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# THE QUARTERLY REVIEW of BIOLOGY



## THE EVOLUTION OF SOCIAL BEHAVIOR BY KIN SELECTION

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### ABSTRACT

*Kin-selection theory (Hamilton's "genetical theory") explains how aid that is self-sacrificing (in terms of classical individual fitness), or "altruism," can evolve if sufficiently beneficial to relatives. It is discussed here in order to clarify the meaning of kin selection and inclusive fitness (the total reproductive value of an individual, both its production of offspring and effects on the reproduction of relatives). Hamilton's condition  $K > 1/r$ , the relationship of benefit/cost and relatedness necessary for advantageous altruism, is reformulated so as to be applicable to altruism by descendants, and from the point of view of any member of a population (e.g., affected parties other than the altruist). A general expression is derived which defines inclusive fitness in terms of a classical and a kinship component. A unit of inclusive fitness—"offspring equivalents"—is defined. An index of the likelihood that altruism will occur in different social and ecological situations,  $K_i$ , is employed to evaluate conflicts of interest among the members of social groups.*

*Specific cases of altruism are discussed with attention to costs and benefits in order to show how kin selection can operate even among quite distant relatives. The probability of altruism is increased if the beneficiary stands to gain a great deal (e.g., in emergencies), if the cost is low (e.g., if the altruist is excluded from reproduction on his own or is in control of an abundant resource), or both; and if the donor is particularly efficient at giving aid or if the beneficiary is particularly efficient at using it, as in the case of the specialized workers and queens of social insects, or if both situations obtain. Phenomena discussed include social responses to food shortages in insects and primates; anti-predator responses of ungulates in variously structured social groups; social grooming and solicitude toward infants in primates; adoption of orphans in a phylogenetically diverse set of animals; "helpers" among birds, mammals, and insects; alarm calls of vertebrates; and dominance-subordinance interactions in vertebrates and invertebrates.*

*Subordinate behavior among primates and other animals living in groups of relatives may sometimes represent a kind of altruism that is advantageous (in terms of inclusive fitness) to*

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the subordinant individual, providing the subordinant individual is a reproductively inferior relative of the dominant individual and contributes sufficiently to the dominant individual's reproduction.

Mutualism (reciprocity and cooperation) and parental manipulation may produce beneficent behavior resembling that produced by kin selection. Mutually beneficent behavior can be maintained by reciprocal-altruistic selection, parental imposition, or the selfish advantageousness of acts incidentally benefiting neighbors, as well as by kin selection. Reciprocal altruism—temporary altruism with the expectation of more than compensating future aid (reciprocation) on the part of the beneficiary—requires meticulous contemporaneous controls on cheating and is therefore probably restricted to intelligent animals, the only documented example being man.

A synthesis of current ideas on the evolution of insect sociality shows how mutualism, parental manipulation, and kin selection could all have operated, either in conjunction or independently, to produce extreme altruism (worker sterility) starting with different kinds of primitive groups. A kin-selection interpretation of insect sociality is given which differs from that of Hamilton in not relying on extraordinarily high relatedness among the members of a colony. The evolution of a reproductive division of labor in insects probably involved differences in reproductive capacity among adults in primitively social groups of relatives, making it profitable, in terms of inclusive fitness, for some (namely, the reproductively inferior individuals) to become altruistic helpers.

Kin-selection theory outlines certain limits to selfishness as well as the conditions under which altruism is advantageous. Inclusive fitness, because it includes the effects of all selfish and social traits on the reproductive value of an individual, is capable of evaluating the selective significance (biological function) of any social act, whether selfish, altruistic, reciprocal, cooperative, or destructive in nature. Thus, it provides an approach which could serve as the basis for a general and comprehensive theory of social behavior.

#### INTRODUCTION

ACCORDING to classical evolutionary theory every characteristic of an organism is a means and a consequence of reproductive competition among individuals, and there should be no example of behavior benefiting another individual at reproductive cost to the performer. Reproductive cost and benefit are measured in terms of *fitness*, the number of adult offspring left by an individual in the next generation in the absence of chance effects (see Williams, 1966). Hamilton (1964a) has recently extended the conventional theory to encompass behavior involving detriment to individual fitness ("altruism") by introducing the concept of *inclusive fitness*. Inclusive fitness consists of two parts: the individual's personal fitness, and his effects on the fitnesses of his neighbors multiplied by his respective fractional relatedness to them. It thus takes into account the individual's total lifetime effect on the gene pool of the succeeding generation(s), both through the production of the individual's own offspring and through effects on the reproduction of other individuals. According to Hamilton's genetical theory of social behavior (Hamilton, 1964a, b), a social act is favored by natural

selection if it increases the inclusive fitness of the performer.

Hamilton's ideas are widely referred to as the theory of "kin selection" (Maynard Smith, 1964). I shall use the term kin selection to refer to the subclass of natural selection by which genetic alleles change in frequency in a population owing to effects on the reproduction of *relatives* of the individual(s) in which a character (allele) is expressed, rather than to effects on the personal reproduction of that individual itself (the domain of classical selection). Just as classical natural selection depends on the likelihood that offspring resemble (genetically) their parents, kin selection depends on the likelihood that other (near or distant) relatives resemble each other, i.e., bear a certain portion of genes identical by descent, so that increasing the reproduction of relatives increases the frequency of alleles like one's own genes in the population.

Kin-selection theory explains social behavior at the level of the individual rather than at the level of the group or the species. Although some authors (e.g., Wilson, 1973) have interpreted kin selection as group selection or "kin-group" selection (Brown, 1974), the idea of inclusive fitness clearly focuses on the contribution of *individuals* to changes in population

gene frequencies, simply including effects on all relatives (rather than just offspring) in the estimation of individual reproductive value. Extensions of kin-selection theory to the group or family level apply only in special circumstances (see Lewontin, 1970, for a discussion of the conditions necessary for group selection in general). In attempting to make widely applicable generalizations about social behavior I have rejected explanations at the group or population level, such as those of Wynne-Edwards (1962) and others, for reasons discussed by Williams (1966), Trivers (1971), Eshel (1972), Maynard Smith (1972), and Alexander (1974). Although selection above the individual level may sometimes affect the frequency of a social gene, contributing to its persistence or extinction, the allele must first become established by selection at the individual level (see Rand, 1967; Levins, 1970; and Alexander, 1971).

In the literature on kin selection, Hamilton and subsequent authors have tended to neglect the idea of inclusive fitness, and have concentrated on the role of a single factor, the degree of relatedness, in the evolution of social behavior. Emphasis on the extraordinarily high relatedness of hymenopteran (wasp, ant, and bee) sisters has created the erroneous impression that very high relatedness is a prerequisite for the operation of kin selection, a view tending to discourage its application to other social animals (e.g., birds and mammals) in which interacting individuals are not always so highly related. This supposition may explain the surprising absence of any direct reference to kin selection in important recent discussions of the functions and evolution of social behavior in primates (e.g., Jolly, 1972; Rowell, 1972) and other vertebrates (e.g., Kruuk, 1972).

This review begins to remedy this problem by outlining social, ecological, and developmental factors which, along with relatedness, influence the evolution of beneficent social interactions. Kin selection has a much wider potential application than is generally believed. It is one of a small set of hypotheses (see below) that should be considered whenever the functional (adaptive) significance of a social interaction is analyzed.

The examples to be cited are intended to illustrate the use of kin selection theory in conjunction with other ideas in the analysis of animal sociality, and are not intended to "prove"

the existence of kin selection nor to show that it is the only possible explanation of the examples given. Some readers will consider certain examples "already explained" by some other plausible hypothesis. They are urged to realize that a single behavior can serve more than one function at once—the benefit to inclusive fitness through aid rendered to a near or distant relative can be an advantage over and above a selfish advantage. The claim that a farmer who saves his brother's life benefits by the consequent increase of genetic alleles like his in the population, through kin selection, does not detract from the biological validity of the farmer's assertion that he did it to get help milking the cows.

Although this review focuses primarily on the evolution of beneficence and altruism, I believe that a model like that presented here—beginning with Hamilton's idea of inclusive fitness—could serve as the basis for a general and comprehensive theory of social behavior capable of evaluating the selective significance of any social act, whether selfish, altruistic, reciprocal, cooperative, or destructive in nature, and at any degree of genetic relatedness. Applications of Hamilton's genetical theory to social phenomena other than altruism are to be found in Hamilton (1970, 1971, 1972), Trivers (1974), and Alexander (1974).

#### HAMILTON'S THEORY

Hamilton defined altruism as behavior benefiting another individual while detrimental to the performer, the benefit and the detriment being defined in terms of personal fitness. He originally (1963) stated that the condition necessary for advantageous altruism is

$$K > \frac{1}{r}$$

in which  $K$  is the ratio of gain to loss in fitness resulting from the altruism, and  $r$  the genetic relatedness (fraction of genes identical by descent) of the two individuals.

According to Hamilton's theory, then, three variables affect the likelihood of altruistic behavior between individuals:

- (1) *The closeness of genetic relatedness* between the aiding and the aided individual. Unreciprocated aid is more likely to occur among rela-

tives, and the more closely related they are the more likely it is to occur.

- (2) *The magnitude of the benefit* to the aided individual, expressed in terms of the consequent increase in his fitness, or reproductive output. The greater the benefit derived from the aid, the more likely it is to be given.
- (3) *The magnitude of the cost* to the altruist in terms of his consequent loss in fitness. The more costly an altruistic act, the less likely it is to occur.

Hamilton (1964b, p. 19) gave the following "generalized unrigorous statement" of the main principle emerging from his model:

*The social behaviour of a species evolves in such a way that in each behaviour-evoking situation the individual will seem to value his neighbours' fitness against his own according to the coefficients of relationship appropriate to that situation.*

#### REFORMULATION OF HAMILTON'S THEORY

Hamilton's expression,  $K > 1/r$ , while attractively compact, cannot be applied directly to all cases of altruism (see below), and tends to obscure the significance of inclusive fitness. The following reformulation modifies  $K > 1/r$  in a series of steps so as to make it both more general and more easily analyzed in terms of classical and inclusive fitness.

#### *Extension to Include Altruism by Descendants*

The condition  $K > 1/r$  assumes that the relatedness of the altruist and the young of the beneficiary is as one-half  $r$ . This is not true for direct ancestors of the altruist, the most important example being parents: in diploid animals,  $r$  with a full sibling is  $1/2$ , not one-half of  $r$  with the parent ( $r$  with the parent is  $1/2$ , and  $1/2 r$  is thus  $1/4$ ). Thus, the form  $K > 1/r$  does not apply directly to the matrifilial societies of social insects, the most discussed application of the genetical theory. (Hamilton, in a personal communication, points out that in such cases the condition does yield proper values if both parents are considered beneficiaries and their degrees of relatedness are summed. However, it seems preferable to have an expression in which both terms can be applied uniformly to any case.) In more recent publications Hamilton (1971-74) has dropped the original  $K > 1/r$  and has substituted another form,

$$K > \frac{1 + F_A}{2r_{AB}},$$

in which  $F_A$  is the inbreeding coefficient for individual  $A$  (the likelihood that two homologous genes in  $A$ , the altruist, are replicates) and  $r_{AB}$  is the probability that a gamete of  $A$  has the same gene as a gamete of  $B$ . Uniform application of the new expression requires the same assumption—that altruist and beneficiary's young are related as one-half the relatedness of the altruist and the beneficiary ("beneficiary" referring to the individual whose reproduction, or fitness, is favorably affected). A more generally and uniformly applicable procedure is to use values of

$$r_{AB},$$

the relatedness of the altruist and the young of the beneficiary. In an outbreeding population the condition thus becomes

$$K > \frac{1}{2r_{AB}}, \quad (1)$$

This modification, while less compact, is perhaps intuitively easier to apply in addition to being more general, since it refers directly to the fitnesses affected and to the relative values of the individuals (young) whose production is altered.

#### *Viewpoints of Non-donors*

Hamilton's condition, like formula (1), applies only to the decision of a *donor* regarding the profitableness of altruism. The degree to which it can be used to predict the results of natural selection depends, among other things, on the degree to which the donor individual is in control of his own reproductive behavior. We must therefore consider the possibility that selection operating on individuals other than the donor might influence the probability of his becoming an altruist—that his altruism might sometimes be forced, reinforced, curtailed, or prohibited through selection operating on influential individuals such as parents (Alexander, 1974) or other members of a cohabiting group. It is even possible that at certain values of  $K$  and  $r_{AB}$ , a beneficiary might advantageously refuse aid—for example, if it were to exact too much from a close relative. (A case in which selection on the beneficiary might

limit altruism—that of robbed wasps of the genus *Trigonopsis*—is given in the section on reciprocal altruism, below.) It is therefore useful to make a version of formulation (1) giving the condition for advantageous altruism from the point of view of any given member (“Ego”) of a population:

$$K > \frac{r_{A_y}}{r_{B_y}} \quad (2)$$

where  $r_{A_y}$  and  $r_{B_y}$  are respectively the probabilities of Ego having a given gene in common by descent with the young of the donor (A) or with the young of the beneficiary (B).

*Expression in Terms of Fitness*

Expressed in terms of fitness, a

$$K \equiv \frac{a_{B_2} - a_{B_1}}{a_{A_1} - a_{A_2}}, \text{ or } -\frac{\Delta a_B}{\Delta a_A}$$

where  $a_{A_1}$  and  $a_{B_1}$  are the would-be personal fitnesses of donor and beneficiary without altruism,  $a_{A_2}$  and  $a_{B_2}$  their fitnesses following altruism by A.

