apparent contradiction and recognized its importance.

"I will not here enter on these several cases, but will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory. I allude to the neuters or sterile females in insect communities. Charles Darwin, *The Origin of Species*, 6th edition.

This question, the principal subject of this chapter, can then be said to be as old as the theory of evolution by natural selection.

"Altruism" in the biological sense is the tendency, given alternate possibilities, to behave toward another organism in such a way as to increase the other's classical fitness to the detriment of the classical fitness of the acting individual. "Classical fitness" indicates (absolute) fitness in the usual sense of an index of the number of offspring surviving to reproductive condition; it is used here to distinguish it from "inclusive fitness," which will be introduced in Section II, B on kin selection. The opposite tendency to altruism is called "selfishness."

Examples of altruism in insects include sting autotomy in some hymenoptera, the tendency of soldiers to place themselves in positions of danger in response to alarm pheromones, the nonoviposition of physiologically capable subordinate females in some species, and defense by suicidal abdomen bursting in workers of the ant *Camponotus saundersi* (Maschwitz and Maschwitz, 1974). Such behaviors are altruistic, as the reproductive potential of the actors is not exactly zero, although they may only rarely leave progeny. Even where caste differentia-
tion is so far advanced that workers are strictly sterile, it is assumed that this is a derived condition, so that altruism remains an issue. The evolution of such differentiation among cooperating individuals is generally seen as a major step in the evolution of eusociality (the most advanced stage in insect sociality, in which groups contain adults of more than one generation and have cooperative brood care and reproductive castes) (See also Chapter 1 for a more comprehensive definition of insect sociality.) The central question of theoretical socioentomology today is "how can natural selection possibly favor such behavior?" Three major answers to this question exist and each is discussed in Section II.

**B. The Superorganism Concept and Its Failure**

Before examining present theory, an historical diversion will serve to emphasize the evolutionary oddness of altruism in animal societies. From about 1911-1950 (Wilson, 1971) much attention was directed to organizational similarities between insect colonies and metazoan organisms, such that the insect colony was seen as a "superorganism" (Wheeler, 1911; Emerson, 1950), with its various members analogous to the cells or tissues of a metazoan body. The ways in which metazoa accomplish their various functions can be analogized with the carrying out of these functions on the colony level by the individual members. It is an amusing pastime to explore the considerable lengths to which the analogy can be taken.

Among the salient features of metazoan organisms which exist in social insects at the colony level are: (1) import, export, and internal transport of materials; (2) control of the inner environment, including water balance and (in homeotherms) temperature; (3) response and orientation to the external environment; (4) negative entropy, i.e., a tendency to higher (somatic or social) organization in resistance to the general trend toward increasing randomness; and (5) replication.

The question of replication of the organismic or superorganismic unit is of special interest. In the superorganism concept, the reproductive and sterile members of a colony are analogous to the germ and somatic cells of the metazoan body. As in metazoan evolution, the evolutionary trend in insect societies is for progressive distinction and determinism of reproductive and nonreproductive units. This is reflected in the dichotomy we draw between "primitively" eusocial (one characteristic of which is usually the absence of distinct reproductive castes) and "highly" eusocial (with clearly distinct castes); this may be semantically unfortunate, but there is no biological reason to object to it.

What, then, are the uses to which the superorganism analogy has been put? Has it "paid for itself"? One can imagine two potential uses:

1. Examination of similarities can throw light on the evolutionary forces which produce analogous features and trends, giving rise to predictions about as yet unknown features and trends in one or the other. To my knowledge, this has
been done only once in the decades that the superorganism was a prominent concept (Lüscher, 1953). Lüscher and his colleagues, considering caste determination in termites as a problem in superorganism embryology, generated testable hypotheses regarding the critical period in the metamorphosis of nymphs into adult forms.

2. Examination of salient differences can lead to the exploration of unique features. According to Emerson (1950), the most obvious difference is the lack of a nervous system analog in the superorganism (though this is also lacking in many primitive Metazoa, and all plants); and Schneirla (1946) pointed to the nature of communication, the existence of castes, and the absence of tradition in the insect colony as outstanding features. Surprisingly, what these and other authors of the time failed to explore was the most striking difference of all: the imperfection in the analogy between the somatic cells and worker individuals, on the one hand, and germ cells and reproductives, on the other. In the metazoan body, somatic cells are genetically identical; the probability is small that two given members of an insect colony will be identical. This creates a basis for competition and natural selection among individuals. If it were not for this difference, then caste differentiation in insects would be unremarkable from an evolutionary standpoint and could be expected to be much more common. Some animal groupings sometimes described as social, such as migratory groups, mating swarms of insects, or nesting colonies of seabirds, have no reproductive division of labor and pose no special genetic problem in this regard. Historically, the superorganism concept has not been used to illuminate this dissimilarity as a basis for seeking solutions to Darwin's dilemma. This constitutes the special failure of the concept.

II. THEORIES ON THE ORIGIN OF SOCIALITY

Theories on the origin and evolution of insect sociality are attempts to account for this feature of "superorganisms," although each has arisen apparently without the benefit of the superorganism concept. Three main theories have been put forward; they are usually known by their special mechanisms: (a) group selection, (b) kin selection, and (c) parental manipulation. These theories will be discussed in the approximate historical sequence in which they were developed, simply because the arguments of each are made with its predecessors in mind. It should be emphasized that the following is a review of theory, not of the literature, so that some historically influential contributions are not mentioned. An additional competing theory for the evolution of eusociality in most bees, the semisocial or mutualistic pathway, is discussed later as a special question. I have not accorded it the same status as the theories mentioned above, because it lacks, in my opinion, their generality, completeness, and clarity.

A. Group Selection

Beaumont (1945) presents a good summary of theory of social evolution of that time. Two main ideas were in discussion.

Roubaud's (1916) hypothesis centered on the primacy of trophallaxis (exchange of alimentary fluids between individuals); newly emerged hymenopterous females are retained in the parental nest and induced to help rear their mother's brood by the attraction exerted by alimentary secretions of these larvae.

Legewie (1924-1925) correctly posed the question as one of selection to overcome the obstacle of "broodegoism," the tendency to rear one's own brood and no other. His hypothesis revolved around the "hypogentialism" of some daughters, i.e., the incomplete development of the reproductive apparatus and concomitant suppression of sexual behavior in favor of maternal behavior. This idea is a precursor to each of the theories discussed below. Like Roubaud's though, it did not address the central genetic question of how it could possibly benefit an individual to subordinate its classical fitness to another.

1. Classical Group Selection

The answer provided by the group selection theory is unequivocal: it doesn't. It benefits the survival and fitness of the group as a whole, but at the expense of the individual altruist. The trait may persist and spread if the benefit to the group is great enough. Numerous papers have explained the possible workings of group selection, but until recently all well-developed models had the same basic mechanism and requirements. A general scenario for such "classical" group selection is as follows (Gilpin, 1975; Levins, 1970; Wynne-Edwards, 1962; among others):

A species comprises small localized populations with little gene flow between them.

Such populations usually contain both altruistic and selfish individuals.

Selfishness, by definition, confers greater individual fitness, so that it spreads rapidly toward fixation in the population.

Populations of mostly selfish individuals are disastrously unfit (sources of unfitness are discussed below) and become extinct.

The extinction of a selfish population leaves its home range open to immigration from another population.

If the new population is made up solely of altruists (through founder effect or genetic drift), it can persist and will later be in a good position to send out propagules to recently vacated home ranges.

If one or more selfish individuals appear in this altruistic population through mutation or immigration, the selfish trait will spread, leading to extinction of that population.
It should be noted that this strictly materialistic conception has nothing to do with any hypothetical "social appetite" or with romantic notions of a willingness to sacrifice for the good of the species; these are still rather widespread, even among biologists.

Classical group selection was first proposed by Carr-Saunders (1922) as a method of population control in primitive human cultures. The maintenance of altruism in Carr-Saunders’s model was cultural, not genetic, but the mechanism of differential extinction of groups of selfish individuals is the same as in the above scenario. Group selection was later extended to animals by a number of early authors, including Haldane (1932), Sturtevant (1938), and Wright (1945). Its most complete examination to date has come from Wynne-Edwards (1962) in a polemic which at least mentioned most animal groups and dealt with a broad variety of behavior.

Although Wynne-Edwards’s model conformed to the above scenario and is a possible case of Sturtevant’s general model, the immediate causes of group extinction in each are opposite. Sturtevant’s model was developed to account for the existence of multiple queens (fertile, egg-laying females) in nests of *Formica rufa* and *F. exsectoides*, which arises through the adoption of newly mated queens by established colonies. Sturtevant hypothesized that the colony depends for its survival on a series of queens, not necessarily closely related, a phenomenon later known as "serial polygyny," so that the colony has greater longevity than any one queen. Colonies disinclined to adopt foreign queens would be less fit and subject to supersedeure by immigrants from adopting populations. Selection would operate on an individual queen in such a colony to advance her fitness at the expense of others, by increasing the ratio of sexuals/workers in her progeny. Such a selfish trait could be expected to spread rapidly through the population over generations until the demands of the sexual brood in most colonies overburdened the diminished work force. The population would have lowered productivity and its home range would be open to immigration. Sturtevant does not specify extinction of selfish populations.

Wynne-Edwards proposed a very different source of population crash. His treatment, drawn mostly from observations of vertebrates, revolves around the dangers of population increase beyond the carrying capacity of the environment. In an analogy to human agreements to prevent overfishing, he interpreted most territorial and much other communication as "epideictic displays" to convey population density information to conspecifics. These conspecifics adjust their reproduction according to this information, thereby avoiding overpopulation, resource depletion and population crash. Social behavior, to Wynne-Edwards, consists of reproduction-limiting "conventions," which take the form of a shift in the focus of intraspecific competition, away from fitness-enhancing rewards to "conventional" rewards which are valueless in terms of individual fitness.

Wilson (1973), in a summary of models of classical group selection, distin-
guishes between (1) selection through \( r \)-extinction (due to population decline to the point where it cannot be maintained), as developed by Sturtevant; and (2) selection through \( K \)-extinction (due to population increase above the environmental carrying capacity \( K \)), as proposed by Wynne-Edwards. He notes that \( r \)-extinction is more likely in invertebrates, while \( K \)-extinction is more likely in vertebrates, and outlines the social characteristics which would be favored by each type of group selection.

\( r \)-Group selection favors "pioneer" qualities, such as clustering of the population, mutual defense, and cooperation: qualities which will serve to rapidly raise and maintain a secure population level.

\( K \)-group selection favors urban qualities, such as reproductive restraint and resource conservation. Mutual aid will be minimal.

Criticism of the invocation of group selection to account for altruism has been of two types.

First, it is unnecessary. Where the phenomena described by Wynne-Edwards (1962) can be satisfactorily explained by more conservative mechanisms (regular individual selection, kin selection, parental manipulation), the principle of Occam's razor demands that we accept these alternatives. It is often maintained (e.g., Williams, 1966) that territoriality, in particular, can be accounted for by simple individual selection.

