Chapter 2

COOPERATION, AGGRESSION, AND THE EVOLUTION OF SOCIAL BEHAVIOR

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I.   INTRODUCTION

Until recently, the relationship between resources and sociality in animals has been poorly understood. Although kin-related models of sociality have been explored extensively (e.g., Alexander 1974; Orlove 1975; Milinski 1978; Sherman 1980; Weigel 1981; Michener 1983), since Hamilton's (1964) seminal work describing the theoretical relationship between social Hymenoptera workers in a haplodiploid system, ecological factors contributing to the development and maintenance of social

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groups have been less extensively modeled. In the mid-1960s to the mid-1970s, Crook and his associates (Crook 1965; Crook and Gartlan 1966; Crook 1970, 1972; Crook et al. 1976) attempted to describe relationships between social systems, resource abundances, and resource distributions for social birds, social mammals, and social and solitary primates. Similar studies have been done with some other animals, such as African antelopes (Jarman 1974), and primates. These types of studies have been sometimes termed socioecology (Crook 1970; Gautier 1982; Terborgh and Janson 1986), because they deal with the ecology of social groups. From an ecological perspective, the primates have been studied most extensively. A series of papers has attempted to document the relationship between food type, mating system, home range, body morphology, and social behavior (Eisenberg et al. 1972; Jorde and Spuhler 1974; Milton and May 1976; Clutton-Brock and Harvey 1977a,b).

The resources hypothesis of sociality suggests that social groups form and are maintained in response to the cooperative benefits that can be obtained by extracting certain types of resource distributions (Crook 1965; Slobodchikoff 1984). These groups may consist of either kin or non-kin. Slobodchikoff (1984) suggested that while kin-related assemblages may be a necessary condition for predisposing some animal groups toward social behavior, such kin-related associations may not be a sufficient condition for sociality to be maintained. Following and extending Crook's (1965, 1970, 1972) arguments, Slobodchikoff suggested that ecological factors such as resource abundances and distributions play a role in determining whether or not a particular group of animals is going to be social.

For example, Hamilton (1964) argued that sociality in the Hymenoptera arises because of the high degree of relatedness that is potentially possible between worker sisters as a result of haplodiploidy. However, while the ants and some bees are social, most species of Hymenoptera are not, and all have the same system of haplodiploidy as the honeybees used in Hamilton's arguments for sociality. The parasitic Hymenoptera constitute an extremely large number of species, yet they are all non-social (Askew 1971). Two major differences between the solitary parasitic Hymenoptera and the social Hymenoptera are the abundance and the distribution of food resources available to the larvae of each group.

The relationship between resources and sociality is expressed in several different models (Crook 1965, 1972; Wrangham 1980, 1983; Terborgh 1983; Van Schaik and Van Hooff 1983; Slobodchikoff 1984). These models each make some similar predictions, and some predictions that are different. Crook (1972) suggested that (1) group size will be high where patchiness of resources is low; (2) group size will be lowest at intermediate levels of patchiness; and (3) group size will increase again as patchiness begins to increase beyond this intermediate level. The logic of this argument, as suggested by Crook, is that at uniform resource distributions a social group can easily defend a particular territory containing necessary resources against other groups or other individuals. As patchiness increases, the members of the group are forced into more direct competition with each other for utilization of each

patch, and the more subordinate individuals will leave the group, causing the group size to drop. As patchiness continues to increase, a larger group size is again more favored, since more individuals would then be available for locating rich patches. Crook also suggested that there is a relationship between resource abundance and group size: the more abundant the resource, the larger the group size of the social group utilizing that resource.