By substitution, we can rewrite formulation (2) as

$$r_{A_y} \Delta a_A + r_{B_y} \Delta a_B > 0.$$

This form applies to both beneficent ( $\Delta a_B$  positive) and harmful ( $\Delta a_B$  negative) acts, whether selfish ( $\Delta a_A$  positive) or altruistic ( $\Delta a_A$  negative), whatever the degree of relatedness of performer (A) and affected individual (B).

Since animals that live in groups often perform behavior (such as alarm calls or cooperative hunting) that benefits more than one individual simultaneously, a more general expression is

$$r_{A_y} \Delta a_A + \sum_{i=1}^n (r_{B_y} \Delta a_B)_i > 0 \quad (3)$$

which sums the effects on the fitnesses of  $n$  individuals of an act by individual A. Since the most commonly considered point of view is that of the performer of a social act, the most commonly useful form of this expression is that in which A and Ego are identical and  $r_{A_y}$  is the average relatedness of the performer and his own young ( $= 1/2$ ):

$$\frac{1}{2} \Delta a_A + \sum_{i=1}^n (r_{B_y} \Delta a_B)_i > 0 \quad (3a)$$

For the case in which Ego is a third party (neither the altruist nor the beneficiary) the condition is:

$$r_{A_y} \Delta a_A + \sum_{i=1}^n (r_{B_y} \Delta a_B)_i - \Delta a_E / 2 > 0 \quad (3b)$$

in which  $\Delta a_E$  is the change in Ego’s personal fitness due to intervention ( $\Delta a_E / 2 =$  cost of intervention).

*Dilution Factor*

I will next try to show how altruism can be advantageous even at relatively low values of  $r_{AB_y}$ . Williams (1966) has objected to explanations involving aid given distant relatives on the grounds that such relatives carry a large portion of competing genes. This raises a very important point. For kin selection to operate positively at low values of  $r$ ,  $r_{AB_y}$  must be greater than the average relatedness of A with all other individuals in the population as a whole ( $\bar{r}$ ). Above this value, as Hamilton (1964a, 1970) has pointed out, the unlike fraction acts to slow (or dilute) the progress of selection but does not alter its direction. This is because the fraction of a beneficiary’s genotype that is not identical by descent contains a random collection of the alleles present in the population at large and therefore neither augments nor diminishes the relative frequency of genes like the altruist’s in the gene pool. These non-identical alleles, therefore, should not be thought of as “competing” genes in the sense that somehow they would oppose or cancel out the positive contribution of the fraction that is identical. For, if this were so, sexual reproduction in outbreeding organisms would be fruitless to an individual, since the non-identical half of its offspring’s genes (those from the parent’s mate) would exactly cancel out the positive contribution of the identical half. It is important to realize that any small above-average degree of relatedness can in fact serve as the basis for kin selection. As long as the relatedness of beneficiary and altruist is even slightly above average, any (even a small) increase in fitness ( $a_B$ ) is profitable to A (providing the ecological cost of A of adding individuals to the population is not too great—see “Cheap Aid and the Effects of Ecological Competition,” below; and Alexander, 1974).

Thus, it would be more precise to write condition (3) by taking the dilution factor,  $\bar{r}$ , into account, as follows:

$$(r_A, - \bar{r}) \Delta a_A + \sum_{i=1}^n [(r_{B_i}, - \bar{r}) \Delta a_{B_i}] > 0 \quad (4)$$

The left side of this expression is like the "inclusive fitness effect" of Hamilton (1964a) except for the involvement of  $\bar{r}$ , the significance of which Hamilton did not discuss until later (Hamilton, 1970).

The consideration of  $\bar{r}$  is complicated by the difficulty of knowing how to define the relevant population to which it should refer—whether that population should be the whole species or some more closely interbreeding (and inter-competing) relatively isolated subunit of the species. As Hamilton has pointed out, it is probably realistic to assume that  $r_{AB} > \bar{r}$  in most social situations: with common patterns of dispersal the unrecognized individuals most likely to be encountered are the ones likely to be most related (here he evidently takes  $\bar{r}$  to refer to the species as a whole, but the same assumption should hold for subpopulations also). Numerical values of  $r$  given in this paper and in the literature assume a large panmictic population in which  $\bar{r}$  is negligible.

#### *The Meaning of Inclusive Fitness*

Expressions (1) through (4) simply restate the basic theorem of Hamilton's genetical theory of social behavior: for a given act (or gene) to be selectively advantageous to a given individual it must cause a net gain in the *inclusive fitness* of that individual. In formulation (3a), effects on the personal (classical) fitness of the performer are represented by the first term; kinship effects are represented by the second term. The sum of the two terms—the entire left side of expressions (3) through (4)—is the effect of the behavior in question on the inclusive fitness of A.

Inclusive fitness ( $a_i$ ), then, is personal (classical) fitness ( $a$ ) plus the lifetime sum of effects on the fitness of relatives ( $\sum \Delta a_B$ ), with each effect weighted according to the degree of relatedness of the individual affected. I shall call this second component of inclusive fitness the "kinship component" ( $a_k$ ) to distinguish it from the personal (classical) component:

$$\begin{array}{rcl} \text{inclusive fitness} & = & \text{classical fitness} + \text{kinship component} \\ a_i & = & a + a_k \end{array}$$

The kinship component is calculated as follows:

$$a_k = 2 \sum_{i=1}^n [(r_{B_i}, - \bar{r}) \Delta a_{B_i}],$$

in which  $n$  is the total number of individuals whose fitnesses are affected by the individual in question during his lifetime, and  $\Delta a_B$  is his total lifetime effect on the fitness of each one (B). (The sum is multiplied by two to make the units of the kinship component comparable to the units of classical fitness—each adult offspring or its equivalent in terms of genes identical by descent = 1.0.)

The unit of classical fitness is adult offspring. I shall call the unit of inclusive fitness "offspring equivalents," valuing each relative (or fraction thereof) added to, or subtracted from, the population according to its relatedness compared to the young of the individual in question. For example, in a diploid organism each offspring is on an average one-half genetically identical by descent to its parent, and its value in terms of classical fitness is 1.0. A sibling, also related by 0.5, is genetically equivalent to an offspring, or worth 1.0 offspring equivalents. A nephew ( $r = 1/4$ ) is worth 0.5 offspring equivalents; a cousin ( $r = 1/8$ ) 0.25; a grandchild ( $r = 1/4$ ) 0.5; and so forth. Suppose an individual raises three offspring to reproductive maturity and in addition gives altruistic aid adding 0.5 to his mother's fitness and 1.0 to his brother's fitness. The aid given his mother is worth 0.5 offspring equivalents and that given his brother is worth 0.5 ( $r$  with the brother's offspring—nieces and nephews—is  $1/4$ , or 0.25). So this individual's classical component is 3.0; his kinship component is 1.0 (i.e.,  $0.5 + 0.5$ ); and his inclusive fitness is 4.0.

In accordance with the present formulation, we can classify all social behavior into two major groups corresponding to the two components of inclusive fitness: first, the primarily "selfish," contributing primarily to the personal fitness component; and second, the primarily "altruistic," contributing primarily to the kinship component by means of positive effects on others. Classified in this way—according to the mode of action of natural selection—"selfish" social behavior includes both overt selfishness, such

as aggressiveness and territoriality, and quasi-altruistic selfishness, such as cooperation and reciprocal (temporary) altruism. However, it should be common to find both components of inclusive fitness augmented simultaneously by a single act.

As pointed out by various authors (e.g., Lin and Michener, 1972) there is ultimately no such thing as biological altruism. Obviously, "altruism" as defined here is ultimately selfish in leading to the spread of alleles like those of the performer in the population. Problems in defining altruism are discussed by Orlove (1974). I shall use the word "beneficent" to describe any behavior raising the fitness of others regardless of its evolutionary basis.

*The Threshold Value of K for Advantageous Altruism ( $K_t$ ) as an Index of the Likelihood that Altruism Will Occur*

Expression (2), above, defines the level of K (the benefit/cost ratio) above which altruism is advantageous. We can call this level  $K_t$ —the threshold value of K for advantageous altruism. When the benefit/cost ratio for a given altruistic act is higher than  $K_t$  from a given individual's point of view, then the altruism is advantageous to that individual.  $K_t$  is calculated by dividing the relatedness of the concerned individual to the young of the altruist ( $r_{A_y}$ ) by his relatedness with the young of the beneficiary ( $r_{B_y}$ ):

$$K_t = \frac{r_{A_y}}{r_{B_y}}$$

The numerical value of  $K_t$  gives the number of extra young that must be produced by the beneficiary to just compensate every one lost to the altruist. This number must be exceeded if a given act of altruism is to be considered advantageous to the individual from whose point of view  $K_t$  is calculated. So the lower the value of  $K_t$ , the more likely is the altruism to occur or to be encouraged as the result of natural selection on that individual or class of individuals. Because it can be applied to the point of view of any individual,  $K_t$  is particularly useful for analyzing conflicts of interest among individuals regarding the desirability of a given kind of social behavior or organization (see Table 1, and the discussion of insect sociality, below).

According to kin-selection theory, a donor is expected to be more altruistic toward close relatives than toward distant ones. But it must be common for altruism to occur in social groups of variously related individuals in which the altruist is unable to distinguish its different degrees of relatedness with others. The theory then predicts that *within groups of variously related individuals who are unable to distinguish between near and distant relatives, altruism will be performed as if  $r_{B_y}$  were equal to  $\bar{r}_{G_y}$ —the average of all values of  $r_{B_y}$  for the possible beneficiaries in an average group of that kind.* In such cases  $K_t = r_{A_y} / \bar{r}_{G_y}$ .

This version of  $K_t$  can be used as an index of the likelihood of observing a given kind of behavior in a given kind of group. For example, suppose we are interested in estimating the

TABLE 1

$K_t$  for different kinds of social organization from different points of view.

( $K_t = r_{EA_y} / r_{EB_y}$  = lowest possible benefit/cost ratio for the social organization (type of altruism) cited to be considered advantageous from "Ego's" (E's) point of view. A = altruist; B = beneficiary.)

KIND OF SOCIETY	DIPLOID SPECIES		HAPLOID SPECIES	
	$K_t$ from point of view of: Altruist	$K_t$ from point of view of: Altruist's Mother	$K_t$ from point of view of: Altruist	$K_t$ from point of view of: Altruist's Mother
Solitary Parental (A cares for own young)	1.00	1.00	1.00	1.00
Filial (A helps siblings)	2.00	1.00	1.33	1.00
Patri-filial A helps parent; brood 50% male, 50% female	1.00	0.50	1.00	0.50



likelihood that orphans will be adopted by subadult females in a species living in nuclear family groups (parents and full sibs) as compared to a species forming clans containing equal numbers of infant siblings and cousins of the potential foster parent. From the adopting female's point of view,  $K_i$  in the nuclear family is 1.00 ( $r_{A_y} = r$  with her own young = 0.50;  $r_{B_y} = r$  with a full sib = 0.50); whereas in the clan,  $K_i$  is 1.33 ( $r_{A_y} = 0.50$ ;  $\bar{r}_{G_y}$  = average relatedness with full sibs, 0.50, and with cousins, 0.25 = 0.375;  $0.50/0.375 = 1.33$ ). In other words, in order to be advantageous to the altruist in terms of inclusive fitness, adoption in the clan must be a third again more profitable (or less costly) than in the nuclear family.

#### THE IMPORTANCE OF COST AND BENEFIT

Hamilton (1963–72) has presented evidence that altruism occurs among close relatives, and has discussed various factors contributing to a high degree of genetic relatedness among the members of social groups. Alexander (unpub.) discusses kin selection among humans. Most examples cited as “problems” for the genetical theory, e.g., alarm calls which carry large distances, and human altruism, involve altruism at relatively low degrees of genetic relatedness. In this section I intend to show that such cases are often the exceptions that prove the rule: when  $r$  is relatively low, the other factors contributing to inclusive fitness are relatively high. That is, the act is either basically selfish (see “Reciprocal Altruism and Cooperation,” below), or is forced (e.g., by parental manipulation—see below), or involves large gains to the beneficiary at relatively small cost to the performer. For example, a trained life-guard who saves a drowning child (non-relative) can at very little risk to himself salvage the child's entire future reproductive effort ( $a_B$  without altruism = 0). Theoretically, the most willing lifeguard should be a physically fit eunuch or post-reproductive individual (who has nothing to lose in terms of personal fitness), and with few living relatives (little to lose in terms of future gains to inclusive fitness through aid to close kin). A good beneficiary is one with high reproductive value (Fisher, 1930), such as a pregnant low-income Catholic teenager about to produce her first child. So costs and benefits to fitness of a given act are age-

dependent (Emlen, 1970); and a large number of other developmental, social, and ecological factors must affect the probability of altruism through their effects on the terms  $\Delta a_B$  and  $\Delta a_A$  ( $K$  of Hamilton). It is thus ironic that these terms have generally been neglected in discussions of kin selection.

In general, the greater the ratio of benefit to cost ( $K$ ) the more likely is the altruism, and the lower is the value of  $r$  necessary for positive selection. There are three obvious general situations in which  $K$  might be large enough to make altruism advantageous at low values of  $r$ : cases of great need (much to gain) on the part of the beneficiary; cases of cheap aid (little to lose on the part of the altruist); and cases in which a small amount of help has a great effect, either because the donor is especially efficient at giving aid (a “super-donor”) or because the beneficiary is particularly efficient at utilizing it.

To simplify the discussion, I shall use Hamilton's  $K$ —the benefit/cost ratio—to refer to the total changes in fitness caused by a social act or role possibly affecting numerous individuals, even though strictly speaking it is only meaningfully applied to interactions between just two individuals having a given  $r$ .