Second, it is impossible. This is due to the restrictive conditions for its operation in nature. The following extraordinary conditions are discussed by Lewontin (1970), Maynard Smith (1964), Williams and Williams (1957), E. D. Wilson (1973), and D. S. Wilson (1975), among others.

a. Extinction Rates of Selfish Populations. Group fitness differences between altruistic and selfish populations must be of such magnitude that extinction is swift, in order for group selection (for altruism) to counteract the opposing (selfish) individual selection. This is generally the central criticism of classical group selection models, since it is doubted that extinction rates can be great enough. Tentative evidence for rapid extinction rates comes from experimental island biogeography (Simberloff and Wilson, 1969; Wilson, 1969), which has produced recolonization rates of such magnitude that the corresponding extinction rates expected by theoretical island biogeography (MacArthur and Wilson, 1967) may be high enough to power group selection.

b. Colonization Rates of Vacated Habitats. Along with high extinction rate, rapid recolonization is necessary for rapid replacement to counteract individual selection. This should not normally be a problem, given high extinction rates.

c. Migration between Populations. Although recolonization must quickly follow extinction of selfish populations, the contrary condition exists that popula-
tions must be strongly localized (Wynne-Edwards, 1963), with little gene flow between them at most times. The reason is clear: if gene flow is high, altruistic populations will constantly be "contaminated" by selfish genes. The greater the gene flow, recolonization rate being equal, the greater is the extinction rate required to counteract the increased pace of individual selection. Group selection is a stopgap strategy, a race in which the only possible outcomes for altruistic traits are defeat or postponement. If gene flow is very rapid, defeat is certain.

d. **Population Size.** Not only must populations be strongly localized, but effective population size must be small. There are three reasons for this.

First, the supposed infrequency of the establishment of pure altruistic populations requires a large number of populations in order that there may be many simultaneous experiments in altruism. Given a species with a certain number of individuals, group selection is facilitated if its distribution is "shattered."

Second, as population size increases above a very low level, the probability of an altruistic trait becoming fixed through genetic drift decreases rapidly.

Third, extinction rates of selfish populations similarly decrease with increase in size of population units (Haldane, 1932).

These conditions have been modeled by Levins (1970) and Boorman and Levitt (1972, 1973). Their general conclusion is that group selection is possible but unlikely. In any event, it is not believable that classical group selection is a general mechanism for the evolution of sociality, including reproductive castes, in insects. The interaction of group selection and extraordinary types of individual selection is discussed in Section II, D.

2. **Competitive Group Selection**

Recently, a new type of group selection not based on differential population extinction has been modeled independently by Matessi and Jayakar (1973, 1976) and Wilson (1975, 1977, in preparation). Rather, it is based on the gradual spread of the altruist gene in mixed populations through the superior fitness of populations with a higher frequency of altruists. For our purposes, a summary of Wilson's model, the "structured deme concept," and conclusions will demonstrate this type of group selection, which I will call "competitive."

Wilson's model is based on species whose life cycle is organized into a nondispersal stage, in which most ecological interactions take place, including mating, and a dispersal stage. During the nondispersal stage populations tend to be subdivided into smaller groups, called "trait-groups," which have little interaction with each other. Trait-groups are the unit of group selection. They usually contain both altruists and selfish individuals.* Dispersal, followed by

*The structured deme concept is not primarily designed to account for altruism, and in fact Wilson (In preparation) predicts the evolution of only weak altruism. It is discussed here for the relationship which it does have to altruism, to solutions it poses to some of the problems facing classical group selection, and its supposed overlap with kin selection.
mating, takes place at discrete generations, and mating is random within trait-groups. Within any trait-group the proportion of selfish individuals will increase in the new generation, but trait-groups with a greater proportion of altruists will increase relative to others (Fig. 1). Under certain conditions, the altruist gene can spread in the species or population. What are the conditions which make competitive group selection more probable than the classical model?

1. Group superiority of altruist-dominated trait groups is not based on sudden replacement of selfish groups. This precludes the necessity of high extinction rates, the main difficulty for the classical model.
2. It does not require long-term isolation of groups.
3. The presence of one or more selfish individuals in a mostly altruistic group does not constitute contamination leading to extinction, but is merely a liability.

Because altruistic group purity is unnecessary, genetic drift no longer has any extraordinary importance. The model does, however, require that at least some trait-groups in each generation be predominantly altruistic, so that it cannot operate under conditions of random (binomially distributed) or less than random

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**Fig. 1.** Illustration of the process of competitive group selection. a = frequency of the altruistic allele A; b = frequency of selfish allele B. A: nondispersal phase; B: selection; C: dispersal phase; D: reassortment into nondispersal phase. (From Wilson, 1975.)
between-group variation in trait frequencies. This is shown in Fig. 1, in which dispersal into trait-groups following mating (C) is not random, so that the right-hand trait-group remains strongly altruist dominated. If dispersal were random, the frequency of altruists in (D) would be close to \( a = 0.55 \) in each group; this would almost certainly lead to a disastrous decline in frequency \( a \) in the next generation. Classical group selection demands total between-group variation, each group being either altruistic or selfish (mixed groups are \textit{de facto} immature selfish groups). Competitive group selection operates between random variation, in which individual selection must prevail, and total variation. Reasons are given by Wilson (1977, in preparation) to expect most species in nature to have variation in this intermediate range.

There are two distinct ways in which variation can be increased above random: differential interactions with the environment and positive assortment of different types at the time of trait-group formation. Where assortment is based on kinship and trait-groups are kin groups, competitive group selection resembles kin selection (defined and discussed below). Wilson (1977, in preparation) states that in this case the two are equivalent, but this is not exactly correct; it is possible for the first to operate in kin groups without satisfying the inclusive fitness (defined and discussed below) requirement of the other.

3. Applications to Insect Sociality

Having shown how group selection is theoretically possible, it remains to be considered how it might have operated in the origin of facultative or obligate castes in insects. On the basis of present theory, group selection cannot be assigned any large role. Even given the immense difficulties of demonstrating group selection in nature, the outstanding fact is that it has rarely been invoked in accounts of the origin of insect sociality, and in no case has a strong case for its influence been made. It has been variously suggested by Wheeler (1923), Richards (1953), and Wynne-Edwards (1962) that sterile castes constitute an attempt to keep the population within the carrying capacity of the environment (\( K \)-group selection). Implicit in this is the idea that social production is less efficient than solitary production. This idea has been supported with evidence by Michener (1964), although he did not draw a group selection conclusion. Wynne-Edwards connected this to his theory of the substitution of conventional rewards for direct fitness-enhancing rewards by suggesting that fighting among spring queens in \textit{Vespula} over nest sites is actually more concerned with population regulation than actual nest site competition. The obvious weakness here is that the nest sites of the subgenus (\textit{Vespula}) to which he referred are primarily abandoned rodent burrows and other underground activities, whose abundance must vary from year to year in a way unlikely to correlate well with other spring conditions important to \textit{Vespula}, such as temperature, rainfall, and prey availability. Besides, in any situation in which insect populations are limited by
nesting availability, which may occur with *Vespula* in some years, the reward is by definition not conventional.

The existence of prominent lines of social species in the bees stands as a major contradiction to *K*-group selection. Food is the only resource which should normally be subject to regular overexploitation by social insects. Unlike the food of predators or conventional herbivores, though, pollen and nectar resources cannot be overexploited by most bees (exceptions are pollen- and nectar-robbers) in a way which damages their future availability. The foraging of bees has quite the opposite effect. While bees can theoretically exhaust all supplies available at one moment, they do not decrease the rate at which new supplies become available. They cannot, therefore, inflict upon themselves the kind of disastrous long-term population crash necessary to *K*-group selection.

The unlikely applicability of their models to social insects was recognized explicitly by Matessi and Jayakar (1976), and implicitly by Wynne-Edwards (1962) by the fact that he mentions them on only 43 of his 653 page opus and never really comes to grips with the question of their evolution.

### B. Kin Selection

#### 1. General Considerations

The question of the origin of altruism was approached in a radically different way through the development of the concept of kin selection. Kin selection can favor the individual fitness of an altruist, but in a way not envisioned by Darwin. Instead of maximizing its bearer's classical fitness, the altruistic trait spreads through behavior which increases the classical fitness of other individuals likely to have that trait, such as close relatives. If such behavior causes more copies of the gene to be produced than would selfish behavior, then it is by definition favored by natural selection. This idea has been expressed by a number of authors, including Haldane (1932) and Maynard Smith (1966), but it first received extensive treatment from Hamilton (1964, 1972, 1974). A discussion of Hamilton's results and those of subsequent authors will satisfy our purposes. This is not to ignore the value of earlier, primarily verbal formulations, but it was only with the publication of Hamilton's (1964) treatment that kinship theory began to exercise a truly revolutionary impact on social evolutionary thought.*

At the present time it is clearly the dominant theory in this subject.

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*The ascendancy of kinship theory over the last 10 years does not constitute a scientific revolution in the strict sense of Kuhn (1962), of having provided a paradigm to replace an earlier paradigm in scientific acceptance; in fact, none existed to be overthrown. Rather, it is revolutionary in the sense of having radically altered the aspect of social evolutionary theory, somewhat similar to the way the development of gel electrophoresis has brought about a "revolution" in population genetics during the same decade.*
They key to the operation of kin selection and the cornerstone of its impact on evolutionary thought is the concept of inclusive fitness. The inclusive fitness \( W_{IA} \) of an individual A is equal to

\[
W_A + \sum \delta W_C \cdot \left( B_{AC}/B_{AA} \right)
\]

where \( W_A \) is A's classical fitness, \( \delta W_C \) is the full effects of A's behavior on the classical fitness of another individual C, \( B_{AC} \) is the coefficient of relatedness between A and C's offspring, and \( B_{AA} \) is A's relatedness to its own offspring. Where two individuals have the same ploidy, relatedness between them is between 0 and 1. Where production is sexual and diploid, and in most other cases, \( B_{AC}/B_{AA} = B_{AC} \), A's relatedness to C; a theoretically important exception occurs in the Hymenoptera.

The expression \( \sum \delta W_C \cdot \left( B_{AC}/B_{AA} \right) \) is called the inclusive fitness effect (Hamilton, 1964; the kinship component of West Eberhard, 1975). Verbally, A's inclusive fitness effect is its effect on the classical fitness of each other individual C, multiplied in each case by the ratio

\[
\frac{A's\ relatedness\ to\ C's\ offspring}{A's\ relatedness\ to\ its\ own\ offspring}
\]

Kin selection is defined here as selection on the inclusive fitness effect. This is slightly different from the original definition (Maynard Smith, 1964) as "selection for characteristics which favor the survival of close relatives of the affected individuals," which is in most cases an operational form of the definition used here. When defined in terms of the inclusive fitness effect, it is clear that the focus of kin selection is the individual, so that it is not a form of group selection, contrary to the view of Brown (1966) and Wilson (1973). Inclusive fitness can be viewed and manipulated like classical fitness, and throughout the rest of this chapter "fitness" will imply inclusive fitness and will be used where there is no need to distinguish between the two.