Wrangham (1980, 1983) and Slobodchikoff (1984) make somewhat different predictions concerning resources and sociality. Wrangham suggested that related females group together to defend resources, while males join groups to have access to females. In this model, the size of the patches determines the group size. Smaller patches lead to monogamy, since the food resources will not support a larger group size. Larger patches lead to polygyny, either with a single male or with multiple males. Slobodchikoff (1984) suggested that the animals did not have to be related in order to band together to defend patchy resources. He further suggested that monogamy would occur primarily when resources were poor in quality and were uniformly distributed, while polygyny would occur when resources were rich in quality, supporting a larger group size, and when resources were patchily distributed.

Terborgh (1983) and Van Schaik and Van Hooff (1983) made similar predictions about the relationship between group size and resource levels, but also suggested that predation would play a role. They suggested that another important component other than food is the protection that is derived from having other members of a group watch for predators. In a cost-benefit formulation of this relationship, Terborgh (1983) and Terborgh and Janson (1986) suggested that costs increase with the food in a patch, while benefits associated with antipredator behavior decrease along some exponential function. The difference between the benefit curve and the cost curve represents the optimal group size at different levels of resource abundance.

Essentially, a common thread through the models is that (1) group size should increase with increasing resource abundance; and (2) at some level of resource abundance, there should be a switch from solitary individuals to monogamous associations, and then a switch from monogamous associations to polygynous ones, first with single male polygyny and then with multiple male polygyny. Differences are that (1) Crook's (1972) model predicts that the lowest group size will be at the intermediate levels of resource abundance and patchiness; (2) Wrangham's (1980, 1983) model predicts that the females are all related while the males are not necessarily related, and that resources have to be defensible by the females; (3) Slobodchikoff's (1984) model predicts that neither the males nor the females are necessarily related, that both sexes would participate in group defense, and that the dispersion of the resources, as well as the abundance, would determine the type of social system present; and (4) Terborgh's (1983) model and Van Schaik and Van Hooff's (1983) model predict that predator protection will modify the effect of food resources on group size.

All the models assume some degree of resource defense, or some sort of aggression between individuals; however, none of the models explicitly deals with the conditions by which such aggression would affect the utilization of the resources and the size of the social group. In this chapter we develop two models that explore the relationship between resources and group size as a function of aggression. We show how aggressive dominance can affect both the size of the social group and the decision to stay and participate in the social group. Finally, we address the question of why animals might stay in a social group without reproducing, and occupy a subordinate status, when they could instead leave the group and breed as solitary individuals.

II.   SOCIAL DYNAMICS: A SOCIAL EQUILIBRIUM MODEL

Social behavior can be viewed as a way for animals to cooperatively exploit resources that they would not be able to exploit as individuals. As such, a relationship can be modeled between resources and the size of the social group. Part of this relationship involves aggression. Aggression can provide a mechanism for controlling the size of the group, for defining the distribution of resources within the group, and for defining the reproductive relationships of the group. In this view, aggression acts as a governor on the social group, translating the available resources into a group size that is able to cooperatively exploit the resources.

The relationship between resources, group size, and aggression can be stated simply. Let us first define these variables:

R_T = total resource
(gs) = group size
n = the amount of resource required by a single animal to breed
a = the coefficient measuring the proportion of resource lost as a result of aggression

The social equilibrium (SE) can then be defined as

$$SE = \frac{R_T}{a \, n \, (gs)} = 1. \tag{1}$$

Let us look at this formula in some depth. The total resource that is available to the animals is R_T. This resource can be food, habitat, mates or other animals, or a combination of these resources. The availability of this resource is modified by a, such that $\frac{R_T}{a}$ represents the fraction of the resource that is actually available to the animals as a result of aggression. A considerable amount of aggression between the animals means that a is large, and the available resource is correspondingly small, while little aggression means that a is small, and the available resource is large.

Another way of looking at the relationship between $\underline{a}$ and R_T is as follows: If we define R_L as the resource lost due to aggression, and R_A as the resource available after aggression, then

$$R_T = R_L + R_A \tag{2}$$

and $\underline{a}$ can be defined as

$$a = \frac{R_T}{R_A} \tag{3}$$

or

$$R_T = a\, R_A \tag{4}$$

Thus, $\underline{a}$ represents the proportion of the resource that is lost through the effects of aggression. The assumption that is made here is that aggression entails a cost in terms of time, energy, and risk of injury, and that the effort expended on aggression can be translated directly into a loss of resource.