#### *Aid During Emergencies*

The probability of altruism among somewhat related individuals is increased in urgent situations, when aid has a large positive effect on the beneficiary's fitness (he stands to lose a lot if not aided) and hence on the altruist's inclusive fitness. Kin-selection theory predicts that altruism toward relatives outside the immediate (nuclear) family may occur during emergencies even in species normally showing little altruistic behavior; and that unusual (extreme) altruism may occur among relatives under stress.

A possible example of extreme altruism among relatives in an emergency is provided by Eickwort (1973) in one of the few published discussions of the role of changes in fitness in kin selection. She assesses the adaptiveness of cannibalism among chrysomelid beetles (*Labidomera clivicollis*), in which eggs and newly hatched larvae are sometimes eaten by older sibs (or half sibs). She defines the conditions under which such cannibalism would be adaptive (from the victim's point of view), and

concludes that "cannibalism is most readily accounted for at [those] points in the life cycle where either the nutritional benefits are great or mortality is high for any reason" (p. 453). Alexander (pers. commun.) points out that such behavior may be the product of selection on the mother beetle, as he compares it to other animals in which parents sacrifice one offspring in favor of another during periods of food scarcity. Indeed, the threshold  $K$  for advantageous cannibalism ( $K_c$ ) is only 1.0 from the mother's point of view, whereas it is 2.0 from the larva's point of view (assuming larvae to be full sibs), a difference that makes it perhaps more likely to evolve by selection on the parent. However, at values of  $K$  (the benefit/cost ratio) greater than 1.0 but less than 2.0 there would be a conflict of interest between parent and larva, and if  $K$  were often at this level larvae might be expected to evolve resistance to cannibalism. Above  $K = 2.0$ , cannibalism is desirable from both points of view.

Other kinds of "altruistic" responses to food shortage have been observed in insects. I have studied a colony of the tropical social wasp *Metapolybia aztecoides* during a period of nutritional crisis—when most of the original (swarm) workers had died or disappeared, and the first offspring workers had not yet emerged to replace them in feeding the numerous large larvae and idle queens present on the nest. The result was that some queens become workers (foragers), evidently in direct response to (i.e., immediately following) strong food-soliciting behavior on the part of hungry nestmates. Not only were the beneficiaries of this behavior experiencing an emergency, but there is evidence that the queens-turned-workers (altruists) were those among the original queens who had the lowest relative reproductive capacity (and hence stood to lose least by becoming non-reproducing workers): they were subordinates in their dominance interactions with other queens, a quality associated with lesser ovarian development in wasps (see Pardi, 1948; West, 1967). Eberhard (1972, 1974) found that nesting females of a primitively social sphecid wasp, *Trigonopsis cameronii*, are allowed in times of need to steal prey from cells stocked by relatives (stealing occurs when the robber has had poor hunting success). The restriction of stealing to periods of necessity may raise  $K$  sufficiently to make it advantageous for the robbed female

to permit the robbery even though, in terms of  $r$  alone, she should prefer to keep the prey for her own young ( $r = 1/2$ ; stolen prey are used to rear young related to her by only  $3/8$ , if the associated females are sisters, which is the most closely related they could be as members of the same generation—see Eberhard, 1974). Some responses of primates to nutritional (ecological) stress, also possibly explainable in terms of kin selection, are discussed in the subsequent section on dominance and subordination.

In many species of social insects the period of founding of the nest is a time of high colony mortality (see Brian, 1965; West Eberhard, 1969; Wilson, 1971), and in some species cooperation and altruism occur during that period among more distant relatives than is usual. In various species of tropical wasps new nests are founded by swarms containing several egg-laying queens and a staff of workers who attend the combined brood, for which the highest possible worker-brood relatedness ( $r_{AB}$ , queens and workers being assumed to be sisters) is only  $1/4$ . There is evidence that in some species, once the initial high-risk period is over, the colonies return to the matrilineal condition, and a high  $r_{AB}$  ( $1/2$  if queens mate only once) is restored (West Eberhard, 1973). A similar phenomenon has been noted by Pisarski (1972, 1973) in long-term observations of formicine ants. Certain species of the subgenera *Formica* and *Coptoformica* live in nesting associations called "polycalic" colonies, in which the members of several individual subcolonies inhabiting separate nests are somewhat related, all of them being ultimately descended (by repeated budding off of polygynous groups) from a single original monogynous nest (queen). Mature, established subcolonies of the polycalic colony function independently, but newly founded ones receive a massive influx of aid (workers) from other nests (i.e., from peripheral relatives), so that there is a rapid initial growth. When a subcolony for some reason begins to decline, its workers move brood and reproductives to another nest, where they are received ("adopted?") without animosity.

Attack by predators, a kind of emergency common in nature, often summons aid from group members who are not the attacked individual's parents and who are not altruistic in other situations. Beneficiaries of such aid are

commonly young (helpless) individuals. Janzen (1970) saw several adult coatis (*Nasua narica*) come to the aid of a young adult male who was being attacked by a *Boa constrictor*. Female coatis and their young live in rather changeable groups usually showing little cooperation or altruism but likely to be members of the same family or extended family (Kaufmann, 1962). Kruuk's (1972) comparative study of group-living ungulates under attack by hyenas amounts to a natural experiment in which he observed different degrees of altruism in the responses of differently structured groups to a "constant" strong predator. It is thus a useful test of kin selection theory, although Kruuk did not directly discuss this aspect. He found a "relation between group size and cohesion and the anti-predator response" (p. 206). Thompson's gazelles, which live in large amorphous herds, generally do not assist each other in defense against predators; whereas eland and buffalo, living in fairly small to large herds (clearly discrete units) show aggression and mutual assistance in their reactions against hyenas; and the families and stallion bands of zebras, small and very distinctive units, show high aggression in defense of their own unit but not of others. Kruuk (1972, p. 205) found it "hard to see why zebra mares should defend only their own foals, whereas eland come to the assistance of calves which are not necessarily their own (but in the same herd)." But the different degrees of altruism seem to correlate, as predicted by kin-selection theory, with the different degrees of genetic identity likely to exist within the groups described. Zebra families and bands roam independently, so that neighboring families are not likely to be relatives. Eland families, in contrast, are part of a stable group more likely to be composed of somewhat related subunits. Opportunities for reciprocation (see Trivers, 1971, and below) would also be more common among eland than among zebra.

Wounded or temporarily disabled individuals are given extra attention in many species. Wounded Bonnet macaques receive intensive grooming by many fellow group members in succession. Dirt and other foreign matter are picked out of wounds and the wounds are licked clean. There seems to be a direct relationship between the seriousness of the wound and the amount of grooming activity (Simonds, 1965). Wild dogs regurgitate food to cripples, infants,

and nursing mothers who don't go out to feed; yet once the pups are weaned, food is refused the mother but given to the still relatively helpless pups (v. Lawick Goodall and v. Lawick Goodall, 1970). Similarly, infant, pregnant, and nursing wolves are regurgitated to by other members of a pack (Etkin, 1964). A mother and two calf zebras were aided by a group of ten adults when attacked by wild dogs, and a whole herd of fifty or so zebras will slow down to stay with a threatened foal (v. Lawick Goodall and v. Lawick Goodall, 1970).

Infant social primates are often helpless to the point of being unable to survive on their own, and can in that sense be considered to be in a constant state of emergency. They are commonly the objects of altruistic attention by adults other than their parents (see Carpenter, 1965; Jay, 1965; Simonds, 1965; review by Jolly, 1972). Attention to infants undoubtedly sometimes has selfish ulterior motives—other or additional selective advantages contributing to personal fitness, e.g., enhancing the social status of the donor (in rhesus monkeys—Jolly, 1972), providing practice in motherhood (in langurs—Jolly, 1972), or perhaps serving to help integrate (identify) the infant group member through intimate contact. But it is also likely to satisfy the conditions for profitable altruism when benefiting somewhat related infants, as in the species mentioned (see references cited). The famous "aunt behavior" of social primates (intense and repeated attention to infants by females other than their own mothers; see Jolly, 1972) may at least in part be due to benefits to the kinship component of the inclusive fitness of the so-called aunts (probably, in fact, relatives). The significance of infants as a class of suitable beneficiaries (individuals not yet competing with adults and with their entire reproductive lives ahead of them, hence with much to gain through altruistic aid) may be dramatized by Moynihan's (1970) observation that caged adult tamarin monkeys utter infantile cries when extremely frightened. This practice, if it occurs in nature, may represent mimicry of the infants' alarm cry and may serve to summon aid to adults (ordinarily less suitable beneficiaries, but possibly worth aiding in an extreme emergency).

A dramatic instance of dire emergency occurs when the dependent infant of a strongly parental species loses its mother. In such cases the

infant will almost certainly die if left alone, so the potential gain in fitness for saving it is very high. In theory, whether or not such orphans are adopted depends on the social structure of the group in which they find themselves—whether or not they are likely to encounter a relative whose inclusive fitness might be increased by giving aid. In practice this seems to hold: adoption of orphans occurs in a taxonomically diverse set of animals, including chimpanzees (v. Lawick Goodall, 1968), baboons, macaques, and langur monkeys (see Jolly, 1972), wild dogs (v. Lawick Goodall and v. Lawick Goodall, 1970), coatis (Kaufmann, 1962), and a primitively social eumenid wasp, *Zethus miniatus* (West Eberhard, in prep.). In all of these cases the adopting individuals were either known siblings (chimpanzees) or other individuals likely to be somewhat closely related as members of extended families or clans (macaques, coatis, *Zethus miniatus*) or other relatively closed groups (langurs, wild dogs). Furthermore, in at least some of these cases the adopting individual was temporarily excluded from reproducing on its own—e.g., was a prereproductive young adult, or, in the case of the wasp, a female without a ready-made cell or larva—i.e., individuals with comparatively little to lose by being altruistic. Part (or all) of the adoptive parent's gain in inclusive fitness may, of course, be "selfish," e.g., as hypothesized by Kummer (1971), who has suggested that adoption of orphaned female infants by male Hamadrayas baboons sometimes serves as the first step toward building a harem.

By contrast, an outstanding refusal to adopt orphans is shown by wildebeest females: even lactating mothers who have lost their own calves refuse to accept bleating orphans who approach them and try to nurse from "udders bursting with milk" (v. Lawick Goodall and v. Lawick Goodall, 1970). Wildebeest cows also seldom show cooperative defense of calves (Kruuk, 1972). The failure to adopt orphans, like the lack of an altruistic anti-predator response, may be explained in terms of kin selection: wildebeests live in very large and amorphous herds, sometimes containing several hundred individuals. If the herds have no internal structure that would increase the likelihood that adjacent individuals are sufficiently related, then the relatedness of a cow with a nearby attacked or orphaned offspring may well be too low

to justify whatever expenditure and risk are involved in saving its life. A similar refusal to adopt helpless orphans has been noted among flying foxes, bats—which, like wildebeest, are highly mobile parental animals living in very large groups, containing many thousands of individuals (Nelson, 1965)—and in elephant seals (Williams, 1966), which also breed in huge groups evidently not showing internal subgroups beyond the nuclear-family level.

#### *Cheap Aid and the Effect of Ecological Competition*

It is obvious that if the benefit/cost ratio ( $K$ ) must be above a certain level ( $K_1$ ) for altruism to be advantageous, then the lower the cost of giving aid the more likely it is to occur, and the more likely it is to occur among relatively distant relatives. Hamilton (1964b) has given several illustrations of low-cost altruism, including alarm calls (see below), social grooming, and the length of post-reproductive lifespan in cryptically and aposomatically colored moth species (see also Blest, 1963). Instances of "cheap aid" might occur (1) when an individual is itself incapable (or nearly incapable) of reproduction on its own—when it is idle, or has nothing or little to lose in terms of personal fitness through altruism (as in the case of postreproductive or sterile adults and those temporarily excluded from reproductive roles, or (2) when the altruism involves a non-storable essential resource that for the donor is in abundant supply.

Individuals temporarily excluded from reproducing, e.g., by virtue of their age or social position, stand to benefit through kin selection by helping reproducing relatives as long as the altruism does not cost too much in terms of their own future reproductive capacity—doing something is better than doing nothing, especially since there is always a certain probability that the "waiting" individual will die before reproducing. There are many examples of such altruism in a wide range of taxa. Among birds, the anis (*Crotophaga* spp.) and various species of jay have been cited as examples of altruistic care of young likely to be siblings by prereproductive adults (Hamilton, 1964b; Brown, 1970). Armstrong (1965) has listed eleven species of birds in which young individuals assist in rearing

younger broods, including a swallow, mannikins, moorhens, wrens, tits, woodpeckers, and the Australian white-winged chough. "Supernumerary" adults reportedly help mated pairs feed the young in black-eared bush tits, banded cactus wrens, little bush tits, and variegated wrens (Armstrong, 1965). And young adult beavers still with their parents help to build and maintain dams prior to reproduction on their own (Bourlière, 1964).

Among primates, subordinate or young adult males are sometimes partly or entirely excluded (temporarily) from reproduction, yet participate in group defense and social grooming benefiting other individuals and their young (e.g., Hall and DeVore, 1965). While such behavior may have functions contributing to classical fitness (e.g., maintenance of a place in the group essential to future reproduction), part of the payoff would be in terms of the kinship component of inclusive fitness whenever the benefited individuals are likely to be relatives (for evidence that they are, see Jolly, 1972; Fox, 1972).