The central principle of kin selection theory is the general expectation that each individual will behave in such a way as to maximize its inclusive fitness. Altruism is expected in all cases where the decrease in classical fitness is offset by a greater increase in the inclusive fitness effect. Or, as Hamilton (1964, 1972, 1974) has expressed it, the individual concerned will behave as if weighing the

*To avoid confusion, I use the subscript C where other authors use \( B \), as the kinship coefficient used is \( B \) (Hamilton, 1972), rather than the more commonly used \( r \). Subscripts for \( B \) will not be used except where necessary. For most of this discussion, \( r \) and \( B \) are interchangeable. Derivation and properties of these and other coefficients of relatedness and relationship are discussed by Crozier (1970), Hamilton (1972), and Orlove (submitted).
ratio of (benefit to the other)/(cost to itself) against probable relatedness. An altruistic act will be adaptive if
\[ K > (1 + F_A) \frac{B_{AA}}{B_{AC}} \]

where
\[ K = -\frac{\delta W_C}{\delta W_A} \]

and \( F_A \) is the inbreeding coefficient of A. Verbally, \( K \) is the ratio
\[
\frac{\text{increase in C's classical fitness as a result of A's actions}}{\text{decrease in A's classical fitness as a result of A's actions}}
\]

\( B \) is usually calculated simply by reviewing the pedigree of affected individuals back to the most recent common ancestor. If it is necessary to go back more than a small number of generations, \( B \) is conveniently set at 0 if inbreeding is small. Unless otherwise stated, inbreeding will be discounted, as a simplifying assumption, in subsequent discussion and calculations.

The inequality (1) was first formulated by Hamilton (1963) in the form \( k > 1/r \), in which \( r \) is Wright's coefficient of relationship and is for our purposes interchangeable with \( B_{AC} \).

In diploid organisms, \( B \) between full siblings is 1/2, between an individual and its nephew or niece it is 1/4, between cousins it is 1/8, etc. Any individual should then be willing to be altruistic toward one or more full siblings as long as \( K > 2 \), but toward cousins only if \( K > 8 \). Similarly, it will turn down an opportunity to rob fitness from a full sibling (this constitutes a special form of altruism) if the benefit to itself is not greater than half the loss to the sibling, while it will rob from a cousin as long as it gains at least one unit for every eight lost by the cousin.

Hamilton (1964) has raised the question of selection for social discrimination, the ability to distinguish between close relatives and others, and between individuals of high and low reproductive potential. Social discrimination by potential altruists has obvious adaptiveness in environments with individuals of various relatedness and reproductive potential. Social discrimination of relatedness is generally more a subject of discussion of vertebrate societies than in the large anonymous societies of highly social insects, but social insects do behave differently toward different conspecific individuals, although strict individual recognition is probably rare. Ant workers, for example, behave very differently toward nest mates and foreigners in most cases (although cases of widespread nondiscrimination are known). Within societies, workers differentiate between other workers and the queen, who may be more closely related to them but who certainly has greater reproductivity. Evidence for relatedness discrimination in
primarily eusocial sweat bees has recently been reported by Barrows *et al.* (1975) and Kukuk *et al.* (1977). In particular, Kukuk *et al.* present indirect evidence that closely related individuals are recognizable by genetically mediated odors.

In viscous populations, individuals may behave as if any other encountered in the home range has a B characteristic of the average for that area, while individuals encountered outside the home range are treated as having the lower B characteristic of the entire population. This sort of discrimination may be operating in spring foundress groups of some social wasps of the genus *Polistes*, which generally aggregate at the parental nest prior to nest founding (West Eberhard, 1969). A wasp will “assume” that any other in the group at its parental nest is a sister and behave appropriately. It is altogether reasonable, given the basic statement of kin selection theory, that, in the absence of direct ability to assess the relatedness of individuals, selection should favor a lower level of intolerance or selfishness toward the population as a whole in more viscous populations with higher average relatedness than in less viscous populations. In *Polistes exclamans*, nest founding is often cooperative in the more southern and western parts of its range in the United States, and rarely so in the northern and eastern parts. West (1968) reasoned that solitary nest founding leads to greater dispersal in each generation and lower population viscosity. Kinship theory would predict, other things being equal, a greater tendency to rob from neighboring nests and greater aggression toward conspecifics away from the nest in the more northern and eastern parts of the range, and also that migration of individuals between nests will be less common. This is a crude and indirect form of social discrimination compared to that practiced in many vertebrate groups, but it can function to fit altruistic/selfish tendencies to the expected B.

2. Kinship Asymmetries in Hymenoptera

The impact of Hamilton’s ideas is heightened by the attention he has drawn to the haplodiploid sex determination system of the Hymenoptera and the novel predictions which can be made on the basis of the asymmetries of relatedness arising from this system.

In the most widely accepted scheme for the evolution of sociality in the Hymenoptera (see Section III, D, 1), the crucial stage comes when some daughters, rather than leaving the parental nest to found their own nests, remain to aid their mother in raising further offspring. This is the stage at which altruism has arisen. How can we account for this phenomenon? Hamilton (1964, 1972, 1974) provides a striking answer to this question by pointing out that, due to male haploidy, a female is related to her full sister by $B = 3/4$, as the half of the genotype of each which comes from their father is identical, while she is related to her daughter by only 1/2 (Fig. 2). She can maximize her inclusive fitness by forsaking the production of daughters in favor of increasing her mother’s production of
Fig. 2. Diagram for the calculation of relatedness in the Hymenoptera under outbreeding. Full squares are females, half squares are males. First generation at the top. Rules for calculating relatedness: (1) If the two individuals in question are a male and his descendant, a female and her son, or a female and a descendant through her son, add up fractions of a full square for which they have identical shading. This is the fraction of a diploid genotype which they have in common. For example, the individuals marked y have 1/4 diploid genotype in common. From the male’s viewpoint, $R = 1/2$, from the female’s viewpoint $R = 1/4$. (2) If between two sisters marked x, $B = 3/4$. If between one of these and offspring of other, $B = 3/8$. If between one of these and grandoffspring of other, $B = 3/16$. etc. (3) All other cases: add up area with identical shading, multiply by 1/2.

daughters, as long as she increases her mother’s production by more than three units for every four units which she herself fails to produce ($K > 3/4$). Hamilton and others have drawn attention to this relationship as a possible explanation for the fact that eusociality has arisen at least 11 times in the Hymenoptera and probably only once, in the termites, in all other insects. Haplodiploidy exists in few other taxa of animals, and in no other is there reason to expect preconditions for sociality.

Differences in male and female genetic "viewpoint" brought about by asymmetries of relatedness provide a basis for other predictions and explanations. The following are some outstanding examples from bhamilton (1964) and Wilson (1971):

1. Male workers are not expected. Unlike females, males are less related to sisters or brothers ($B = 1/2$) than to daughters ($B = 1$; Fig. 2), so that there is no genetic basis for the habit of aiding their mothers in producing siblings of either sex. There is also no basis for males aiding their mates; while a male is related to his daughters by 1, he is unrelated to his mates’ parthenogenetically produced sons, and unless he can discriminate the sex of larvae, brood care is a poor investment (Hamilton, 1971). Male worker castes are unknown in the Hymenoptera and male brood care or other "work" is rare and often apocryphal.
Kinship theory expects workers of both sexes in the termites, and this is of course the case. There is some question of the likelihood of male workerness* in hymenoptera even in the presence of selection for it, as the behavioral prerequisites are virtually unknown among males of solitary species.

2. A female will prefer raising her own offspring to helping sisters to raise theirs. A female is more related to her offspring \( B = 1/2 \) than to nephews and nieces \( B = 3/8 \); Fig. 2).

3. A female will prefer to raise sons \( B = 1/2 \) rather than brothers \( B = 1/4 \). The strongest evidence for this is the general retention of a functioning reproduction in workers, even in species in which mated workers are unknown or rare (see Lin and Michener, 1972, for references), and the habit of honey bee workers laying male-producing eggs upon the removal, death, or decline of the queen is well known.

4. Single mating by females will be the rule. This is conspicuously not the rule in highly social hymenoptera (see Wilson, 1971, Ch. 17, for references) and appears to constitute a testing drawback to the kin selection principle. With multiple matings by queens, the extraordinary relatedness of sisters disappears (Fig. 3), while mother–daughter relatedness is unaffected. This problem will be dealt with separately below.

3. **Special Factors**

Hamilton (1964, 1972, 1974) has dealt mainly with the right-hand part of the inequality

\[
K > (1 + F_A) \frac{B_{AC}}{B_{AS}}
\]

and its derivatives. Reproductive potential of interacting individuals is assumed to be equal, and in his manipulations he has generally treated \( K \) as equal to 1. As recognized by Hamilton, this simplifying assumption is not a general case, and variation between individuals provides a basis for values of \( K \) greater than 1. The implications of such values of \( K \) and the situations in which they can arise have been most completely developed by West Eberhard (1975). We will discuss here the effects of different values of: (1) Benefit to the recipient \( C \) (the numerator in \( K \)) and cost to the actor \( A \) (the denominator in \( K \)), (2) inbreeding; and (c) closeness of relatedness.

a. **Benefit to Recipient \( C \) and Cost to Actor \( A \).** West Eberhard (1975) discusses three ways that \( K \) \( = - \delta W_c / \delta W_A \) can be increased to levels where altruism is favored at low \( B_{AC} \)

*"Workerness" here refers to the state of being of the worker caste. It is not equivalent to "workerliness," the state of being workerlike. An analogous and more important distinction is made between "queenness" and "queenliness."
i. The recipient C has much to gain. Or it has much to lose if aid is not forthcoming. Such a situation in social insects can be sought at the time of nest founding or under emergency conditions. Lin and Michener (1972) have discussed the high value of cooperative nest defense in the early stages of colony development in ground-nesting bees. West Eberhard gives as an example of emergency altruism the tendency under colony nutritional crisis of some gynes* of the social wasp *Metapolybia aztecoides* to become workerlike foragers.

ii. The donor has little to lose, or little to gain by robbing from C, so that the cost of altruism is low. West Eberhard calls this “cheap aid.” In the example cited above from social wasps, there is evidence that the gynes which become foragers are those with the lowest reproductive capacities, so that they have the least to lose by becoming more workerlike (though they also would appear to have the least to lose by letting the larvae starve, if they have been laying fewer eggs). Similarly, H. R. Hermann and I (personal observation) have noted that individual readiness to attack in *Polistes annularis* is inversely correlated with behavioral queenliness. At extraordinary high $K$, any above-average $B$ can favor kin-selected altruism. In cases where $W_A = 0$, through complete sterility or lack of opportunity, $K$ is infinitely large if $\delta W_C > 0$. The example is given by Lin and Michener (1972) and West Eberhard of the tendency of army ant workers which have lost their queen to join any conspecific colony which they encounter; it is assumed that army ant populations are viscous enough that the workers’ relatedness to any such colony is significantly above average. Unless it can be shown, though, that this is a frequent phenomenon, I doubt that it could have the impact for selection to act and would suggest that such joining is merely an “accident.”

iii. A small amount of aid has a large effect. This is dependent not on an emergency situation, but on extraordinary abilities of the individuals involved. It can arise either through the evolution of donors which are especially efficient at giving aid (“superdonors”) or recipients which are especially efficient at utilizing it. In the case of the highly social insects, the queens and workers are each highly derived forms, and one has only to think of ecitonine army ants, in which the workers not only have little to lose (low $\delta W_A$), but are especially efficient at accomplishing worker tasks, while the queen during the statary phase is a highly physogastric super-egglayer (high $\delta W_C$).

b. Inbreeding. The relatedness $B$ is a function of genealogical relationship and of inbreeding in the population. In the simplest case, where the population is

*Following Michener (1974, and elsewhere), a “gyne” is a potential or actual queen. It is most usefully used for individuals whose future queenness is uncertain. Unlike Wilson (1971), then, I use “polygynous” in a broader sense than “multiple-queen.”*
outbred, $B$ can be calculated from family history alone. Figure 2 diagrammed a hymenopterous genealogy under outbreeding and gave rules for calculating $B$.