Given this assumption, the proportion $\underline{a}$ can be subdivided into resource loss through intra-group and inter-group aggression. If R_g is the resource lost through intra-group aggression, and R_i is the resource lost through inter-group aggression, then

$$R_L = R_g + R_i \tag{5}$$

Substituting equation (4) into equation (2), we have

$$R_L = R_A\,(a - 1).$$

With a substitution of R_g and R_i from equation (5), we have

$$a = \frac{R_g + R_i}{R_A} + 1 \tag{6}$$

Group size (gs) can be seen to depend on the interaction of the resources and aggression in the system. A rearrangement of the social equilibrium formula shows that group size is expressed as

$$(gs) = \frac{R_T}{a\,n} \tag{7}$$

This means that for a constant ratio of $\frac{R_T}{n}$, as (gs) increases, $\underline{a}$ decreases, and as $\underline{a}$ increases, (gs) decreases (Fig. 1). At first glance, this may seem counterintuitive. It seems to say that there is less aggression in a big group than there is in a small group. The argument is not quite that simple. The argument says that a smaller group will lose more of the available resource, whether through intra-group or inter-group aggression, than a larger group. This includes the cost of social interactions between the group members as well as the costs of defending the resource against non-group members. Even given that, however, the logical extension is that the costs of aggression decrease with increasing group size.
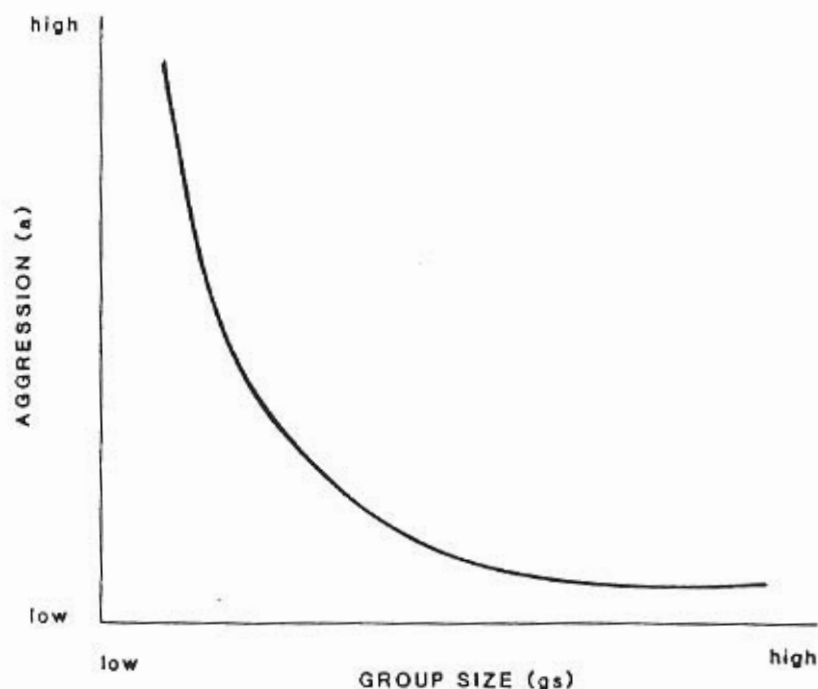
Fig. 1. The relationship between group size and aggression.

III.   SOCIAL DOMINANCE

Many social groups set up dominance hierarchies even as the group is forming. Examples of dominance hierarchies in animals such as the primates have proven to be ambiguous as to whether the dominant animals have significantly more access to resources than subordinate ones. By viewing dominance hierarchies, however, as a way of limiting aggression within the social group, and thus decreasing a while increasing the fraction of R_T that becomes available to the group, it can be seen that both dominant and subordinate animals can stand to benefit by limiting the costs of aggression.