In temperate-zone populations of the social wasp *Polistes fuscatus* females which are physiologically capable of reproduction (mated, overwintered females with ovaries containing large eggs which they sometimes lay), but which emerge late from hibernation, become sterile workers on the nests of other females (West Eberhard, 1969). There seems to be a very high premium on starting colonies early: nearly all colonies are founded within two or three days in the spring, indicating that latecomers are at a marked reproductive disadvantage. They may have a lower personal fitness because of any one or a combination of such factors as the reduced availability of suitable nesting sites, the shorter length of the remaining growing season, the reduced chance of getting helpers, or physiological (reproductive) inferiority as indicated by their behavioral subordination to queens (see West, 1967; West Eberhard, 1969). Such factors might make it preferable for them to help another rather than to go off on their own, even though the highest possible  $r_{AB}$ ,  $(3/8)$  for doing so is slightly lower than the  $r$   $(1/2)$  with their own young (all overwintered females are of the same generation; therefore the closest relationship they could share is that of sibling hymenopteran females:  $r = 3/4$ ;  $\bar{r}$  with nieces and nephews =  $3/8$ ).

The importance of the cost of altruism is indicated by the restraint sometimes shown in giving aid. Low-cost altruism occurs among groups in which individuals normally refuse to give high cost aid or give it only in situations of urgent necessity. *Metapolybia* (wasp) queens who become workers participate in relatively low risk activities (brood care and building on the comb), and undertake to forage (a higher risk activity, involving greater expenditure of energy and exposure to rain and predators) only when the colony is in a trophic crisis, as explained above. Gazelle females, which singly do not usually aid the offspring of other gazelles which are under attack by groups of hyenas, occasionally will do so in the company of others (e.g., several may perform distracting behavior near a fawn threatened by a single hyena) or in some less dangerous situation, e.g., when a fawn is injured but is not under attack (from Kruuk, 1972). Coatis who groom and guard the young of temporarily absent females do so with less intensity than they show to their own young (Kaufmann, 1962).

An example of category (2)—facultative low-cost altruism in times of abundance—may be represented by the feeding behavior of wild chimpanzees. When food is abundant the chimps make a lot of noise upon discovering a rich source of fruit, and thereby attract other groups to the site. However, when comparatively little fruit is available they forage on their own or in two's or three's (rather than in larger groups) and are quiet (Reynolds, 1970). Even if the noise arises from fighting over food rather than being an evolved signal, it constitutes an announcement that benefits the (presumably) rather unrelated individuals of other groups. That altruism should be more common when times are good is an idea quite natural and "obvious" to humans, which suggests that we go by the same rule.

The facultative nature of generosity in chimpanzees illustrates a further point. Just as the low cost of altruism in times of abundance makes altruism more likely, so should scarcity of a resource (the high cost of sharing) be associated with selfishness, even at high values of  $r$ . If there is very strong competition for some resource, a potential donor should refuse to aid (and may even eliminate) its closest relative. Thus mammalian littermates and sibling nestlings among birds push each other

aside even though they are (except for their parents) each other's closest relatives (see Alexander, 1974, for a discussion of this effect of ecological competition, and the possible role of parents in controlling such behavior). The cost of altruism (the denominator of  $K$ ) is thus clearly a function of the intensity of competition between donor and beneficiary. In general, we should find that *the greater the intensity of reproductive or ecological competition between two individuals, the less the probability of altruism between them*. The probability of altruism thus depends on such ecological parameters as the so-called carrying capacity of the environment, population size, and population (or social) structure (since not all age or behavioral classes are equally competitive). This consideration immensely complicates the determination of  $K$  in nature. There is certainly no species for which the total ecological cost to conspecifics of adding another individual to the population (or subtracting one from it) is known.

#### *Super-Donors and Super-Beneficiaries*

The workers of social insect colonies are prime examples of super-donors. If it is advantageous to be a helper, it is probably more advantageous to be a more efficient helper; hence the extreme morphological and behavioral specializations of the sterile workers of some social insects can be viewed as products of selection on workers as individuals rather than as (or in addition to) products of selection at the level of the colony (selection on mothers), the traditional way of interpreting such adaptations (Darwin, 1859; Wilson, 1971). Although in most conditions the two kinds of selection would produce the same results, this is not always the case—see section on insect sociality (below). The beneficiary's capacity to use aid must keep pace with the donor's ability to provide it, or increased efficiency in giving aid will be selected against (will have no effect). It is therefore not surprising to find the most extreme examples of worker polymorphism accompanied by the most exaggerated super-reproductive queens (e.g., in the army ants, *Eciton*—see Wilson, 1971).

There is a corollary of this line of reasoning which helps dispense with some supposed problems for Hamilton's theory: the better the helper the more advantageous it is to be a helper

rather than a reproductive individual, and the less important it is to be closely related to the beneficiary. That is, a worker, as a super-donor, is in a sense "trapped" in altruism, not only by being a relatively poor (or even sterile) reproductive individual, but also by being such a good donor that she cannot afford to be anything else if there is a relative ( $r > \bar{r}$ ) around to be helped. Thus, if a worker's mother dies, and with her the worker's evolutionary *raison d'être*, she might be expected to serve a less closely related reproductive individual. If the altruist is completely sterile, as in the case of some social insects, the denominator of  $K$  ( $a_A$  before altruism) goes to zero and  $K$  approaches infinity; so the sterile worker, while she will prefer to help her mother, should in the absence of the mother, or if unable to distinguish her from other reproductive females in the vicinity, find it advantageous to help a female with any, even slight, degree of relatedness greater than  $\bar{r}$ —anything is better than nothing. This may help to explain the behavior of queenless army ant workers, which reportedly will join a passing colony and aid the "foreign" queen (Schnierla and Brown, in Lin and Michener, 1972). However, even in cases of complete sterility (laying workers are apparently unknown in army ants—see Lin and Michener, 1972),  $r_{AB}$ , of the orphaned worker and the adopted queen must be greater than  $\bar{r}$  or it would be more advantageous for an orphan to die unemployed. It seems likely that this condition is satisfied in the case of the army ants, which represent a relatively "viscous" population, since the virgin queens are wingless and colonies reproduce by fission (Schnierla and Brown, 1950); hence an orphaned worker can be fairly certain that the first queen she encounters will be quite closely related to her on her mother's side.

The extremely high  $K$  of a super-donor may in some cases also help to explain the problematical existence in ants and polybiine wasps of multi-queen colonies, in which several queens band together, apparently in order to reap the advantages of rapid colony establishment, and the workers care for the broods of various females in addition to that of their mother. Strictly in terms of  $r$ , the worker's own mother is the only reproductive individual qualified as beneficiary. Accordingly, workers of multi-queen colonies should rebel and go off to

reproduce on their own, or should learn to discriminate between their mother and other queens. However, in the case of a super-donor the choice is not between helping the mother or reproducing on her own; it is between helping the mother or some other, at least slightly related female, or nothing. Also it should be remembered that the worker is interested in maximizing the mother's reproduction, and if aiding other females contributes to the efficient integration of a multi-queen colony favorable to the mother it is likewise usually favorable from the worker's point of view. Thus, the multi-queen society can be viewed as a group of queens for whom cooperation (reciprocity) is advantageous to individual queens and, hence, to their workers.

Among vertebrates, various examples can be cited of altruism involving efficient beneficiaries, that is, superior reproductives or individuals in a relatively good position to capitalize on aid. Dominant individuals aided by subordinates will be discussed in a later section. Adults possessing an already established nest or territory are superior beneficiaries, especially if the nest is complicated or costly in terms of building time or energy (or both), or if suitable space is in short supply. At least some of the species already mentioned as having non-reproducing helpers make complicated nests or other structures connected with breeding—e.g., the anis, beavers, and *Polistes* wasps. Experienced males with established harems among baboons and macaques offer similar examples of individuals with a reproductive advantage who are sometimes the recipients of aid by reproductively excluded individuals (see Crook and Gartlan, 1966).

#### *Alarm Calls*

Alarm calls, which can confer great benefit at low cost, may sometimes be examples of altruism among individuals of low  $r$ . An individual under attack by a predator stands to lose his life if not warned; and various factors tend to reduce the likelihood of the alarmist himself being attacked. These factors include (1) the alarmist's awareness of the predator's presence before the predator is aware of or prepared to attack him; (2) the possibility that more than one individual may give the alarm (either through simultaneous perception of the

predator or contagiousness of the alarm signal), and thus reduce the risk of alarm-giving by providing more than one distraction to the predator; and (3) the evolved ability, at least in some species, of alarmists to give signals difficult to localize (Marler, 1955, 1957). The combination of these factors acting to raise the value of  $K$  might make the value of  $r$  relatively unimportant in the evolution of alarm signals. Furthermore, any gain in the kinship component of the alarmist's inclusive fitness would be multiplied if more than one somewhat related ( $r > \bar{r}$ ) individual were helped simultaneously—a situation that is possible if the predator or parasite is capable of attacking more than one individual at a time or in quick succession.

Other explanations of alarm calls not involving kin selection are discussed by Maynard Smith (1965), Williams (1966), and Trivers (1971). Williams (1966) sees the warning signals of mammals (e.g., the raised white tails of deer) and of birds (e.g., the distraction and warning display of tail feathers in a bird taking flight) as primarily a device for protecting their own offspring, and he cites as evidence the fact that he knows of no such warning devices in species not showing well-developed parental care. He considers such signals non-adaptive (pathological or neutral) when given in the absence of the young. "As long as pathological social behavior is frequent (see Williams, 1966), it seems misguided to regard as adaptive any behavior that happens to benefit some individual. Selection in relation to low values of  $r$  must often be so weak that it gets lost in the evolutionary noise" (G. C. Williams, pers. commun.). Since other readers may share Williams' doubt concerning the importance of selection at low values of  $r$ , it seems worth pointing out that, while it may prove difficult to demonstrate—just as it is difficult to demonstrate any example of weak selection in nature—nevertheless weak kin selection, if and when it occurs, should follow the same rules as conventional natural selection. That is, a unit of inclusive fitness gained through aid to relatives is exactly equivalent to a unit of classical fitness in so far as prediction of the results of reproductive competition among individuals is concerned. My intention is mainly to point out that high values of  $r$  are not necessary for kin selection to be possible—that behaviors such as alarm signals have characteristics that might enable them to be

selected positively through a contribution to the kinship component of inclusive fitness, whether or not they have originated or been maintained also, or even primarily, by selection in other contexts.

THE SIGNIFICANCE OF DOMINANCE AND SUBORDINANCE  
AMONG RELATIVES

Dominance-subordinance interactions are common among animals living in groups, including birds (see Collias, 1944; Watts and Stokes, 1971), mammals (see Etkin, 1964), and insects (see Pardi, 1948, 1950; Free, 1955). Among some primates dominance hierarchies seem to be important in determining the social and reproductive roles of individuals; so a proper interpretation of the functions of dominance and subordinance is critical to understanding primate social organization and, in turn, its relation to human society.

The selective advantage of being *dominant* is clear whenever, as commonly is the case, the dominant individual has improved access to some resource(s) (such as food, mates, or nesting sites—see above references) vital to or at least enhancing its survival, reproduction, or both. The significance of subordinance, however, is not so obvious, and remains the subject of controversy. Indeed, interpreting the significance of dominance hierarchies resolves to one question: why do certain individuals accept a subordinate social and reproductive role with respect to others when that means giving in to or even aiding a reproductive competitor? Answers commonly given to this question are: (1) that subordinance reduces the destructiveness of intragroup competition and is thus selectively advantageous to the group (e.g., Etkin, 1964); (2) that dominance relations serve to control population size by restricting breeding to a small number of individuals (e.g., Wynne-Edwards, 1962; Woolpy, 1968); and (3) that a dominance hierarchy (and subordinance) is the result of compromises among competitors (Williams, 1966), that is, the subordinate is a hopeful potential dominant who temporarily or permanently has lost out in competition with others.

Reasons for doubting the validity of interpretations like (1) and (2), based exclusively on group-selection, are given by Williams (1966) and Maynard Smith (1972). The present theory

suggests a possible individual-level interpretation in addition to (3), namely, that in certain circumstances, submissive behavior may be a form of altruism that is advantageous to the subordinate individual by increasing its inclusive fitness.

In the case of a temporarily weak individual it seems obvious that avoiding fights might increase the chance of future reproductive success by reducing the risk of injury and the squandering of energy in prolonged conflict with a recognizable superior (see Maynard Smith, 1972). However, subordinance is not always passive. It often serves to channel the lower ranking individual into a different social role (see Markl, 1971, 1973), perhaps involving risky and energy-consuming altruism toward dominants and their young. For example, subordinate female *Polistes* wasps feed and defend the dominant queen and her larvae; subordinate male baboons participate in the care and defense of infants and mates not their own (Hall, 1960); and subordinate male flying foxes, excluded from reproduction for the year, stay at the periphery of the breeding group where they give alarm calls presumably benefiting dominant, breeding males (Nelson, 1965). Even passive deference to a competitor is a kind of altruism, since it allows the dominant individual prior access to resources which might be depleted by him, and there is a certain probability of the subordinate's death without reproduction (losing out in the waiting game). The present model enables us to specify the conditions under which advantageous, altruistic subordinance could occur: if and when

- (1) dominance reflects superior hereditary endowment (e.g., intelligence, experience, ability to produce or rear offspring, physical strength), or superior reproductive capacity, or both;
- (2) the subordinate's behavior (deference or aid) contributes to the reproductive output of the dominant;
- (3) the individuals involved are relatives ( $r > \bar{r}$ ); and
- (4) these factors (those affecting fitness and relatedness) are quantitatively related such that, following the period of subordinance (altruism), the theoretical conditions specified at the beginning of this paper (expressions 3 and 4) are satisfied.

The more closely related the members of a group, the more likely it is that subordinance



functions in this way; but marked differences in reproductive capacity could lead to advantageous subordination among quite distant relatives.

If dominance-subordination relations function as hypothesized here, one would expect the evolution of an ability to discriminate the dominance interval (sufficient difference in dominance) necessary to indicate advantageous subordination, individuals adopting the subordinate deference or aid behavioral syndrome whenever that level was surpassed. The required dominance differential should be adjustable to suit ecological conditions; e.g., in times of resource abundance, a relatively poor reproductive individual might better be able to make it on his (or her) own.