The general effect of inbreeding, as in diploid organisms, is to increase $B$ toward unity (if both have the same ploidy). Two views exist on the effect of inbreeding on the origin of altruism leading to eusociality. Hamilton (1964) generally viewed it as a factor decreasing the scope of selection for selfishness, thereby facilitating the evolution of altruism. In addition, Hamilton (1964) considered it necessary to invoke at least a mild inbreeding from population viscosity to account for some situations, most notably polygyny in polybiine wasps. Inbreeding should be neutral, though, with regards to the ratio of unrelatedness \((1 - B_{\text{daughter}})/(1 - B_{\text{full sister}})\) in Hymenoptera, which remains at 2 for all inbreeding values. Hamilton's (1972) later conclusion, supported by Trivers and Hare's (1976) more developed argument and by Starr and Duffield (In prep.), is that inbreeding will aid the development of within-colony altruism through a greater identity of interests but will not especially encourage sterility. Trivers and Hare conclude that it will actually depress the likelihood of eusociality evolving. It seems from this that high inbreeding favors a passive, or simply nonselfish, rather than an active manifestation of altruism.

One factor which makes inbreeding in the Hymenoptera appear likely a priori is the effect which male haploidy has in countering the ill effects of inbreeding. All alleles expressed are effectively dominant in males, so that any lethal or subvital ones will be exposed to selection in every generation. Males are required each generation for the production of females ("generation" is used here in the usual sense, not in its occasional sense of "brood" in species with several broods of workers every generation). Snell (1932) proposed that this accounts for the evolution of mating flights, with pairing or copulation high in the air, so that weak males or those with a poor sensory apparatus are excluded from reproduction.

c. Closeness of Relatedness. One sizeable difficulty for the "three-fourths relatedness hypothesis" for the Hymenoptera is that the key condition that all sisters have the same father is at best doubtful in most species. We are ignorant with regard to primitively social species, and it is known that this condition is frequently not met in highly social species.

The best-studied species is the honey bee *Apis mellifera*, for which Taber (1954) calculated that queens usually mate six or seven times. Taber and Wendel (1958) give a figure of seven to ten matings, with some sperm transfer in each, as usual for *Apis*. The average between-sisters relatedness declines rapidly with multiple mating (Fig. 3), and if more than two males contribute equally $B$ is less than 1/2, the relatedness between a female and her offspring, $K$, then, must rise above 1 for the principle of kin selection to obtain. If mates of the queen are unrelated, her daughters will each be related by either 1/4 or 3/4, depending on
whether they have the same father. The possibility that females can distinguish female larvae of the same father is not suggested here (however, see Kukuk et al., 1977), so that a female is expected to behave toward female brood as if \( B_{AC} = \bar{B}_{AC} \) in each case. This assumes that they can distinguish between female and male brood, or at least the cells in which they are raised, which is probably not universally true. If the mother queen produces equal numbers of daughters of \( n \) males, average between-sister relatedness

\[
\bar{B} = 1/4 + 1/2n
\]

This goes from 3/4 at \( n = 1 \) to 1/4 when \( n \) is infinitely large. This dilemma of low \( \bar{B} \) may be solved in two ways.

Between-sisters relatedness is actually higher than 1/4 + 1/2n, due to unequal contribution by males. A male can father more than 1/n of the queen’s daughters if there is either unequal sperm contribution to insemination or to fertilization of eggs. Unequal insemination can most easily arise if the first male’s sperm occupy and hold more than 1/n of the spermatheca capacity, or if the last male’s sperm forces out some of the others. Even if insemination is equal, unequal contribution to progeny will arise with either (1) variation in sperm vitality; or (2) variation in sperm distribution in the spermatheca and either (a) the spermatheca habitually holds more sperms than are used in the queen’s lifetime, or (b) the queen produces more than one distinct brood of sexuals in her lifetime. There is some scant evidence for satisfaction of condition (2). Taber (1955) reports no appreciable mixing of sperm from different males for *Apis mellifera*. With incomplete mixing, \( \bar{B} \) between a worker and the sexual brood she rears will be higher than that calculated from insemination data if either condition (2a) or (2b) obtains. Condition (2b) is well known for many social Hymenoptera, especially ants, in which the queen is long-lived and produces multiple sexual broods over an extended period.

If equal progeny contribution of males is not assumed, the between-sisters relatedness takes the more general form

\[
\bar{B} = 1/4 + 1/2 \left\{ \frac{1}{2} \sum_{i=1}^{n} f_i^2 \right\}
\]

where \( f_i \) is the contribution of the \( i \)th male (adapted from Wilson, 1971). The effects of unequal contribution can most simply be demonstrated by taking the case where the first male (or the last) makes a contribution greater than 1/n, while all others contribute equally. In this case

\[
\bar{B} = 1/4 + 1/2 \left[ f_1^2 + (1 - f_1) f_2 \right]
\]

As \( n \) becomes very large and \( f_2 (= f_3 = f_4 = \ldots = f_n) \) approaches zero, \( \bar{B} \) approaches \( (1/4 + 1/2 f_1) \). Figure 3 compares curves for \( \bar{B} \) when contribution is equal and when \( f_1 \) is 1/2, 2/3, and 3/4. The initial dropoff as \( n \) approaches 2 is not
spectacularly affected by raising of $f_1$ above $1/n$, but after that the curve "bottoms out" much more quickly at high $f_1$ and differences in $\bar{B}$ are readily apparent. As well as comparing $\bar{B}$ at different $f_1$, for a given $n$, it is interesting to compare the values of $n$ which produce a given $\bar{B}$ at different $f_1$. For example, if a honey bee queen mates equally with eight males, $\bar{B} = 5/16 = 0.31$. If, however, $f_1 = 1/2$, then $\bar{B} = 0.39$, which is also the value of $\bar{B}$ if the queen mates equally with 3.6 males. If $f_1 = 2/3$, then $\bar{B} = 0.49$, the value of $\bar{B}$ for $n = 2.1$ if all contribute equally. I call this value of $n$ which produces a given $\bar{B}$ if all males contribute equally the effective promiscuity $P_e$. In the above example, then, where $f_1 = 2/3$, $P_e = 2.1$. $P_e$ is not a simple function of Hamilton's (1972) index of promiscuity $(1 - r_s)$; under complete outbreeding, $P_e = 1/r_s$, where $r_s$ is the correlation between sperms drawn at random from the spermatheca.

Returning to the basic inequality of kin selection (1), if a female can produce an extra sister at the same expense as that of producing a daughter, so that $K = 1$, then probable relatedness must be greater than $1/2$ for kin selection to favor such an action. Figure 4 plots necessary $f_1$ against $n$ for maintaining $\bar{B} = 1/2$ or $P_e = 2$, for our simplified case where all males but one contribute equally. If $n = 8$, then $f_1$ is slightly less than 0.70, close to the value for $n = \infty$. It is unlikely that
any male contributes 70% of the sperm in the honeybee (Taber, 1954), but the other factors mentioned above may raise $\bar{B}$. The inbreeding coefficient and the components of $K$ must also be known in order to precisely test the kin selection relationship in any case.

The other suggested solution to the apparent dilemma of multiple insemination is that this is a derived condition in each highly social phyletic line. A number of authors have raised this idea, among them Alexander (1974), Hamilton (1964, 1972), and Lin and Michener (1972). The general hypothesis is that monogamy was originally necessary, when there was little reproductive difference between females ($K \leq 1$), but that an increasingly social mode of reproduction yielded increasing productivity, a trend which would lend itself to the evolution of sterile castes. Once a nonmating caste evolved, queenness is no longer an option for these individuals, though their classical fitness may not be zero.

Solitary and moderately social species of the Hymenoptera in which males are known to have more than enough sperm to fill the spermatheca support this idea (see above authors for original references). The adaptiveness of increasing $P_e$ is not obvious. It has been suggested by Lin and Michener (1972) that multiple mating is an outbreeding device, serving to counter the effect of male haploidy and some breeding habits in increasing phylogenetic inertia, but this has not been developed beyond the level of a suggestion.

![Graph](image)

**Fig. 4.** Necessary $f_s$ as a function of total number of males inseminating the mother for sisters to have average relatedness $\bar{B} = 1/2$. This is the same as necessary $f_s$ for $P_e = 2$. 
C. Parental Manipulation

1. General Considerations

The concept that worker offspring are produced through selection on the queen in Hymenoptera and on the queen and king in termites is, in my opinion, the most obvious of the three theories; it is the only one which was clearly anticipated by Darwin.* The closest Darwin came to anticipating either group selection or kin selection was his vague hypothesis that selection might operate at the level of the colony. In the superorganism idiom, this identifies the phenotype on which selection operates, but does not say which of the colonies several genotypes will thereby be favored. In view of Darwin’s ignorance of Mendelian genetics, any more precise statement would have been surprising. Parental manipulation was the last of the three theories to receive serious treatment, however, so that it is most conveniently discussed in the light of the alternative it poses to other models.

The manipulation involved in parental manipulation is of parental investment. "Parental investment" is a commitment of energy or resources by the parent to the fitness of an offspring, at some expense to the parent’s ability to invest in other (present or subsequent) offspring (Trivers, 1972). The central idea in Alexander’s (1974) development of the parental manipulation theory is that the parent will manipulate investment in such a way as to maximize its own fitness. Where there is conflict over investment distribution between parent and offspring, the parent is expected to prevail. The parent will disperse or concentrate investment according to the plan which provides the highest yield. Offspring in social insects can then be likened to grownup eggs, and workers to grownup trophic eggs (West Eberhard, 1975).

It should be emphasized that manipulation can be strictly genetic, as well as behavioral or physiological. In its most extreme form, the parent may not manipulate the offspring in any sense of having personal control, but merely in the sense that the offspring is genetically programmed to behave so as to maximize the parent’s fitness at some possible expense to its own. This type of parental manipulation is more likely to be found in insects, in contrast to the behavioral manipulation expected in social vertebrates. It is consistent with the parental manipulation concept to say that insects may even be under parental influence in this manner after the parent’s death.

Evidence for this general theory as applied to halictine bees was presented by Michener and Brothers (1974), who used the term "queen control" for behavior by the queen to enforce workerliness in some daughters. It was shown that the queen controlled the activities and oviposition of these daughters, and the con-
Conclusion was reached that division of labor and castes did not evolve primarily through selection on the workers to maximize their inclusive fitness, but on the queen to maximize her classical fitness.

Conflict of genetic interest between parent and any given offspring except its last is expected in sexual species. While an offspring's inclusive fitness is its classical fitness plus its inclusive fitness effect, the parent’s inclusive fitness is identical to half the summed classical fitness of the different offspring plus its own inclusive fitness effect.* If we introduce the reasonable assumption that the parent's fitness effects on its siblings, cousins, parents, etc., are insignificant at this stage, we can conveniently ignore the parent's inclusive fitness effect. The conflict, then, is between the parent’s classical fitness and the offspring’s inclusive fitness. Any offspring should "want" to increase its classical fitness at the expense of any sibling C as long as it does not thereby harm its own inclusive fitness, i.e., as long as \( \delta W_A > - \delta W_c(B_{ACY}B_{AY}) \). A parent will only favor such action by an offspring if it increases his/her number of grandoffspring, i.e., if \( \delta W_A > - \delta W_c \). The reasoning behind Alexander’s (1974) proposition that evolution should consistently favor parental "victory" in situations of conflict, i.e., that a trait favoring offspring victory cannot spread in the population can easily be stated verbally. Suppose such a trait appears in one offspring in a brood; that individual will receive more parental investment than it would otherwise have done. The same trait will appear in some of that individual’s offspring, probably in increased proportion, so that its classical fitness, if measured in terms of grandoffspring, will actually be less than it would otherwise have been. This trend will continue in each generation, rapidly decreasing any initial advantage to the trait.

This exposition does not constitute a proof that such a trait cannot possibly persist and spread over generations. This will require models which take into account relative \( \delta W \) of parent and offspring, type of genetic dominance, and the sexual nature of the organism involved (Alexander employs the simplifying assumption of asexuality).

2. Genetic-Interest Asymmetries in the Hymenoptera

The parental manipulation theory has some attractive features with regard to the Hymenoptera. Most obviously, multiple insemination creates no problem for pure parental manipulation, as it does with kin selection, as mother–daughter relatedness is independent of relatedness between daughters. The situation is complicated if kin selection and parental manipulation operate together. One unattractive feature of parental manipulation is that it has provided no explanation for the hymenopteran near-monopoly on eusociality.

*Equating parental classical fitness with half of the sum of offspring classical fitness is a slight revision in usage, but it does not alter the meaning of "fitness" for our purposes.
The difficulty in distinguishing between social effects resulting from kin selection and parental manipulation is that they often give rise to very similar predictions, and where it is theoretically possible to distinguish between them the area of distinction may be smaller than the imprecision in present data. If our theory also contains imprecisions, then we are reduced to interpreting data from nature in such a way as to suit our preferences.

As indicated above, parent–offspring conflict will normally revolve around the offspring's inclusive fitness and the parent's classical fitness. In termites, for example, the offspring is expected to try to increase its fitness by absorbing more investment up to the point where it is costing siblings two units for every unit of benefit to itself; the parent will be willing to continue investing in offspring C only as long as the ratio is $1:1$ or better ($K > 1$). If $K < 1/2$, parent and offspring are agreed that the parent should not invest; if $K > 1$, they are agreed that the present should invest. The zone of $bk$ for which kin selection and parental manipulation make opposing predictions is $1/2 < K < 1$. In the Hymenoptera the zone of conflict is comparable; if the sex ratio is balanced, its lower limit is $1/2$ for male offspring and $B_{sisters}$ for female offspring. The large difficulties in obtaining believable data on investment, $K$ and $B$ have so far impeded efforts to resolve this most interesting theoretical question.

Trivers and Hare (1976), in a recent examination of the implications of haplodiplody for inclusive fitness, have examined two sources of parent–daughter conflict, one of them arising strictly out of relatedness asymmetries, and in doing so have pointed out a radical new way to make and test predictions based on ideas of who wins in parent–offspring conflict. They start from the observation that females, although they are related to full sisters by $3/4$, are related to brothers by only $1/4$, so that average relatedness will be $1/2$ if the sex ratio is balanced. In this situation, a worker can increase her inclusive fitness (while lowering her mother's fitness) in either of two ways: (1) by laying some of the male-producing eggs herself or letting sisters do it, so that at least some new males are sons ($B = 1/2$) or nephews ($B = 3/8$, if $P_e = 1$), rather than brothers; or (2) by investing differentially in brood of the sex to which she is more related.

If $B_{AM}$ is A's average relatedness to male brood and $B_{AF}$ is her average relatedness to female brood, then $x$, the expected preferred ratio of investment in males/females is equal to

$$x = \frac{B_{AM}(\text{relative value of a male})}{B_{AF}(\text{relative value of a female})}$$

If inbreeding and multiple mating are not significant factors and if workers lay all male-producing eggs, then $x$ for the queen is $1$, and for nonlaying workers is $1/3$. Using sex ratio data and dry weights for samples of 21 species of ants for which they believe the above conditions of inbreeding, promiscuity and maternity are met, Trivers and Hare calculated a rate of investment not significantly different
from 1/3, while significantly different from 1. They drew the provisional conclusion that the workers were winning, a conclusion supporting kin selection theory. They report that the sparse data available for termites do not contradict the expected $x = 1$ for all individuals.

In Trivers and Hare's treatment the $x$ values for queens, laying workers, and nonlaying workers are calculated and considered, but not of males, the reasoning being that queens are in a position to behaviorally affect the ratio of investment, while males can have little behavioral impact. In the broader concept of parental manipulation used here, though, the possibility must be admitted that males can manipulate investment ratio and maternity of their grandsons through their daughters' behavior. Starr and Duffield (in preparation) discuss the preferred ratio of investment of males, how it relates to Trivers and Hare's treatment and conditions in nature which are most conducive to using such analysis to make distinct predictions for kin selection and parental manipulation effects.

**D. Synergistic and Antagonistic Action**

Having reviewed the effects of group selection, kin selection, and parental manipulation in producing altruism, we can consider how these different effects can interact. Although each of these produces effects which are distinct in theory, they have been much less well distinguished in nature. There are three reasons for this: (1) very few people are really trying to distinguish them; (2) such data as $B$, $P_e$, $F$ and the components of $K$, all of which are necessary to calculate $W_i$, are difficult to obtain; and (3) there are broad areas of overlap in the predictions flowing from these effects. Figure 5 diagrams the different areas of classical fitness effect and inclusive fitness effect which provide scope for the operation of group selection, kin selection, and parental manipulation. The area of interest for the question of altruism is below the $SW_A = 0$ line. Genes with effects below this line decrease individual A's classical fitness. Area A is of interest with respect to pure group selection. No form of individual selection favors altruism in this area, as it maximizes neither A's classical fitness or inclusive fitness, nor the classical fitness of A's parents. Any situation in which it could be shown that a class of behavior existed with effects in this area would constitute strong evidence for group selection.

Area B is of interest for two reasons. If group selection is operating, the presence of an inclusive fitness effect above zero will dampen an opposing effect of selfish individual selection and will therefore facilitate successful group selection for altruism. This is the hypothetical situation described by Williams and Williams (1957), in which the units of selection are groups of siblings. A conclusion of Levin and Kilmer's (1974) computer simulation was that pure group selection (area A) could most likely not serve as the primary force in the evolution of altruism, but that its most important role may be in synergistic
association with kin selection. Where C is A's parent and group selection is not significant, area B is also of interest as the area in which parental manipulation promotes offspring altruism, while kin selection on the offspring opposes it. It is the area of parental victory. The opposite outcome is represented by area E.

Area C is the area of kin-selected altruism. If behavior in this area can be demonstrated, it is trivial that natural selection may also favor groups containing such individuals over those which do not. It is not trivial, however, that parental manipulation can also operate in this area, if C is A's parent. If it can be shown that the offspring can win in parent–offspring conflict situations (other than those in which there is a qualitative difference in the source of classical fitness of each, as when workers lay some male-producing eggs in the Hymenoptera), then the possibility exists, for values in area B, that greater between-sibling relatedness will ease altruism through parental manipulation. If, however, parental manipulation is supreme and the offspring cannot possibly win, then between-sibling relatedness is irrelevant.

The diagonal line of slope $y + x = 0$ is the line along which A's effects on its own classical fitness and on the classical fitness of others (inclusive fitness effect) exactly cancel each other. All behavior with effects below this line (A, B, and F) is inconsistent with kin selection. Area F is of tangential interest as the area which is inconsistent with kin selection, although it causes increased classical fitness for A, because A's selfishness against relatives is too great. Behavior in area D is favored by all types of individual selection and is therefore quite unremarkable.
III. SPECIAL QUESTIONS

We will now consider four special evolutionary questions in the light of these theoretical viewpoints: (1) the social evolution of termites; (2) the origin of social parasitism; (3) polygyny in some species of Polistes wasps; and (4) pathways to eusociality in the Hymenoptera.

A. The Social Evolution of Termites

Theory around the social evolution of termites is much less developed than around the Hymenoptera. I am unable, for example, to find any mention of the subject in a recent two-volume, 1195-page work on the biology of termites (Krishna and Weesner, 1969–1970). The termites lack two very useful footholds which have allowed substantial theoretical progress with the Hymenoptera: (1) a broad gradation in social levels, such as exists most outstandingly in the bees and provides scope for comparative study; and (2) the asymmetries in relatedness arising out of male haploidy.

In order to consider the impact of the different theoretical selective effects on the early evolution of termite sociality, let us consider what special selective pressures may have been important.

The presocial ancestor of termites is presumed to have lived in and fed on rotting wood, which is digested with the necessary aid of intestinal symbionts, as do some extant species. These are eliminated along with the lining of the hindgut at each molt, so that a newly molted termite must obtain a fresh supply of symbionts. The presence of similar intestinal symbionts in the gregarious rotting-wood roach, Cryptocercus, as well as other biological and morphological apparently synapomorphic characters, have led to the widely accepted idea that termites are derived from a Cryptocercus-like ancestor. The importance of these intestinal symbionts cannot be denied, as dependence on them effectively precludes the option of solitariness before adulthood. Lin and Michener (1972), among others, have suggested this as a possible driving force in the evolution of termite sociality. Clearly, it serves as a preadaptation by mandating group cohesion, but it has not been shown how it can select for higher components of sociality.

A suitable food supply/microhabitat for Cryptocercus (i.e., a single rotting log) would appear to be a very good one by the standards of group-living insects, and the same may have applied to the ancestral termites. An established colony can therefore be especially stable and productive. Due to the extreme patchiness of food/microhabitat distribution and the apparently relatively large hazards of nest founding, it is plausible that this greater stability makes for a colony survivorship curve over time which is especially convex downward.

Neither these selection factors nor present forms of termite sociality stand in
clear contradiction to any of the three theories. Classical group selection is favored by the extreme hazards of colony founding, danger of local extinction and low effective population size, while the discrete dispersal stage at long intervals is favorable to the competitive group selection model. Williams and Williams (1957) considered their model of selection between groups of relatives to be well applicable to termites. It is unlikely, though, aside from the general unlikeliness of group selection in insects, that group selection alone could produce sterile castes, as the success of altruistic groups depends on the maintenance of the trait in the reduced brood of each altruist.