Evidence indicates that the model's conditions are satisfied in various phylogenetically diverse species, including social wasps, cercopithecoid primates (see below), bumblebees (Free, 1955), Welder brush turkeys (Watts and Stokes, 1971), kookaburras (Parry, 1972), and wolves (Woolpy, 1968). A quantitative test of the model has been made using data obtained in a study of dominance behavior and reproductive success in a natural population of *Polistes* wasps. In this case it was possible to show that subordinate females were very likely sisters of aided dominants, and that they did sufficiently better (in terms of inclusive fitness) than solitary reproductive individuals as to satisfy the conditions just outlined for advantageous subordinate altruism (West, 1967; West Eberhard, 1969).

The present hypothesis offers a possible explanation for the "wife sharing" of Tasmanian hens described by Maynard Smith and Ridpath (1972), since a pair of males forming a breeding group with a single female are brothers, and such "trios" have a higher productivity (1.45:1.0) than male-female pairs. In this case both males mate with the female, but the relative contributions of each as fathers is not known. Nor is it clear that dominance relations are established between them at some time, although the authors have stated that "it is certain that one of the males could drive out the other" (p. 449) if it were to his advantage to do so. If both gain equally by the arrangement, then I would regard this as a case of mutualism (reciprocal altruism or cooperation, see below) that does not necessarily involve altruism by kin selection.

Some primates have behavior and reproductive patterns which, in so far as they are known, fit the present interpretation remarkably well. For example, the dominance rank of male baboons depends on such factors as their health, fighting ability, ability to enlist the support of other males, and experience or intelligence (see discussion in Crook, 1972). That is, dominant males are likely to be "superior" individuals both in terms of inherited characteristics affecting their physical strength and intelligence, and in terms of their ability to protect and maintain a group of females and young. Fox (1972) discusses the evidence, in sum positive, that dominant baboons and macaques leave more offspring during their lifetimes than do subordinates. Thus the association of dominance, superior survival and reproductive capacity, and enhanced fitness required by the model is present. Furthermore, baboons and macaques tend to stay in groups of close relatives and are probably capable of recognizing at least some of their close kin (see Fox, 1972), a situation making advantageous altruistic deference or aid even more feasible. Unfortunately, the numerical data on kinship and individual reproductive success that would allow a quantitative test of the model are not available for any primate group.

This model also provides an interpretation for another dominance-related phenomenon observed in primates—the formation of one-male groups in regions or seasons of food scarcity, and the association sometimes observed between multi-male groups and food abundance (Crook and Gartlan, 1966). Crook (1972) points out that reducing the number of males present in a group is "adaptive," in that it allows a greater proportion of the available food to be apportioned to females responsible for rearing young, and he further discusses the advantage of the single-male social organization to the breeding individuals and to the group as a whole. But the explanation must ultimately focus on the males who leave the group in deference to the others: how could such behavior be advantageous to them as individuals? One obvious possibility is that during food scarcity males who break away from the breeding group get more to eat, either because they can forage more widely or effectively, or because they don't have to share with others. Solitary or small-group feeding in regions or

in times of food scarcity occurs independent of dominance relations in chimpanzees (Reynolds, 1970), hyenas (Kruuk, 1972), and flying foxes (Nelson, 1965). The present model suggests an additional possible interpretation for species having dominance hierarchies: males who leave the breeding group may be subordinates who, having found reproductive deference to the dominant male advantageous, as just explained, find it advantageous to carry their altruism one step further and leave the group in time of food scarcity, thus increasing the dominant male's probability of reproductive success and therefore the subordinate's own inclusive fitness. When food is more abundant, and staying with the group would not cause undue nutritional stress, it might benefit the subordinate's inclusive fitness more to stay on as a defender. Crook (1972) has also discussed the theoretical relationship of group size, defense effectiveness, and resource availability per capita. He shows how, at some point, to add another male will not increase defense effectiveness, while it will be costly in terms of energy (resources) to the breeding individuals and their young. A subordinate male would also have to consider the effects of leaving or staying on his own chances of breeding in the future (e.g., the effects on his survival and well-being, social status, proximity to females, etc.).

Stated in terms of the general theory presented above, this model of dominance and subordination predicts that a contending individual will profitably and willingly give in to a relative if dominance cues indicate that the benefit/cost ratio,  $K$ , is above a certain level ( $K_t$  from the subordinate altruist's point of view). What happens if that condition is not satisfied? One of two situations must then be true: either the individual in question is clearly dominant to the other, sufficiently so as to make the *other* a contented subordinate altruist; or there is a conflict of interest between the two, each one wanting the other to become altruistic and neither one wanting to concede because the benefit/cost for doing so is too low. Conflict of interest becomes more important among more distant relatives. For example, if the contenders are diploid siblings, conflict occurs whenever  $K$  is between 0.50 and 2.0, whereas, for cousins, the conflict range is considerably greater, including all situations for which  $K$  is between 0.125 and 8.0; and this range contin-

ues to increase as relatedness declines. Whenever there is a conflict of interest, fighting should escalate until one contender reaches the level at which the cost of continued fighting outweighs the potential benefit of winning, and the individual gives in. In this case the first to give in, the "subordinate," would not be expected to be altruistic. So it is of interest that in *Polistes* wasps close contenders are the most vicious and persistent fighters; and prolonged fighting among near equals can lead to one of the pair leaving an established nest and reproducing independently—giving in to, but not aiding, the other (West Eberhard, 1969).

The interpretation of dominance-subordination interaction as a means of channelling individuals into the social (reproductive) roles most advantageous to them as individuals is not expected to apply to all the diverse examples of dominance-subordination behavior found among animals. But it does seem necessary to revise hypotheses about the functions of dominance hierarchies by taking into account the possibility of individually advantageous subordination.

#### KIN SELECTION IN RELATION TO OTHER FACTORS IN THE EVOLUTION OF ALTRUISM

Alexander (1974) points out that there are three general ways in which selection can act to produce beneficent social behavior: through kin selection, parental manipulation, and reciprocity. The second category is expanded here to include the additional possibility of altruism imposed by relatives other than parents, for example, by adults who adopt orphans or by socially dominant individuals in a position to manipulate the behavior and resources of others. I shall call such forced beneficence "imposed altruism." The purpose of this section and the next is to define the relations among kin selection, imposed altruism (particularly parental manipulation), and reciprocity, especially in the evolution of extreme altruism (worker sterility) in the social insects, where all three factors may have played a role.

#### *Imposed Altruism*

Altruism by parental manipulation is the only kind of beneficence imposed by selection on individuals other than the donor the theoretical

nature of which has been discussed in the literature (Alexander, 1974; Trivers, 1974). It is probably by far the most common kind, because parents are often in a position to manipulate the phenotypes of offspring (see Alexander, 1974), and offspring are the individuals least likely to rebel inasmuch as their interests often coincide with those of their parents owing to the high degree of genetic similarity between them (see Table 1).

According to the parental-manipulation hypothesis (Alexander, 1974), altruism can sometimes be forced on individual offspring if parents with altruists among their brood reproduce more than parents with an entirely selfish brood, even when the altruism is disadvantageous to the altruist in terms of its own inclusive fitness. Illustrative examples include the trophic eggs of insects (crickets: West and Alexander, 1963; ants: Wilson, 1971), in which some gametes or zygotes are sacrificed to assist (feed) others, and the "controlled cannibalism" of hawks and owls in which larger young eat smaller ones in times of food shortage (Ingram, 1959, from Alexander, 1974).

In applying this hypothesis, it is critical to consider the extent to which offspring can be expected to rebel against parental manipulation. In what circumstances will there be a parent-offspring conflict regarding the advantageousness of altruism by offspring, and to what extent can offspring escape parental control? It is clear that parents and offspring will not always agree regarding the desirability of altruism, since  $K_i$  from the two points of view differs (see Table 1). Trivers (1974) has analyzed parent-offspring conflicts of interest and has emphasized the fact that offspring are expected actively to resist parental manipulation when it is counter to their own best interests. In cases of parent-offspring conflict, who can be expected to win? Alexander (1974) argues that the parent is likely to dominate the situation, being stronger and in control of resources on which the young are dependent, and in a position to manipulate the phenotypes of the young. Furthermore, he argues, offspring are future parents and are likely to be selected against as adults because they are likely to produce inferior (rebellious) broods. Trivers (1974) points out that although the contest is weighted in favor of the parent in cases of parent-offspring conflict, there are some signs

of resistance in the behavior of offspring, e.g., during the weaning process in mammals. It seems clear that selection of offspring can favor an escape from parental manipulation as long as the benefit (increase in fitness because of rebellion when young) outweighs the cost of producing a rebellious brood as an adult (see Trivers, 1974).

Like altruism by kin selection, altruism imposed by parental control is only advantageous when the beneficiary is a relative—it will occur primarily among groups of kin. Exactly the same kinds of altruistic behavior can be produced by both kin selection and parental manipulation and the benefit/cost ratio at which they can advantageously occur overlaps (see Table 1). How, then, are we to know which kind of selection is responsible for a given case of altruism? Although it is possible to discuss in precise theoretical terms the conditions under which each kind of selection will occur and the situations in which conflict of interest is expected (see Trivers, 1974 and below), I know of no sure and practical way to distinguish all cases of kin selection from all cases of parental manipulation in nature. Presence or absence of the parent at the scene of the altruism is not an adequate criterion, since offspring altruism by selection on parents can theoretically occur even after the death or in the absence of the parent (see Alexander, 1974). The most that can be done is to discuss the various factors that make one explanation seem more likely than the other in a given case. For example, the "altruism" of a human infant sacrificed in favor of a sibling seems more likely properly explained by selection on parents (see Alexander, 1974) than by (kin) selection on offspring, considering the strength and influence of the parent and the physical helplessness of the human baby. On the other hand, similar sacrificing (cannibalism) of immature beetles can be explained credibly by either kin selection (Eickwort, 1973) or parental control. The two kinds of argument are illustrated in detail by parallel sets of interpretations applied to phenomena observed in social insects (see below).

An obvious opportunity for non-parents to impose altruism occurs when a peripheral relative adopts an orphan and assumes the manipulatory powers of parenthood without the same genetic responsibility. It seems likely that foster parents might sometimes impose

altruism of a different kind or degree than that imposed by true parents. For instance, when the adoption occurs in a species that shows altruism characterized by parental manipulation favoring siblings, the foster parent could channel advantages to its own offspring that normally would have been destined for offspring of the true parents of the adopted individual.

To the degree that worker altruism is imposed by reproductive adults in social insects (see below), the conditions for control by relatives other than parents occur in several kinds of colonies. These cases differ from adoption in vertebrates in that control by non-parents is a regularly occurring part of the normal colony cycle, and could conceivably have preceded parental control in the evolutionary history of the species. In certain social wasps (e.g., *Polistes canadensis*, West Eberhard, 1969, and *Mischocyttarus drewsenii*, Jeanne, 1972) the reproductive cycle involves succession of a queen by a daughter of sibling who takes over a colony containing the ex-queen's workers and brood; and in *Polistes* species it is quite common for a newly founded nest to be conquered and controlled by a new arrival (possibly but not certainly a close relative of the original foundress) up to several weeks after nest initiation (Yoshikawa, 1955; West Eberhard, 1969, and pers. observ. on *P. carnifex* more than six weeks after nest founding), so that the first workers (altruists) are daughters of a deposed queen. The possibility of some degree of control of altruism by non-parents also exists in the polygynous (multi-queen) social Hymenoptera, in which there are complex interactions among the several queens and their immature and adult offspring (Naumann, 1970; West Eberhard, 1973); as well as in queen-recruiting ants (e.g., *Myrmica rubra*) in which the number of colony queens is augmented by the incorporation of additional gynes, at least sometimes sisters of those already present (Elmes, 1973).

In general, the same theoretical considerations regarding escape and rebellion that apply to parental manipulation should apply to control of altruism by other relatives. The more distantly related the dominating individual, the more the altruist is expected to resist imposed altruism. There should be very strong selection against altruism benefiting non-relatives without compensating beneficial consequences for

the donor or its relatives—a kind of social parasitism which might sometimes evolve from relative-imposed altruism.

#### *Intraspecific Mutualism*

Mutualism or cooperation—a beneficent exchange in which both donors gain—can occur either among relatives or non-relatives. It seems useful to distinguish at least four kinds of intraspecific mutualism in order to analyze the way in which natural selection acts to maintain the performance of mutually beneficent acts:

- (1) *Mutualism maintained by reciprocal-altruistic selection.* Temporarily altruistic acts are performed mutually with each donor expecting more than compensating future beneficent behavior (reciprocation) on the part of the beneficiary, so as to result in a net gain in classical fitness of both participants. Possible example: reciprocity among humans (Trivers, 1971).
- (2) *Mutualism maintained by kin selection.* Each individual act is advantageous to the performer in terms of inclusive fitness—no reciprocation is required. However, individuals associate with kin because of the increased probability of being the recipients of similar ("reciprocal") aid. That is, the group owes its existence at least partly to the advantageousness of being able to dispense aid to (and receive it from) relatives. Possible examples: the sphecid wasp *Trigonopsis* (Eberhard, 1972, 1974); group-hunting species such as wolves (Woolpy, 1968) and wild dogs (van Lawick-Goodall and van Lawick-Goodall, 1970); communal nursing of young by lions (Schaller, 1972).
- (3) *Mutualism imposed by parents.* Mutualism among siblings could be the result of selection favoring parents whose offspring live together in cooperating groups (see Alexander, 1974). Possible example: "semisocial" groups of sisters in *Allodapula* bees (Michener, 1968).
- (4) *Mutualism maintained by ordinary selfish behavior incidentally benefiting neighbors.* The selfish behavior of an individual warning, feeding, or defending itself or its young can simultaneously benefit other individuals in the vicinity—e.g., by showing them the way to food, chasing off parasites, predators, or both; or by warning of danger. Groups may form and stay together because of this mutual advantage (see Williams, 1966). In this case the beneficent behavior costs the performer nothing beyond the expenditure justified by benefit to its own classical fitness. Possible examples: breeding

aggregations of wildebeest (Kruuk, 1972); nesting aggregations and foraging flocks of colonial birds such as the piñon jay (see Brown, 1974); nesting aggregations of certain bees, e.g., *Lasioglossum zephyrum* (Batra, 1966; other examples in Michener, 1958, 1969; Lin, 1964).

Most mutualism among non-relatives or distant relatives is probably of type (4). Under special conditions (see Trivers, 1971, and below), non-relatives can also engage in reciprocal altruism (type 1). But mutualism maintained by reciprocal-altruistic selection alone is probably a rare or unstable phenomenon in most species, for reasons to be discussed below.

When mutualism occurs among relatives, it can be maintained by selection operating in any of the four ways listed, or in any combination of them; so for mutualistic groups of kin it will often be difficult to know for sure which kind(s) of selection are actually operating. This problem is illustrated by the following example. Eberhard (1972, 1974) has described the behavior of some primitively social sphecid wasps (*Trigonopsis cameronii*) in which females likely to be close relatives nest in small groups, each female provisioning her own cells but occasionally stealing prey from those of neighbors. Robbing females show altruistic restraint in not stealing at every opportunity, and apparently do so only in time of "need" (following poor hunting success). Robbed females are altruistic in permitting robberies, and only rarely attempt to prevent them even when present at the time of the robbery. Is such reciprocal pillage to be regarded as stealing or as sharing? At least three interpretations must be considered: (1) the behavior may represent reciprocal altruism (sensu Trivers, 1971), in which a female permits some stealing in the expectation of being able to get provisions in the same way on a future bad day; (2) it may be Hamiltonian altruism, in which each female permits limited (in accord with  $r$ ) stealing by close relatives such as to benefit the kinship component of inclusive fitness, and limits her own stealing so as not to lower her inclusive fitness by excessively harming relatives (see Eberhard, 1972); or (3) it may be an instance of maternal control, in which a group of daughters distributes food among themselves in a manner that maximizes the total number of young produced by the sibling group.

Each of these three explanations is theoretic-

ally distinctive, in that each permits a different level of profit and loss due to stealing. These levels can be specified as follows. For an act by individual A (donor) benefiting individual B (beneficiary) let

$B_b$  = profit to B of aid,

$C_b$  = cost to B of reciprocation,

$B_a$  = profit to A from beneficent behavior of B,

$C_a$  = cost to A of original beneficent act,

$2r_B$  = relatedness of and young of B  $\times$  2 = increase in inclusive fitness of A for each offspring added to B's reproduction (expressed in offspring equivalents),

in which all costs and benefits are expressed in terms of fitness (offspring).

The conditions for positive selection are then:

- (1) For reciprocal altruism from the point of view of A:
  - a. Pure reciprocal altruism (kinship disregarded):

$$B_a > C_a$$

- b. Reciprocal altruism among kin:

$$B_a > C_a - 2r_{B_y}(B_b - C_b)$$

or, in species for which  $r_{B_y} = r_B/2$  (e.g., outbreeding diploid animals):

$$B_a > C_a - r_B(B_b - C_b);$$

- (2) For mutualism maintained by kin selection, from the point of view of A:
  - a. Altruism by A benefiting B:

$$B_b > C_a/2r_B,$$

- b. Altruism by B benefiting A (if not satisfied, A should refuse aid from B):

$$B_a > 2r_{B_y}C_b$$

- (3) For reciprocal beneficence among siblings with parental control (condition for advantageous mutualism among brood from parent's point of view):

$$B_a + B_b > C_a + C_b$$

or

$$B_a > C_a - (B_b - C_b).$$

(Note that when  $r_{B_y} = r_B/2$ , as in the case of outbreeding diploid species, expression (2a) is identical to Hamilton's (1964b)  $K > 1/r$ .  $B_b > C_a/2r_{B_y}$  becomes  $B_b > C_a/r_B$ , or  $B_b/C_a > 1/r_B$ , in which  $B_b/C_a \equiv K$ . Expression (2b) simplifies to  $B_a/C_b > r_B$ .

The brood-manipulating parent (case 3) is interested only in the summed individual fitnesses of the brood—the total number of grandchildren (descendants) produced—regardless of the kinship interactions and reciprocal debts important among the young themselves. Thus the evolution of mutualism may sometimes involve conflict of interest between parent and offspring. Selection on a parent might favor participation by offspring in a mutualistic group containing non-siblings (Alexander, 1974). Such a group could engage in mutual aid maintained by any one (or any combination) of the other three kinds of selection, and the above conditions (1, 2, and 4) would have to be satisfied from the *parent's* point of view.

Trivers (1971) has outlined and discussed the theoretical characteristics of "reciprocal altruism." He and later authors (Eshel, 1972; Hamilton, 1972; and Markl, 1973) have noted that reciprocal altruism and kin selection are likely under the same conditions (low dispersal rate; life in small stable groups; long period of parental care; and high benefit/cost ratio). Comparison of expressions (1a) and (1b), above, shows precisely how much kinship affects reciprocal altruism, namely, by subtracting the quantity

$$2r_{B_y}(B_b - C_b)$$

from the required reciprocal payoff. Note that for interspecific mutualism ( $r_{B_y} = 0$ ) this factor becomes zero, and this and the very special circumstance when  $r_{B_y} = \bar{r}$  are the only situations in which kinship effects can be ignored (when  $\bar{r}$  is included in this expression it is subtracted from  $r_{B_y}$ ; so when  $r_{B_y} = \bar{r}$  the effect of kinship is zero). Even when reciprocal-altruistic selection is primarily responsible for a given beneficent act (e.g., in humans) the performer should demand more in return from a beneficiary of distant or unknown relatedness than from one of certain high relatedness. In view of these considerations it is probably an over-simplification to regard even human mutualism as resulting "only from reciprocal-altruistic selection" (Trivers, 1971, p. 46), especially since during the period of human history when biological selection was still operating to produce the basic characteristics of the human reciprocal system man probably lived in the

kinds of groups favoring kin selection (Trivers, 1971, p. 45).

Maintenance of reciprocal altruism depends on some meticulous mechanism for recognizing and punishing a cheater *during its own lifetime*. Otherwise there is a premium on cheating among reciprocating members of the same species. Any small energy-saving or risk-avoiding failure to reciprocate to a beneficent conspecific individual is reproductively advantageous, and such cheating should become more and more exaggerated in successive generations until the system breaks down because of the disadvantage to those being cheated of continued association with cheaters.

It might be supposed that this eventual dissolution of the group would constitute adequate punishment of the cheater, whose descendants are deprived of the advantages of group living. But in this event the non-cheater, whose descendants are also deprived of mutualistic aid, actually loses more than the cheater, who at least gains (rather than loses) by the act of cheating. Inter-deme selection could eliminate cheating from a population by extinction of cheater-containing groups, but only if *all* of the following conditions were to hold: (1) group-living must be obligatory, so that cheaters lose as much by dissolution of the group as non-cheaters; (2) groups composing the population must be genetically isolated from each other (have a migration rate so low that it does not outweigh mutation rates), so that the temporarily successful cheaters are not able to infiltrate neighboring groups of non-cheaters before selection has operated to extinguish them along with their original group; and (3) non-cheaters must be able to colonize new areas with offshoot groups and thus propagate their kind, so that group-by-group extinction does not eventually lead to extinction of the entire population or species. Since such conditions are probably quite rare (conditions 2 and 3, for example, require both movement from place to place and genetic isolation), the reproductive advantages of failure to reciprocate should usually lead to the spread of this tendency whenever it occurs unchecked by contemporaries, even among species for which mutualism is essential to individual survival, since the long-term disadvantage—the breakdown of reciprocity and the extinction of descendants—cannot be foreseen.

In the case of humans, the problem of checks on cheating is resolved by the unusual development of human intelligence and memory, which makes it possible to discover cheaters and immediately limit reciprocation toward them (see Trivers, 1971). Human reciprocity is the only example of mutualism thus far shown to fit the conditions of reciprocal altruism as distinct from other kinds of intraspecific mutualism (Trivers, 1971). Trivers has considered one other possible example—the warning calls of birds, which he interprets as involving no reciprocally beneficent behavior by the beneficiary, and no checks against cheating. The mere survival of the warned individual repays the call-giver by preventing predators from specializing on the caller's species and locality. Viewed in this way, warning calls are not really *reciprocal* altruism, since only one member of the interacting pair (the alarm-giver) is temporarily altruistic; and no checks on cheating are required because the altruism is "automatically" repaid in the course of purely selfish behavior by the beneficiary. Hence the example does not really fit Trivers' model which, while not very explicit on this point, seems to require that *both* parties be (temporarily) altruistic. (See, for example, section 3, p. 37, of Trivers, 1971. The emphasis given checks on cheating throughout that paper also implies altruism by both parties, as just explained.) If the model in fact requires only one party to be temporarily altruistic, then it is trivially applicable to many phenomena clearly better considered as ordinary selfishness (e.g., mating behavior, in which a male donates sperm to a female, thereby enabling her to reproduce at the risk of wasting his effort unless she survives to provide the delayed payoff—his offspring).

Trivers has also applied the model to interspecific mutualism in a useful analysis of cleaning symbioses among fish. That discussion, again, involves an example of mutualism with only one party—the host fish—temporarily altruistic (the cleaner's contribution is seen as selfish feeding on the host's parasites), and Trivers' interpretation parallels those of other authors—e.g., Borradaile and Potts, 1958; Moynihan, 1962; Williams, 1966; and Janzen, 1966, 1967—who have explained interspecific mutualisms in terms of unadorned classical selection.

While Trivers (1971) expects reciprocal al-

truism to be found in many species, a model of reciprocal altruism requiring temporary altruism by both participants (and therefore contemporaneous controls against cheating) leads instead to the conclusion of Williams (1966) and Hamilton (1972) that the phenomenon is probably restricted to intelligent animals and, hence, to a few species of mammals (Williams, 1966). If reciprocal altruism does occur in non-humans it will probably be difficult to demonstrate, even in terms of checks against cheating. Differential beneficence by an individual toward different members of a group might not always indicate recognition of differentially reciprocating companions (or checks against cheating). It could represent control of other kinds of social parasitism, such as preemption by non-relatives or distant relatives of beneficence destined for relatives, or even outright stealing.

#### THE ORIGIN OF EXTREME ALTRUISM IN INSECTS

In terms of altruistic behavior the most social animals by far are insects. In all of the more than 24,000 known species of eusocial (i.e., possessing a worker caste) wasps, ants, bees, and termites, at least some of the brood of each reproductive female (queen) is made up of complete altruists—individuals (workers) whose entire lifetime reproductive effort is dedicated to rearing the young of others, and for whom group living is absolutely obligatory. The variety and exaggeration of social traits among insects offer an ample testing ground for any general theory of social behavior.

According to the view traditional in entomology, the reproductive division of labor originated when the mother of a subsocial group (a mother with her own young) become so long-lived as to cause a generational overlap and lead to a society in which the offspring would help the mother rather than go off on their own. This traditional account (Darwin, 1859; Wheeler, 1928) implied that the mother, or family, is the relevant unit of selection in bringing this about, since the evolution of sterility is obviously impossible by classical selection operating on workers (in terms of individual fitness).

In recent years there have been three major new interpretations of the evolution of insect sociality, each of them involving one of the three

hypotheses applied to altruism in the previous section—kin selection, reciprocity, and parental manipulation. Each of these hypotheses will be discussed separately below. A fourth kind of explanation often referred to involves selection at the level of the colony: namely, colonies with specialized workers and reproductives out-reproduce (presumably in terms of daughter colonies) colonies without those specialized groups, in much the same way that a multicellular organism with specialized organs might do better than one not having a division of labor among its cells. The last hypothesis (colony control) has seldom been clearly set forth as an explanation of the *origin* of sterile castes. It has mainly served to explain how, given a group with some individuals specializing as workers and others as reproductives, the two castes can develop morphological and behavioral adaptations contributing to the success of the group as a unit. Selection at the level of colony, or “family,” was first mentioned by Darwin (1859), is inherent in the “supraorganism” concepts of Wheeler (1911) and Emerson (1959), and was recently cited by Wilson, (1971) as the most feasible explanation for the evolution of insect altruism (although Wilson did not explicitly choose it over the kin-selection hypothesis discussed at length in the same book, and he sometimes—p. 342—acknowledged that the queen is the “ultimate focus” of selection).

“Colony-level selection” is an undesirable term even when it implies selection on mothers, since it is certain to be understood by some readers to imply selection operating at a level higher than the individual—e.g., on groups or populations, a generally unjustified interpretation (see Introduction). Both “colony-level selection” and the old “supraorganism” concept have in common the error of considering the workers as extensions of the queen’s soma, an idea which fails to acknowledge the quite important fact that, unlike a multicellular organism, an insect colony contains a number of genetically different individuals who must be considered actual or potential reproductive competitors.

#### *The Three-Quarter-Relatedness (Haplodiploidy) Hypothesis*

Hamilton introduced the idea of inclusive fitness in 1963, and with it the novelty of being

able to consider the evolution of sterility from the individual daughter’s point of view. He argued that the frequent occurrence of social altruism among the Hymenoptera may be owing to the great advantage to workers (in terms of inclusive fitness) of helping their mothers rear their sisters ( $r_{AB} = 3/4$ ) rather than of reproducing on their own ( $r_{AB} = 1/2$ ). The unusually high relatedness of female hymenopterans and their sisters ( $3/4$ , vs. the more common  $1/2$  for diploid organism) is the consequence of the haploidy of hymenopteran males, that makes all the paternal genes of sisters identical instead of only half identical (providing the mother has mated only once) (see Hamilton, 1964b).