The supposed large hazards involved in nest-founding and high productivity of established colonies are consistent with kin selection theory and neutral to parental manipulation.

The condition $K > B_{\text{AAB}}/B_{\text{AC}}$ presents no special problem where C is a parent of A, as $B_{\text{AAB}}/B_{\text{AC}} = 1$. The factors discussed above which increase values of $K$ can apply to termites; the superrecipient nature of the royal pair and high productivity of the homeostatic mature nest raise the numerator of $K$, while the hazards of nestfounding and superdonor nature of soldiers and some workers lower the denominator.

Clear sources of parent–offspring conflict, conducive to an analysis of which is winning, are not evident in termites. One possibility exists in species with supplementary reproductives. When either the queen or king dies, she/he is normally replaced by an offspring of the same sex, which is raised to reproductive condition and mates with the surviving parent. If the offspring of the previous royal pair were not inbred, between-sibling $B$ for offspring of the new pair will be 3/4, while these new offspring will be related to offspring of the old royal pair by 1/2. This raises the possibility that the extraordinary $B$ between new offspring can serve as a basis for workerlike altruism. This is subject, though, to the unlikely condition that the offspring can detect this situation or to the condition that such transitions take place frequently enough that between–worker $B$ at any given time is probably significantly above 1/2. This second condition may be met in the primitive state, in which royal longevity was presumably much closer to that of workers than in the highly eusocial condition.

If a given individual "decides" not to be a worker, given the presence of a functioning royal pair, two options exist. The simplest is to become a regular new reproductive and leave the nest in the mating season. The other is to attempt to usurp the position of the reigning queen or king or to mate with the appropriate individual and competitively produce offspring. Unlike hymenopterous immatures, termite nymphs are not channeled into castes by trophic differentiation, out of their own control. Rather, they respond to chemical cues from the queen and/or king and develop accordingly. Why doesn't every nymph differentiate into a reproductive and mate with its parent, inasmuch as this would lead to the production of offspring of relatedness $B = 3/4$? One answer is that in some
species the workers kill and eat any supernumerary reproductives (Hamilton, 1972), so that there is little scope for such “disobedience” to caste-regulating chemical commands. This destruction of “renegades” is not a general phenomenon, however (A. M. Stuart, personal communication), which leaves open the possibility that individuals assume the caste characteristics most valuable to the fitness of the primary reproductives, sometimes in opposition to their own fitness. It is not a strong case one way or the other, but the current state of theory regarding the termites is such that even such speculation can be admitted.

B. Social Parasitism

The question of the origin and fate of social parasitism is relevant to the selective forces on individuals in a society. “Social parasitism” is used variously in the literature; here it will mean the exploitation by a foreign (to the colony) organism of the social machinery of an insect colony, to the colony’s detriment. Although there is no special ecological uniqueness to such exploitation, it raises different evolutionary questions than more regular forms of parasitism of social insects. I see two possible origins of such parasitism (see also Chapter 8 of this volume).

1. A foreign organism penetrates the colony by providing the “password” which allows it to pass for a colony member and gain the benefits of membership. Such an interloper is not expected to assume the “obligations” of membership, such as brood care, foraging, temperature control, etc. Large ant and termite colonies are commonly host to a phyletic diversity of organisms, some of which are clearly parasitic on the colony’s social machinery. Such a situation presents interesting questions of the colony’s security system and the chemical and tactile signals which maintain it, but it poses no special genetic problem.

2. It is believed that in some groups social parasitism originated in conspecific robbing, usurping, or cheating (any selfish behavior in a normally altruistic or mutualistic context). Emery (1909) noted a general tendency in ants for social parasites to be closely related to their hosts. Emery’s rule (so called by LeMasne, 1956) has given rise to the following suggested pathway to permanent obligate social parasitism in the Hymenoptera:

a. The tendency exists within a species for gynes which are disadvantaged, for example, by a late start in nest founding in regions where seasonality is important, to attempt, sometimes successfully, to usurp a conspecific nest from the resident queen. If successful, the usurping gyne then proceeds to establish her own colony in the normal fashion. For example, the bee *Hoplitis anthocopoides* usually nests away from others. When nests are close together, two tendencies appear: communal nesting, with more than one female sharing at least part of the nest, and nest usurpation (Eickwort, 1975).

b. The insurgent gyne not only usurps the nest, but also makes use of the
present or emerging workers to raise her brood to maturity, after which her own offspring take over the work and the colony cycle proceeds as normal. This stage may be common in bumble bees. Bohart (1970) records observations of *Bombus huntii* in which a nest is usurped by a succession of gynes, and R. C. Plowright (personal communication) reports that it is rare to excavate functioning bumble bees in nests in Ontario and Manitoba without finding at least one dead gynae in each, evidence that usurpation is at least commonly attempted.

c. A tendency develops for the insurgent queen to produce fewer and fewer worker offspring in favor of sexual offspring, and to rely increasingly on the host workers.

d. The usurping queen never produces workers, and her daughters show degeneration of workerlike features, so that parasitism is obligate. This is most apparent in bees, where the reduction (in females) of the pollen basket indicates the inability to collect pollen; any species of bee with this feature can be identified *a priori* as an obligate parasite.

Despite its attractiveness, the generality of the above pathway has lost ground in recent years. MacDonald and Matthews (1975) point out that the facultative social parasite *Vespula squamosa* is not closely related to either of its common hosts, *V. maculifrons* and *V. vidua*. Plowright and Stephen's (1973) taxonomic analysis of the obligate social parasitic bumble bees *Psithyrus* concluded that this genus is indeed monophyletic, a conclusion which negates the schema of Reuter (1913, Ch. 23) and Richards (1927) for the evolution of *Psithyrus* from multiple species of *Bombus* facultatively parasitic at stage (a) or (b).

Despite accumulating counterexamples, there are *a priori* reasons to believe that advanced social parasitism can sometimes arise from occasional intraspecific cheating or from taking advantage of a situation in which aid is given on the basis of kinship or parental manipulation.

Nest sites, especially for ground-nesting species, are often scarce. Nest usurpation may be advantageous relative to finding and outfitting one's own nest or to going without a good nest site. Behavioral adaptations for nest usurpation (e.g., in *Hoplitis anthocapoides*, Eickwort, 1975) and intraspecific robbing of food stores (common in *Apis mellifera*, Bohart, 1970) are widespread in social hymenoptera, even in species whose colony livelihood is not normally gained by such means, so that the transition to regular kleptoparasitism can be gradual.

Group selection provides no special viewpoint on the evolution of social parasitism. This is not surprising inasmuch as such models are developed to account for the opposite phenomenon. Competitive group selection provides an explanation for the maintenance of occasional kleptoparasitism in a population, but does not account for the evolution of separate permanently parasitic species.

Situations in which "reciprocal altruism" or other forms of mutualism prevail should be fertile ground for the beginnings of social parasitism. In more colloquial terms, an individual which has a mutualistic relationship with another but
lacks a means of enforcing the arrangement is "just bending over asking for it"; such circumstances will favor the fitness of cheaters. This is aside from the question of whether sterile castes can possibly evolve on the basis of mutualism (Section III. D. 2). I have not used Maynard Smith's (1976) method of analysis to determine whether opportunistic cheating can be an evolutionarily stable strategy (ESS), but mutualistic "honesty" can probably not be an ESS unless

1. Honest individuals can retaliate against cheaters;
2. The mutualistic giving is simultaneous or a long series of reciprocal actions, so that cheating is impossible or unimportant;
3. The benefits of mutualism and the probability of a cheated party absconding are large; or
4. One of the above is supplemented by above-average relatedness among participants, so that the benefits from cheating are dampened by a significant negative inclusive fitness effect.

The possibility of social parasitism arising out of such a situation is similar to the idea of Sturtevant (1938) that multiple-queen colonies in ants present an opportunity for individual queens to produce only sexuals and not workers, to the detriment of other queens.

Michener (1958, 1969, 1974) and Lin and Michener (1972) have proposed a mutualistic route to eusociality in most bees (Section III. D. 2). If this indicates that mutualism, as a precondition for sociality, is widespread in bees, then we might expect unusual opportunities for social (and other) parasitism in this taxon. It is interesting, then, that 30 of the 115 genera of bees found in North America are exclusively parasitic and that the parasitic habit has had at least 16 separate origins in bees (Bohart, 1970). This is not a hard, falsifiable hypothesis, as the opposite situation, a singular lack of the parasitic habit in bees, could be taken as an indication of the necessity to develop effective defenses against parasitism, precisely because of this special vulnerability.

The question arises of how a species can divide into two sister species, one of which is parasitic on the other. Dobrzanski (1965) rejected Emery's rule on the grounds that this situation could not evolve if the parasitic and host groups were never allopatric. Wilson (1971) likewise recognized the unlikelihood of sympatric speciation and suggested the straightforward pathway:

One nonparasitic species
Divided by barrier into two populations
Speciation
Barrier removed, species sympatric
One species becomes specialized as a parasite on the other

This pathway is not qualitatively different from the probable pathway taken by parasites not closely related to their hosts. The essential difference is in the necessity of some period of allopatry and in the special opportunities which a
closely related species has for penetrating its host’s defenses through deception, as it will more likely have the necessary signals in its behavioral repertoire. In this case, Emery’s rule is an observation of nothing remarkable and exceptions, if they were not known, would be expected.

An alternative pathway can be imagined, which is based on species with facultative intraspecific parasitism, such as some species of Bombus or Vespa:

Single species with occasional intraspecific parasitism
Barrier separates species into two groups
Nest usurpation or other parasitic habit, becomes more common in one group (A), more important in its life economy
Some divergent evolution, leading to lowered fitness of potential hybrids
Removal of barrier, two groups sympatric
Increased parasitic tendency in group A; at the same time disruptive selection leads to speciation
Species A evolves obligate parasitism on species B

A number of factors can accelerate the evolution toward obligate parasitism. If anti-parasite defenses in group B are less effective than in group A at the time of barrier removal, members of B will present an easy target for members of A. In addition, if population viscosity and the inclusive fitness effect is a factor in dampening the parasitic habit in group A, during the allopatric phase, this will be less a factor as a greater proportion of potential hosts in the sympatric phase are unrelated.

Social parasitism between sister species should arise more commonly in geographical areas where conditions favor speciation. If social parasitism is a stable, long-term strategy, this condition would best be met in a stable environment with fine niche differentiation, as is presently the general case for the tropics. If, on the other hand, social parasitism is generally a dead-end or limited strategy, one would expect centers of social parasitism in areas with much disruption and rapid turnover in barriers, such as exist, for example, in mountainous areas of the north temperate zone. The geography of social parasitism has not, to my knowledge, been the subject of intensive study, but we have some indications. Of the social parasitic species of ants, 56% of known species are in the palearctic region, 27% in the nearctic, and only 17% from the rest of the world (Kutter, 1969). Even considering our relative ignorance of tropical insects and the greater landmass of the holarctic region, this disproportion is remarkable. Bohart’s (1970) figure of 26% wholly parasitic genera for North American bees has already been noted; Bohart was unable to say whether this is remarkable on a world scale. The richness of social parasitic ants in the Alps has frequently been noted, and the majority of North American social parasitic species are from limited mountain ranges in the West (Wilson, 1975).