Three objections are commonly raised regarding the  $3/4$ -relatedness argument: (1) that such (matri-filial) sociality is not prominent in other haplodiploid groups; (2) that comparable altruism has been achieved by workers of diploid species (termites) or in other social groups for which  $r_{AB}$  is less than  $3/4$ ; and (3) that the observed occurrence of multiple mating among the social Hymenoptera means that the relatedness of sisters is sometimes lower than  $3/4$  (for example, two matings would reduce the relatedness of sisters to  $3/8$ , and would eliminate in one stroke the advantage, in terms of  $r$  alone, of rearing sisters rather than daughters) (see reviews by Hamilton, 1964b, 1972; Wilson, 1971; Lin and Michener, 1972; and Alexander, 1974). A fourth point is usually overlooked, namely, the fact that the extraordinary  $3/4$ -relatedness applies only among *females*. Hymenopteran sisters are unusually highly related ( $r = 3/4$ ), but the relatedness of sisters and brothers is unusually low ( $1/4$ ); and if the queen’s brood contains equal numbers of each sex the average worker/brood relatedness is only  $1/2$ —the same as  $r$  for diploid siblings. So unless there has been some mechanism for assuring that more aid goes to the females than to the males of the queen’s brood, the unusual  $3/4$ -relatedness of hymenopteran sisters cannot have been responsible for the frequent evolution of matrifilial societies in the Hymenoptera as Hamilton suggested (Trivers, unpubl.). Hamilton (1972) in fact discussed the point that this asymmetry in the relatedness of haplodiploid siblings should mean that workers would be comparatively unwilling to help rear brothers, and would be inclined to



replace the queen's male-producing eggs with their own; but there is so far little evidence that workers do in fact channel more aid to the females of the immature brood.

These considerations place severe limitations on the situations in which the  $3/4$ -relatedness could have been important in hymenopteran social evolution. Not only would there have to have been temporal and spatial overlap of generations, but also a limitation to single matings on the part of females and separation of or discrimination between the male and female broods. One cannot rule out the possibility that these conditions were satisfied. Since eusociality (worker sterility) has arisen only a few times in all the history of all the many thousands of species of Hymenoptera, exceptional (improbable) conditions could very well have been involved. Even if multiple mating were to prove universal among *eusocial* Hymenoptera, it is conceivable that one or more of the several origins of eusociality among insects occurred in species already having single matings at that stage in their history. Indeed, multiple mating may have evolved secondarily in some social Hymenoptera to supply the extra sperms needed to fertilize the huge number of eggs produced by specialized queens. Spatial or temporal separation of the two sexes in the brood is also conceivable, although so far it is unknown in the few studied primitively social species. Workers do commonly lay (unfertilized) male-producing eggs in many social species. Information concerning this phenomenon has been recently reviewed by Wilson (1971), Lin and Michener (1972), and Hamilton (1972). Theoretically, given a perfect 50:50 sex ratio, all a worker has to do to capitalize on its  $3/4$ -relatedness with its sisters is to lay one male egg, and thus raise her average relatedness with the brood slightly above that with her own offspring.

Lin and Michener (1972) construed the persistence of male production by workers to be evidence *against* kin selection, and concluded that "the larger the productivity of the joiner or worker, the less relevant is the coefficient of relationship to an understanding of the evolution of the worker caste" (p. 142). Their conclusion that eusocial colonies (by definition those having workers with reduced reproductivity) "without altruism are possible if male production by workers is important enough" (p. 132) involves the mistaken idea

that the workers can be viewed as a group whose collective productivity can be summed and compared with that of the queen(s), the altruism of the sterile working workers somehow being cancelled out by the productivity of the others (for laying "workers" do not simultaneously work—Lin and Michener, 1972). Even if every worker is seen as reproducing during some period of her life, she could not recompense the potential offspring she lost in assisting the mother, unless the colony is visualized as somehow perfectly mutualistic, in which case it would not usually be called "eusocial."

Although the  $3/4$ -relatedness of hymenopteran sisters offers a dramatic hypothetical illustration of how kin selection can operate, it is unfortunate that Hamilton and others have allowed the whole case for kin selection in the social Hymenoptera to rest on this point. As has been pointed out repeatedly in this paper, kin selection involves not only relatedness but the benefit/cost ratio ( $K$ ) of the changes in fitness incurred by beneficiary and donor. A discussion of multiple mating in highly social species is seen to be quite beside the point when one realizes that the number of times the mother mates is of little or no consequence to a daughter once she is sterile—even workers capable of laying eggs certainly have a greatly reduced individual reproductive capacity compared to that of their mothers, making  $K$  very high (if the altruist is completely sterile  $K$  approaches infinity). Thus, the more general kin-selection argument cannot be demolished by any of the above four arguments, since they all concern relatedness alone. Hamilton himself has not fully used the complete theory in its own defence. Although he has devoted much attention to factors that tend to raise relatedness, he has tended to neglect factors that would raise the benefit/cost ratio.

I believe it would be wise to replace the  $3/4$ -relatedness argument with a kin-selection hypothesis less heavily dependent on relatedness alone. It should consider factors that make altruism more profitable than selfishness even at  $r = 1/4$  (the lowest average  $r$  possible among offspring of a single mother), including such parameters as the potential (sacrificed) fitness or reproductive capacity of the altruistic worker, and the effect of her aid on the mother's reproduction. Individual differences in reproductive capacity among the members of a brood

may have been of great significance in the evolution of worker sterility, as will be discussed below.

### *The Semisocial Hypothesis*

Michener (1958) has suggested that "semisocial" groups, composed of differentially reproductive females of the same generation, have been important ancestors of the eusocial societies of bees, and has proposed the semisocial route to sociality as an alternative to the subsocial route (by which the original group is a single female and her offspring). This idea was originally proposed (Michener, 1958) in a form contradictory with the (later) genetical theory, involving as it did a "division of labor" among possibly unrelated females. However, in the examples cited by Michener (1958)—those for which sufficient geneological information and long-term individual histories could be inferred—a *reproductive* division of labor (as distinct from a non-reproductive one involving temporary specialization in foraging or guarding) appeared only among matrifilial societies or semisocial groups frequently consisting of sisters. Thus, at its most critical pass—the transition from selfish to altruistic behavior—the semisocial route does not differ from the subsocial route. Although the semisocial route is therefore not strictly an "alternative" to the subsocial route regarding the kind of group in which altruism actually originates, this hypothesis introduces two important points regarding the evolution of insect sociality: (1) that factors other than degree of relatedness, such as the necessity for cooperative defense against parasites and predators (Michener, 1958; Lin, 1964), probably favored group living and mutual beneficence with or without kinship; and (2) that such groups are common among the Hymenoptera and represent a class of pre-eusocial behavior different in important ways from isolated subsocial females, and hence offering a different situation in which social evolution might occur. Hamilton (1964b, 1972) has regarded the subsocial route as more likely than the semisocial, mainly on the basis of his objection to the suggestion of sociality among unrelated females (an aspect now less emphasized by Michener—see Lin and Michener, 1972); and Michener considers the "kin-selection" hypothesis (3/4-relatedness hypothesis)

inadequate to explain altruism among semisocial groups of somewhat distant relatives (Lin and Michener, 1972). This "controversy" evaporates once it is realized that such factors as parasite-predator pressure raise the value of  $K$  and hence lower the value of  $r$  necessary for altruistic behavior by kin selection. So Michener's basic hypothesis in its present form (Lin and Michener, 1972) is not incompatible with the genetical theory.

Viewed in terms of the theory being presented here, mutualistic (cooperating) groups like those described by Michener represent one response (cooperation and reciprocity) to the same conditions (conditions producing difficulty for solitary individuals), which given a different population structure (family groups rather than more genetically diffuse aggregations) might produce a reproductive division of labor (altruism). One would expect that, given a group of selfish cooperators, the advantage of cooperating with relatives rather than non-relatives and thereby of contributing simultaneously to self and kin might lead to a localization of families within the larger aggregation. This could set the scene for the evolution of a highly developed reproductive division of labor through kin selection (see Lin and Michener, 1972), maternal control, or both (Alexander, 1974—see below).

### *The Maternal-Control Hypothesis*

Alexander (1974) has recently proposed a maternal-control hypothesis as an alternative to Hamilton's explanation of insect sociality. He argues that selection among reproductive females could favor using some offspring to help rear others in the same way that some mammals advantageously resorb some fetuses in order better to nourish others and that some insects use a portion of their eggs (trophic eggs) as food for older young. According to this hypothesis a sterile worker is, in effect, a grown-up trophic egg—it has been reared to adulthood but is likewise sacrificed in favor of its siblings; and mothers with some altruistic brood do better in competition than those who produce only selfish offspring. Major points supporting this hypothesis as applied to insects are as follows (after Alexander, 1974).

(1) Maternal control solves the problem of the initial spread of altruism (because of the

increased fitness of mothers with an altruistic brood), which cannot benefit an altruist by kin selection unless the beneficiary also carries the allele for altruism—a condition that would not hold for the original (mutant) altruist.

(2) The origin of (diploid) termite eusociality, a “problem” for Hamilton’s hypothesis because the 3/4-relatedness hypothesis does not apply to diploid organisms, can be explained by supposing that the young originally stayed in the parental nest in the hope of using that costly resource for themselves, and thereby gave the parents (a monogamous pair) the opportunity to use them as helpers.

(3) No insects are known to tend their offspring to adulthood and overlap with them without having sterile castes, a situation suggesting that it is selection on mother-offspring interactions rather than sibling interactions that is involved in eusociality.

(4) Workers have apparently not evolved the ability to discriminate between sibs and half-sibs among the brood of a mother who has mated more than once, as they might be expected to under kin selection. The maternal control hypothesis predicts the absence of such discrimination, since all members of the brood have the same value from the mother’s point of view.

(5) The absence of male workers in the Hymenoptera is easily explained by selection on mothers, since female Hymenoptera can commonly control the sex of their offspring and hence produce as many as necessary of the sex best suited to altruism (in this case the females, hymenopteran males rarely contributing to the care of young).

(6) Modes of caste determination among eusocial insects are evidence of maternal control, since they usually involve the direct or indirect influence of the queen during the preadult (larval) period.

(7) The question (raised by Hamilton, 1972) of why the queen honeybee has a specialized sting that is used exclusively to kill a close relative (sister) can be explained by selection on the mother, who, once she has provided a certain number of workers, might find it more desirable to have only one daughter queen survive if that for some reason would increase the total reproductive efficiency of her descendants.

(8) The facultative altruism of subordinate

*Polistes* females which inhabit new spring nests (in the absence of the mother) can be explained if queens gain by producing daughters who cooperate in certain conditions at the expense of all but a single dominant reproducing queen (also a daughter) and thus can build new nests more swiftly. This situation offers an example of imposed altruism performed in the absence of the individual favored, for obviously the old (mother) queen need not be present at nest founding for such daughter altruism to evolve because of the superior reproduction of females having such broods.

Alexander (1974) has recently discussed Hamilton’s explanations of various characteristics of eusocial behavior. He finds maternal manipulation a “more compelling” explanation. However, his discussion refers mainly to the 3/4-relatedness hypothesis. If a broader view of kin selection is taken—one that comprehends changes in fitness, and not just relatedness—plausible kin-selection arguments can be provided on each of the above eight points, independent of the problematical 3/4-relatedness idea. The following parallel sets of arguments illustrate how parental control and kin selection are often suggested by exactly the same data.

(1) The initial spread of altruism can be explained within the bounds of kin-selection theory if altruism is facultative and is directed only toward reproductively superior relatives, as seems to be the case in certain social wasps and bumblebees (see discussion of dominance relations, above). If the original (mutant) facultative altruist happens to be a superior reproductive individual (has a high potential classical fitness), her altruism would not be expressed phenotypically. She would produce a large brood of likewise facultatively altruistic young who could then engage in profitable facultative altruism among themselves, and thereby cause the allele to spread through the enhanced reproduction of beneficiaries. If she should happen to be a reproductively inferior individual (although not completely sterile), she would engage in temporary or part-time altruism toward superior relatives when  $K > K_0$ , while also producing her own smaller brood of young likely to bear the allele for facultative altruism. In the first case, the allele would be spread but not expressed by its original bearer; in the second case, it would be selected against for

one generation only. Dominance interactions (see above) among cohabiting individuals could have been a preadaptation enabling facultative altruists to know when to give aid and to whom.

(2) Kin selection on offspring would also favor altruistic aid to termite parents in the circumstances specified by Alexander. The threshold for advantageous altruism ( $K_t$ ) is then low because the parents are monogamous and monogamy assures that all young are full siblings ( $r_{AB} = 1/2$ ). The parent who already possesses a nest and mate (high potential benefit) is in a good position to capitalize on aid; and the offspring is in a relatively poor position to reproduce on its own, not having an established nest or mate, and therefore has little to lose by becoming at least temporarily altruistic.

(3) An association between overlap of generations and sterile castes would likewise support a kin-selection interpretation, which also points to mother-offspring relations, not sibling interactions, as being of primary importance in the evolution of insect sociality (for the young of the worker's mother are more closely related to a worker than are the offspring of her siblings). [Actually, an overlap of generations without worker sterility is known to occur among wasps: *Macromeris violacea* and *Stenogaster depressigaster*, Williams, 1919; *Trigonopsis cameronii*, Eberhard, 1974; *Zethus miniatus*, West Eberhard, in prep., but that fact neither supports nor detracts from either hypothesis.]

(4) The ability to make fine distinctions among variously related close relatives is not expected to be an inevitable consequence of kin selection, which should be able to produce a degree of altruism appropriate to the average within-group relatedness. Inability to distinguish sibs from half-sibs, if it is observed, may simply indicate the difficulty of evolving a dependable discriminating cue (worker/brood relatedness even with multiple mating varies continuously from 0 to 1.0). Such discrimination is possible even with maternal control of altruism as long as it does not hurt the mother (i.e., as long as the entire brood is still adequately cared for). So presence or absence of this ability does not really distinguish between the two hypotheses.

(5) The threshold for becoming a mother-aiding altruist by kin selection is twice as high for males as for females ( $K_t = 2.0$  and  $1.0$ , respectively); and the threshold value is less

likely to be reached by males because of their relative lack of preadaptions for the efficient performance of aid (worker duties). It seems likely that hymenopteran males could develop worker-like behavior if it were to their advantage, in terms of inclusive fitness, to do so. I have seen male Hymenoptera carry out every common worker duty except bringing prey and building material to the nest. *Polistes* males forage (for themselves) at flowers and return to the nest site, feed larvae, and fan (part of nest temperature regulation) (West Eberhard, 1969); *Trigonopsis* males stationed on a nest will chase approaching predators (ants) (Eberhard, 1974); and the male of an unidentified *Trypoxylon* species applied mud (brought by a female) to the nest (pers. obs.). Alexander (1974) suggests that a "genetic revolution" would be required to make hymenopteran males into workers, but moderate reform might be sufficient.

(6) Maternal control of caste in *eusocial* species does not eliminate the possibility that worker altruism originated by daughter choice (kin selection), since once worker sterility or partial sterility had evolved the daughter would be trapped by her low personal reproductive capacity into agreeing with the best interests of her mother regarding caste ratios ( $K$  for workerness from the sterile daughter's point of view stays well above  $K_t$ —the denominator of  $K$  approaches 0—as long as the queen, whose offspring are the daughter's closest available relatives, is reproducing). Furthermore,  $K_t$  for imposing mother-aiding altruism on sisters is the same (0.5) as it is for imposing altruism on daughters from the queen's point of view, so a queen and her workers have no conflict of interest regarding the situations in which brood females should be made into workers rather than queens.

(7) When factors other than close relatedness are considered, one would not expect closely matched superbeneficiaries such as honeybee queens to behave altruistically toward each other even if they are sisters. It is in the best interests of a highly specialized reproductive individual, poorly equipped to give aid, to reproduce on her own; and her own offspring are worth more to her ( $r = 1/2$ ) than are her sister's offspring ( $r = 3/8$ ).

(8) A kin selection explanation of subordinate workerness in *Polistes* has already been discussed

above (see West Eberhard, 1969).

Both sets of explanations seem tenable. It is difficult to choose between them because the conditions favoring each hypothesis overlap (see Table 1), and the two kinds of selection are not mutually exclusive (they can operate either alone or together to produce the same result). One conclusion that can be drawn from the above parallel analyses is that the wishes of mother and daughter often coincide. It is possible, at least theoretically, to define exactly when they agree (when  $K$  is less than 0.5 or is greater than 1.0); and also to show that under certain conditions (when  $K$  falls between 0.5 and 1.0), there is a conflict of interest between them, selection on the mother favoring daughter altruism and selection on the daughter opposing it.

The problem of a mother-daughter conflict of interest is critical in understanding the evolution of insect sociality. Unless there is a saltatory increase in  $K$ , conflict is inevitable as  $K$  changes from the low values that favor solitary or selfish reproduction to the higher values that favor altruism. Such a stage must have occurred during the multiple evolutions of insect sociality, and a similar situation is created in the normal ontogeny of colonies if a queen's reproductive powers decline as she grows old. In theory, selection on daughters can favor an escape from maternally imposed altruism when there is a conflict of interest. In practice, escape is virtually impossible to demonstrate, since knowing whether to call a given instance of behavior (e.g., oviposition by workers on the maternal nest) "escape from maternal control" or "agreement between mother and daughter" depends on knowing the *precise* value of  $K$  for that situation (0.51 would give one answer, 0.50 the other), and the calculation of  $K$  involves such unmeasurable parameters as the fitness a worker *would have* if she reproduced on her own, or that a particular queen would have without aid.

The interpretation of male production by workers illustrates the complexity of this problem. It is common (some say almost universal—see Hamilton, 1972; Lin and Michener, 1972) for workers to lay eggs, even among highly social insects. Hamilton (1972) cited this as evidence of worker control of altruism, and Alexander (1974) has shown how it could occur by selection on mothers. Either one or both

interpretations could be right, depending on the value of  $K$  in a given case. When  $K$  is greater than 2.0, male production by the mother is favored by selection on both mother and daughter. This condition—the daughter's aid enabling a queen to produce more than twice as many males as the daughter could—must often be met in eusocial colonies, considering the relatively poor trophic and reproductive condition of most unfertilized females (workers), which characteristically have lower dominance or food-getting status (or both), reduced fat reserves, and rudimentary ovaries compared to queens (in wasps, Richards and Richards, 1951; in ants, Wilson, 1971; in bees, Michener, 1969). At values of  $K$  between 0.5 and 2.0, there would be disagreement between mother and daughter regarding which should produce males, each preferring to do it herself; and at  $K$  lower than 0.5, male production by workers would be favored by selection on both mothers and daughters, for example, if the mother's reproductive powers were declining severely (as might occur in ageing females), or if the available workers had brought the mother (queen) to her maximum possible reproductive rate.

Lin and Michener (1972) pointed out another context in which selection on queens might sometimes promote male production by workers. It would shorten the generation time for the expression of male-transmitted genes and hence increase the rate of evolution (the speed of responding to changed conditions) of the queen's male descendants. However, their added suggestion that the queen "will transmit more genes to subsequent generations by devoting that productivity to diploid females rather than haploid males" (p. 154) is erroneous. Although it is true that a diploid female has twice as many genes as a haploid male, only half of them come from the queen, the other (paternal) half coming from the queen's mate.

Interpretation of worker oviposition is further complicated by the fact that workers, being unmated females, produce only males. Hence the advantageousness of doing so (and to the mothers of allowing it) is affected not only by the reproductive condition of the queen, but also by the sex ratio in the population as a whole, and the fact that daughter-produced males compete with the queen's own sons (see Alexander, 1974). One situation in which worker oviposition should commonly occur by

selection on both mothers and daughters is following the death or disappearance of the mother queen, when worker-brood relatedness, dropping from  $1/2$  to  $3/8$ , makes daughter altruism less desirable from both points of view.

I know of at least one example in the social Hymenoptera which seems to indicate that the daughters behave according to their own advantage rather than the mother's. Following the death or disappearance of a queen *Polistes canadensis*, the daughters fight among themselves for possession of the colony, and cause an almost complete cessation of reproductive activity (egg-laying and nest enlargement) for as long as five weeks, after which the defeated females go off and found new colonies (West Eberhard, 1969). Evidently the stakes are high from the daughters' point of view, inasmuch as starting a new colony may be relatively risky and expensive, whereas conquest of the old colony means inheriting both a nest and a staff of workers; but the mother would clearly be at an advantage were any one of the evidently closely matched daughters to take over the original nest, while the others began new ones without delay. (A staunch maternal manipulationist could possibly argue that the mother would benefit enough by the dominant female taking over the nest that selection in her favor would justify or compensate for such long and costly fighting).

This example raises the question of how far into future generations maternal control could be expected to operate. Projection of a parent's best interests into the future would certainly be limited by lack of foresight into changing conditions, which must often make it advantageous to leave even immediate descendents a wider range of choice and flexibility. However, there are clear examples of parents manipulating their broods in ways that do tend to maximize production of grandchildren rather than of offspring, e.g., the fattening of reproductive offspring beyond the degree necessary for mere survival, so as to make them superior reproductives (of grandchildren) even when that means rearing fewer of them. This raises the further general question of just what it is that selection maximizes—whether number of children, grandchildren, great-grandchildren, or  $n$ th descendents (see Alexander, 1974)—and it shows another way in which classical fitness is an inadequate measure of an individual's total

reproductive (genetic) contribution. Inclusive fitness can include effects on future generations but does not specify how many generations should be included. In threshold cases of hymenopteran sociality there must sometimes be a reduction in mean fitness of the offspring—a paradox for classical theory (Hamilton, pers. commun.).

#### *Conclusion: A Synthesis*

Although the above hypotheses are presented by their respective authors as separate and independent theories, all three of them are perhaps best seen as appreciations of historically neglected factors in the evolution of insect sociality—as new insights, not as mutually exclusive theories. There is no reason, as I have argued, why Hamiltonian kin selection, Michenerian mutualism, and Alexanderian parental manipulation cannot all have contributed simultaneously or sequentially to produce the evolution of sterile castes; and it seems fruitless, *in making generalizations*, to argue in favor of one idea to the exclusion of the others (although this may be an important question in discussing a particular well-studied case). Rather, it seems necessary to acknowledge that all three sets of hypothetical factors could have operated, either alone or in some combination, especially in view of the fact that the several origins of worker sterility could each have arisen in a different combination of circumstances, making a uniform explanation impossible.

How, then, are we to visualize the steps leading to eusociality in insects, given this set of three possibly interacting hypotheses? Beginning with a solitary female who does not overlap in time or space with her adult offspring, four kinds of primitive groups of adults might conceivably form: a patrilineal group (parents and adult offspring), formed when parents become longlived and adult offspring remain in the parental nest; a filial group, of adult siblings remaining together without the parents; an extended family group, containing variously related adults who tend to stay in the same place generation after generation; and a "semisocial" group of non-relatives (or quite distant relatives) occupying the same nest or nesting area.

Unreciprocated reproductive altruism of the kind found in eusocial insects (worker sterility)

can evolve only if the beneficiary is a relative or group of relatives (see Alexander, 1974). This will ordinarily mean that it originates among relatives. So the formation of patrifilial, and filial, and extended family groups can be considered preadaptations for eusociality. What about semisocial groups of non-relatives? The only kinds of beneficence that can evolve in such groups are reciprocal altruism and cooperation. Could mutualism among non-relatives ever represent a significant step toward eusociality? I think it could, since the occurrence of cooperation and reciprocal altruism is likely to lead to the formation of subgroups of relatives in which cheating is less important, and this, in turn, could lead to the evolution of unreciprocated altruism by kin selection or parental manipulation. So, if the primitive group is composed of mutualistic non-relatives, an extra step is involved in reaching the stage in which eusociality can evolve.

Whether by maternal control or daughter choice, altruism performed unequally by different members of a filial, patrifilial, or other kin group is only likely to evolve if it is the temporarily or permanently inferior reproductives in the group who become altruistic. In the case of maternal control, mothers for whom offspring with inferior reproductive potential are effective altruists are likely to win over those for whom superior reproductives are sacrificed, or for whom the altruism is performed irrespective of reproductive capacity. Likewise, in the case of altruism by daughter choice, altruistic dedication of superior reproductives to aiding inferior reproductives would be highly disadvantageous to the altruists and possibly even to the beneficiaries (if close relatives) and there should be some mechanism guaranteeing that it not occur (see discussion of the function of dominance interactions, above). Thus, *a linkage of reproductive inferiority and altruistic behavior is expected to evolve* especially among social organisms in which altruism is very costly in terms of personal fitness (in contrast to low cost altruism, which is theoretically more likely in well-off individuals—see above). Exceptions might occur during emergencies, e.g., when the mother's life or a large portion of her reproductive investment (such as nest, or brood) is endangered unless help is recruited, even if that means the sacrificing or volunteering of a superior individual. But inferior ones should

still become altruistic first.

Differences in reproductive capacity among the members of a brood may thus represent an important preadaptation for eusociality. Such differences could originate because of incidental or regularly occurring differences in diet, environment (temperature, or other seasonal conditions), genetic makeup, social conditions (e.g., sibling competition) during ontogeny, or various combinations of these. Or they could be the result of maternal manipulation of these factors, as Alexander (1974) has suggested. Whatever their origin, these differences could have the effect of forcing altruism by daughter choice (kin selection), through lowering the daughter's personal potential fitness so that it is more advantageous to her to become a helper (either of sisters or mother) rather than to reproduce on her own. Thus eusociality could sometimes be the product of a combination of parental manipulation and kin selection, initiated by maternal manipulation of reproductive capacity and concluded by the daughter's subsequent adaptation (as a helper) to her altered capacity for independent reproduction.

Kin selection, mutualism, and parental manipulation may not represent an exhaustive list of the possible contexts in which eusociality can evolve. One obvious additional possibility is that altruism might sometimes be imposed by selection operating on relatives other than parents, e.g., siblings or aunts, as already discussed in the section on imposed altruism.

#### A LIMIT TO SELFISHNESS

The majority of social interactions, even among close kin, are probably competitive rather than beneficent in nature. Indeed, as Alexander (1974) has pointed out, an individual's closest relatives are his closest competitors because of their proximity and dependence on the same, often limited, resources.

Although the present discussion has dealt mainly with beneficent social behavior, this biological view of sociality suggests certain limits to selfishness, as Hamilton (1964a, b; 1970) has already pointed out. Ecological and social (intragroup) competition among individuals should follow the same rule applied to beneficent behavior. It will be selected for if it contributes to the inclusive fitness of the performer. Accordingly, selfish behavior that causes exces-

sive harm to a neighbor, or exacts more than the performer can use is selected against—precisely, when the kinship component of inclusive fitness becomes negative and exceeds the personal benefit of the act. Expectations regarding harmful and spiteful behavior have been formally considered by Hamilton (1970) and shown to conform generally to the predictions of the genetical theory.

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