Richards (1927, 1953) gives as an alternative explanation for the apparently greater abundance of social parasites in the north temperate zone the difficulty of founding nests. Added to this must be the greater importance of precise timing of
nest initiation in the shorter and more exact northern season, and the fact that nests which are suitable targets for usurpation (typically, those in the immediate preemergence stage) will be more available at the right time, due to the greater synchrony of the nesting cycle among different nests.

Thus far the question of insect social parasitism has been discussed only with respect to the Hymenoptera. The reason for this is simple: social parasitism is unknown among the termites. Termite colonies, like those of ants, are host to various symbionts, but no termites are themselves social parasites. Given the paucity of sophisticated social evolutionary theory related specifically to the termites, it is not surprising that no testable theory exists to account for this unanimity. But some useful speculations have been made. Lin and Michener (1972), in their discussion of possible outbreeding mechanisms in the Hymenoptera, point out that (diploid) male termites do not cause or experience any special loss of genetic variability, so that no special outbreeding devices are necessary. Lin and Michener interpreted the acceptance of “joiners” in some primitively social species as a possible outbreeding device, and noted that it involves increased vulnerability to social parasitism.

Richards (1953) suggested that the necessity of both a resident queen and king in termites poses an unusual difficulty for the evolution of parasitism, as it would demand that two reproductives successfully penetrate the host colony. This should not bar the possibility of occasional usurpation within the species, as a single reproductive could depose the reigning queen or king, but of course this habit is not conducive to speciation or to long-term parasitism of other species. Richards also points to the ready production of supplementary reproductives in some species as a force against usurpation. The habit in some species of destroying supernumerary reproductives may function as an additional defense against usurpation.

C. Polygyny in Polistes

Wilson (1971) defines “polygyny” as the coexistence in a colony of two or more egg-laying queens. A slightly broader meaning will be used here, to include cases in which two or more gynes coexist, some of which do not function as queens.

Primitively eusocial wasps of the genus Polistes have attracted much scientific attention because of their intermediate social level, large size, open accessible nests, and their general piquancy. Polistes colonies in the initial stage can be monogynous or polygynous, with the characteristic mode of nest founding varying from species to species and sometimes within a single species from one part of its range to another. In polygynous species or populations, the gynes which found a new colony (foundresses) are generally thought to be sisters. In the early part of the nesting cycle they engage in a period of dominance interactions which
results in a hierarchy, with only one of them assuming the characteristic queen’s role, while the others become workerlike “auxiliaries.” This pattern of nest founding is most completely studied in *P. fuscatus* in North America and *P. gallicus* in Europe (Deelecurance, 1950; Pardi, 1948), and the following discussion will have these species in mind.

That selection pressures for and against polygyny are still operative is shown by the fact that each of these two species is polygynous in only part of its range. Interestingly, while *P. gallicus* is polygynous in the southern part of its range and monogynous in the northern part (Hamilton, 1964), the opposite trend is true for *P. fuscatus* (D. L. Gibo and H. E. Dew, personal communication). The pattern for *P. exclamans* in North America is roughly opposite to that for *P. fuscatus* (D. L. Gibo and H. E. Dew, personal communication), which militates against a purely climatic explanation. “Monogynous” and “polygynous” are relative terms here. In North America there is a gradual transition in characteristic mode of nest founding, with occasional uncharacteristic colonies being found even at the extremes; the same is probably true for *P. gallicus*.

The key evolutionary question is why the auxiliaries remain on the nest and aid the dominant gyne by becoming workerlike. When their subordinate position becomes obvious, why do they not invariably leave to attempt to found their individual nests? This question posed substantial difficulty for Hamilton (1964), as the foundresses are of the same generation, so that $B_{\text{AC}}$ is at best $3/8$ (if foundresses are full sisters), while $B_{\text{AA}}$ is $1/2$. West Eberhard (1969) emphasized relative reproductive potential rather than relatedness and reformulated the general expression $K > \frac{1}{B}$ to apply to this specific case:

$$\frac{P_{e+1} - P_e}{P_j} > \frac{1}{B}$$  \hspace{1cm} (2)

where $P_e$ is the productivity of the colony without a particular auxiliary, $P_{e+1}$ is the productivity with the addition of that auxiliary (joiner), $P_j$ is the auxiliary’s productivity if she attempts to nest on her own, and $B$ is the auxiliary’s relatedness to the (egg-laying) queen.

West Eberhard used the coefficient $r$; I have taken the liberty of substituting $B$. The joiner (A) and queen (C) are of the same generation, so that $B_{\text{AA}}B_{\text{AC}} = 1/B$, and we can use the simpler expression.

A number of factors favor the satisfaction of this relationship in the north temperate zone, both by way of decreasing $P_j$ and $P_e$, and increasing $P_{e+1}$. The tendency for *Polistes* in North America to nest almost exclusively under the eaves of buildings and in other man-made structures where these are available (personal observation) suggests that nest sites were much scarcer before the coming of European civilization, so that the value of joining a foundress group with a nest site was greater relative to that of seeking one’s own. The density of colonies to be found in occasional, presumably prime, nest sites today suggest
that their availability may still be limiting at times. This cannot be stated with any
certainty, as the characteristics of desirable nest sites have not been systematically
studied for any species. This restriction is made more severe by the short
north-temperate season, which probably exacts a severe penalty for late nest
initiation, both through a decrease in available time itself and through the re­
duced probability of being assisted by auxiliaries (West Eberhard, 1969). It may
be difficult to show a firm correlation in nature, due to the possibility that those
wasps which are attempting late nest initiation are physiologically inferior and
have tried unsuccessfully before. Lin and Michener (1972) and Lin (1964) have
emphasized the superiority which multiple-foundress groups give to pre­
emergence colonies in bees where predator and parasite pressure are important
factors in colony survivorship.

*Polistes fuscatus* nests are reported to be most susceptible to destruction by
birds shortly before emergence of the first worker brood (D. L. Gibo, personal
communication), an indication of the value of a defense force at this stage.
Bumble bee nests in the same stage are reported by Voveikov (1953) to be most
susceptible to usurpation.

Another circumstance favoring polygyny would be a foraging bottleneck in
this early stage, with the danger that a single gyne would not be able to provision
a large enough brood to ensure rapid colony growth. There is a general similarity
between the suggested hazards involved in solitary nest founding in *Polistes* and
those postulated by Hamilton (1972) as pressures promoting sociality in termites.

An auxiliary’s value to her colony \((P_{e+j} - P_e)\) will be governed by her ability
to work and the ability of the queen to translate that work into brood, as discussed
in Section II, B, 3. There is good evidence that generally \(P_{e+j} > P_e\) [Noonan
(personal communication), Owen (1962) and West Eberhard (1969) for *P. fuscatus*
in Michigan; Starr (personal observation) for *P. annularis* in Georgia].

What, then, limits the size of foundress groups? It has been shown by Michener
(1964) to be a general rule in the Hymenoptera that productivity per female for
surviving colonies decreases as colony size increases. The applicability of this
rule has been confirmed for *P. fuscatus* and *P. annularis* in the references cited
above. As foundress-group size increases, then, the value of each additional
auxiliary decreases and must reach a point where it no longer pays to join. If
colony defense is the key factor, with most pressure coming from a single species
or type, then one would intuitively expect foundress-group size distribution to
cluster around the maximum size at which an extra foundress still provides a
large enough increment in colony survivorship. If, on the other hand, active
defense is unimportant, as appears to be the case where ants are the principal
threat to polistine wasps (Jeanne, 1975; Richards and Richards, 1951), then the
greater linearity of the curve for \((P_{e+j} - P_e)/P_j\) should produce a more disperse
size distribution with a more gradual dropoff in frequency at the upper end.

The positive correlation between subordinance and reduced ovarian develop­
ment suggests that the foraging activities of auxiliaries are responsible for this decrease in $P_J$ ("nutritional castration," Marchal, 1897; Plateaux-Quenu, 1961; Spradbery, 1965). This raises the possibility that one important function of harassment by the queen of behaviorally queenlike gynes is to decrease their $P_J$ and consequently the probability that they can increase their fitness by leaving the colony. The importance of the progressive reduction of $P_J$ once dominance is established can be seen if we add to the inequality (2) the term $P_J'$, to indicate the classical fitness of an auxiliary on the nest, which at any moment is her probable lifetime reproductivity:

$$\frac{P_{e+1} - P_e + \frac{1}{B} P_J'}{P_J} > \frac{1}{B}$$

(3)

Although $P_J'$ increases total colony production, West Eberhard implicitly left it out of $P_{e+1}$.

$P_J'$ can rise above zero in either of two ways: (1) through occasional egg laying, despite vigilance of the queen. This is probably uncommon in *P. fuscatus* or *P. gallicus*; (2) Through succeeding to the queen position either by conquest (probably uncommon) or through the disappearance or decline of the queen. Hamilton (1964), Ghiselin (1974), and Lin and Michener (1972) have emphasized this latter source of classical fitness for auxiliaries. The possibility that the gyne in question is the one who becomes dominant through the normal course of dominance interactions is not considered, as the question is why she accepts an initially assured subordinate position.

In the species under discussion, it is the habit of the workers to drive off auxiliaries soon after worker emergence, so that $P_J'$ will approach zero as the preemergence stage draws to a close. This raises the hypothesis that in the beginning condition (3) obtains, but condition (2) does not, i.e., $P_J' > 0$, so that $P_J'$ is the decisive factor in keeping an auxiliary on the nest. As $P_J'$ approaches zero, condition (3) can be maintained by (1) increasing the difference between $P_{e+1}$ and $P_e$ through devices associated with superdonorism and superrecipientism (I know of no evidence for such an effect in *Polistes*), or (2) decreasing $P_J$. This clearly happens through seasonal decrease in opportunities and the independent physiological reproductive decline of auxiliaries.

It is possible, then, that dominance harassment by the queen and subsequent (physiological or behavioral) "demoralization" of auxiliaries serves to maintain the queen's position, through preventing desperate conflict by auxiliaries as subservience less and less serves their fitness. Productivity of auxiliaries after they are driven from the nest is unknown, but it is probably usually very small.

Marking of new gynes in the fall indicates that foundress groups in north temperate *Polistes* comprise mostly sisters [Noonan (personal communication) and West Eberhard (1969) for *P. fuscatus*; Starr (personal observation) for *P.
annularis]. This raises the question of selection on the parents for manipulation, necessarily genetic, of offspring to nest cooperatively. The necessary condition for the maximization of parental classical fitness (in grandoffspring) through polygyny is

\[ P_{e+1} + P_{1}' > P_e + P_1 \]  

if all foundresses are sisters. The attraction in a parental manipulation explanation for polygyny derives from the fact that condition (4) is more easily satisfied than condition (3). This is evident if Eq. (3) is changed into its equivalent

\[ B(P_{e+1} - P_e) > P_1 - P_1' \]  

and Eq. (4) into its equivalent

\[ (P_{e+1} - P_e) > P_1 - P_1' \]  

Because the area of potential conflict between parent and offspring (potential auxiliary) revolves solely around the F\textsubscript{2} generation (grandoffspring of the parents), and not around both F\textsubscript{1} and F\textsubscript{2}, and because all relevant females are inseminated gynes, it is probably not possible to use asymmetries of relatedness in the manner of Trivers and Hare (1976) to create divergent testable predictions for the effects of kin selection and parental manipulation. Rather, we must rely on the area of conflict in total production where

\[ (P_{e+1} - P_e) > (P_1 - P_1') > B(P_{e+1} - P_e) \]  

In a population where this relationship obtains, parental manipulations will predict joining, while kin selection will not. A verbal restatement of Eq. (7) is: joining generally entails a loss in classical fitness; the value of the joiner to the colony’s productivity, multiplied by the fraction of unrelatedness \((1 - B)\), is greater than this loss in classical fitness. If Eq. (7) does not obtain, kin selection and parental manipulation theory will predict the same effects. Presently available data in the literature cannot be used for this purpose, and the testing of the question presents two substantial difficulties: (1) values of \(P_1\) and \(P_e\) cannot be obtained for any colony for which \(P_{e+1}\) and \(P_{1}'\) are available, and vice versa, but must be inferred from comparisons between colonies. Large, accurate sample sizes are therefore required. In nature, the colony and not the investigator will dictate which set of values can be obtained directly. (2) Condition (7) is satisfied only for a narrow range of values of \((P_{e+1} - P_e)\), the width of which approaches zero as the inbreeding coefficient (and therefore \(B\)) approaches 1. For populations for which \(B(P_{e+1} - P_e) > (P_1 - P_1')\), joining is consistent with each theory and we are left with the question, untetstable under present theory, of which selective effect originally promoted joining.

It is consistent both with kin selection and parental manipulation that position in the dominance hierarchy be positively correlated with reproductive potential
and that individual gynes rapidly recognize their relative positions and avoid unnecessary fighting. West Eberhard (1975) has pointed out in this connection that variability in reproductive potential will favor rapid establishment of stable hierarchies, so that such variability may be an important preadaptation for polygyny. If such rapid equilibrium in foundress groups is an important factor, and if parental manipulation is the key selective factor, it will sometimes be in the parents’ interests to artificially create variability by handicapping some offspring of \( P_j \) and \( P_j' \), in the interests of increasing \( P_{x+j} \). This need not necessarily be accomplished by the mother personally, but could be done by workers through nutritional or physical means. Caste determination of brood by workers is well known in honey bees (nutritional) and ants (nutritional or physical). If it exists in \( Polistes \) in the limited sense that workers vary the reproductive potential of future inseminated and overwintered gynes, it will probably be less easy to detect than in these other groups. If fall conditions or expected winter or spring conditions are such that nest founding in the spring will probably be an unusually propitious matter, so that optimum foundress-group size is smaller, selection on the queen mother would favor the production of an unusually large number of gynes of queen caliber. One way to test for such a phenomenon is to simulate the environmental conditions which correlate with autumn cues to the queen or workers of conditions to come, but this is of course a difficult proposition which cannot be lightly entertained, even if there are no theoretical difficulties. At present I see no practical way to resolve the kin selection/parental manipulation question of polygyny in \( Polistes \) with any certainty of obtaining conclusive results.

D. Pathways to Eusociality

1. Familial Pathway

Discussion of the origin of reproductive altruism and workerness has so far been based on the assumption that the key step is the habit of some offspring remaining in the parental nesting and helping their mother to raise additional offspring. This viewpoint is the prevalent one, and works treating the subject, where they do not actually point to a series of steps from solitary to eusocial life, generally assume that the familial route is universal for social insects (e.g., Allee, 1927; Ribbands, 1953; Richards, 1953). A number of authors have proposed evolutionary pathways for the Hymenoptera or some subgroup (Emery, 1894; Evans, 1958; Evans and West Eberhard, 1970; Roubaud, 1916; Spradbery, 1973; Wheeler, 1926). The most complete and least hypothetical of these, inasmuch as each stage is based on extant species, is that of Evans, of which the plan of Evans and Eberhard is an expansion and refinement. Evans’s schema, which applies to the wasps (Vespoidea) and wasplike hymenoptera, is a 13-step progression from solitary to moderately eusocial. It is summarized below.
Evolution of hunting, nest construction, and provisioning cycle toward flexibility in the order of components; from single-cell to multiple-cell nests; from mass provisioning to progressive provisioning and to the habit of macerating prey and feeding it directly to larvae.

Increased longevity of females; generation overlap; some adult female offspring remaining in the parental nest, caring for their own brood and building cells.

Increased division of labor; some females sometimes caring for brood other than their own.

Increasing division of labor; increasingly distinct reproductive castes, terminating in the condition found in *Vespula* and *Vespa*.

The key stages for our purposes are (9), in which generation overlap and nest sharing for the first time offer regular opportunities for robbing and egg replacement and, with mutual nest defense, of cheating; and (10), in which cooperative brood care and the beginnings of reproductive castes appear. It is possible to account for stage (9) with the unremarkable hypotheses that personal vigilance makes robbing by nest mates unprofitable and that females retaliate against cheaters. The primitive reproductive division of labor which arises in stage (10), however, poses the sharp question which is at the heart of theoretical socioentomology. Stages (4) and (5) in Spradbery's (1973, p. 310) scheme for the Vespoida are equivalent to Evans's (9) and (10).

**2. Semisocial Pathway in Bees**

Students of insect sociality have not been unanimous in hypothesizing the familial route for all Hymenoptera. In the light of modern theory, though, the only exception which demands serious attention is the semisocial route proposed by Lin and Michener (1972) and Michener (1958, 1969, 1974) to account for the evolution of eusociality in most nonalloidapine bees. The pathway proposed in the earliest of these is from solitary to quasisocial (cooperative broodcare by individuals of the same generation, not necessarily related) to semisocial (cooperative broodcare plus reproductive castes) to eusocial (see Fig. 1, Chapter 1).

Rather than treating joining as a special case for kin selection, Lin and Michener (1972) and Michener (1969, 1974) treat it as something not explained by kin selection. Their first point, that the maximum relatedness under outbreeding between joiner and queen is that of full sisters, so that no extraordinary $B_{ACY}$ obtains, can be discounted in the light of subsequent theory on the components of $K$ and selective forces for large $K$. If joiners are frequently not sisters, though, the necessary $K$ may rapidly become prohibitively large, especially as $K$ at primitive stages will tend to be small.

The explanation of these authors to this apparent dilemma is simply that no kin selection is necessary, because the associations are not altruistic but mutualistic, on the average beneficial to the classical fitness of each female. In the absence of reproductive castes, this can occur in any situation where two or more females will each be more productive working together than separately. Situations in which this could occur include those where
1. Nest construction is particularly difficult or prime nesting sites sufficiently scarce that it is preferrable to build an "apartment house" rather than individual "cottages.

2. Food resources come in nutritionally large but infrequent packages.

3. Defense against predators and parasites is much more effective with more than one defender. This is the situation emphasized by Lin (1964), Lin and Michener (1972), and Michener (1958, 1969, 1974)

In addition, Lin and Michener have suggested that even in the more derived semisocial stage the subordinate individuals are not necessarily altruistic. If they are reproductively somewhat disadvantaged at the time of joining, either through physiological inferiority or lateness in nesting, it may be better for them to give up exclusive rights to a dubious solitary nesting opportunity in favor of a small share in a much more successful operation. This can happen if workerlike auxiliaries have some small egg-laying opportunities qualitatively like those of the queen or, more interestingly, if they have part or all of the male-producing "franchise."

It is much less easy to account for a transition from semisocial to eusocial. This is evident if we pose the question as, "How can sterility evolve on the basis of aid given to nonrelatives?" Lin and Michener (1972) hypothesized that once semisocial colonies exist and joining is a regular event, selection could favor those colonies which produce their own auxiliaries. This would have the advantages of insuring the presence of auxiliaries and the benefits they confer, and of adding a greater-than-zero inclusive fitness effect. This latter effect would add to the advantages of previously mutualistic associations. The question which arises is whether such a hypothesis constitutes de facto discarding of the semisocial pathway, since the route proposed, except for this diversion into quasisociality and semisociality, is the same as that accepted for other hymenoptera. The implicit suggestion is that the semisocial condition provides a behavioral habit of joining and accepting, which serves as preadaptation for joining by daughters.

The semisocial hypothesis has its origin not in a priori models of how selection should operate, but rather in observations of social organization in phyletic lines of bees. The model of what must have happened preceded the explanation of how it could have done so. The actual evidence for the semisocial pathway (Knerer and Plateaux-Quenu, 1966; Lin and Michener, 1972; Michener, 1958, 1974; Michener and Lange, 1958; among others) will not be reviewed here. The interpretation of the evidence has been widely challenged (Alexander, 1974; Hamilton, 1964, 1972, 1974; West Eberhard, 1975; Wilson, 1971), and a properly meticulous examination is beyond the scope of this chapter. The principal kinds of evidence for this pathway are: (1) demonstrations of the importance of nest defense; (2) cases of occasional joining by apparently unrelated individuals;
(3) two species of supposedly permanently semisocial halictid bees; (4) the frequency and nature of semisocial stages in colony ontogeny in primitively eusocial groups; and (5) the general absence of intermediate familial-route stages without morphological castes in bees.

In addition to different interpretations of these types of evidence, the existence of permanent semisocial species is not universally accepted. It is widely doubted that such a social structure could persist in the absence of high relatedness.

At present, the semisocial pathway stands as a useful basis for a discussion of some features of social evolution, but not as a plausible theory (at least in the minds of most theoretical socioentomologists with whom I come into contact). Two lines of evidence are lacking for its substantiation: (1) incontrovertible evidence of the existence of permanent semisociality in nature, with colonies frequently initiated by unrelated females; and (2) a robust theoretical demonstration of how such permanent semisociality can exist and how it can lead to eusociality. At present, the best tools for such a demonstration are genetic modeling (e.g., Orlove, 1975) and evolutionarily stable strategy analysis (Maynard Smith, 1976). Either of these could be used in attempts to show how a trait for mutualistic honesty could prevail over a cheating trait in the early stage, and later how a trait for sterility could attain prevalence over both.

IV. CONCLUSION—STATE OF THE SCIENCE

In this chapter I have attempted to review the state and content of present theory on the origin and evolution of insect sociality. As is usual with any attempt to review key questions in an active field, the best measure of eventual success is the degree to which such an overview contributes to its own obsolescence, and in fact this has been a conscious consideration here. I have attempted, therefore, also to indicate questions which are particularly ripe for further development, both in general and specialized areas. One special case I have not reviewed is the fascinating question of the forms, origin, and adaptive significance of polygyny in polybaine social wasps. Present knowledge is still relatively fragmentary, but these wasps stand to be actively studied over the next few years. In the area of general theory, what is needed most is data to test specific predictions. Theory has so far outstripped reliable data that new theory is being built on disperse data collected for other purposes, and in some cases on previous theory itself. The obvious reason for this is that collection of such data is difficult and expensive. Breakthroughs in techniques for sampling key data, particularly the relative productivity of colonies and the different components of relatedness, will constitute major contributions.
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