The social equilibrium model may be modified to express this relationship. Under conditions of resources being more abundant than the social equilibrium formula predicts for a given group size, dominant animals may have more access to resources than subordinate ones. In this situation, if k_i is the proportion of resource garnered by a single individual, and $\overset{(gs)}{\Sigma} k_i = 1$, with (gs) being the number of animals in the social group, an unequal distribution of resources can be obtained between dominants and subordinates under the condition of the inequality

$$\frac{\iota \, k_i \, R_T}{a \, n \, (gs)} > 1 \tag{8}$$

In this circumstance, $\underline{a}$ is expected to be high, and as (gs) increases with a corresponding decrease in $\underline{a}$, an unequal distribution of resources through social dominance is expected to disappear (Table I).

IV. DISPERSAL AND REPRODUCTIVE DOMINANCE

So far, we have seen what happens when the sociality equilibrium equals 1 or exceeds 1. But what happens when the equilibrium drops below 1? As group size increases, $\underline{a}$ continues to decrease. However, the critical ratio of $\frac{R_T}{n}$ becomes too small for some animals to have enough resources available to be able to breed. Although the predicted strength of cooperation in the social group should increase (as $\underline{a}$ decreases), the choice for some animals becomes (1) to stay in the social group and not breed, or (2) to leave the social group and try to find another group that has not yet approached its sociality equilibrium of SE = 1.

The choice of whether to stay or to leave should depend on two probabilities. One is the probability, P_d, of surviving as a solitary individual and finding another group where breeding is possible. The other is the probability, P_b, of breeding eventually by staying in the social group. If $P_d > P_b$, the animal should leave, and if $P_b > P_d$, the animal should stay.

If the animal stays, its chances of breeding decrease with increasing group size once SE < 1. The probability of breeding can be approximated

Table I. Characteristics of Social Systems under Different Conditions of the Sociality Equilibrium

SE > 1	SE = 1	SE < 1
Social dominance	No dominance	Reproductive dominance
All animals breed	All animals breed	Some animals breed
High aggression	Low aggression	Low aggression
Low cooperation	High cooperation	High cooperation
Unequal resource distribution	Equal resource distribution	Unequal resource distribution

through the sociality equilibrium formula, by the approximate relationship, when SE < 1, or as follows:

$$P_b = \frac{R_T}{n \, (gs)} \tag{9}$$

This probability function is shown in Fig. 2. The consequence of this declining probability of reproduction is reproductive dominance (Table I).

A constraint here is that the animal's share of the resource must be enough to allow the animal to survive, if the resource is food, space, or other animals exluding mates. If r is the minimum resource needed to support one non-breeding animal, then the animals' share of the resource cannot fall below r. If it does, then the animal must leave the group and disperse.

V. MAXIMUM GROUP SIZE

The social equilibrium equation (1) can be used to predict the maximum group size that should be possible for a given amount of a resource. When n represents the amount of resource needed by each and every animal in the group (i.e., when all the animals in the group breed), the maximum group size is predicted by equation (7), or

$$(gs)_{max} = \frac{R_T}{a \, n}$$

But what if there is reproductive dominance, and not all animals in the group need or use resources in the same way? For example, in honey bee colonies, there is usually only one reproductive female per colony, while ant colonies have one to several reproductive females (Wilson 1975).

We can define this situation with a few additional terms. If n is the minimum amount of resource needed to support one breeding animal, then let us say that r is the minimum amount of resource needed to support one non-breeding animal. Then, if only one animal breeds in the group, the maximum group size will be

$$(gs)_{max} = \frac{R_T - n}{r} + 1 \tag{10}$$

This can be expanded to a more general case of x number of breeding animals and y number of non-breeders. The maximum group size under these conditions becomes
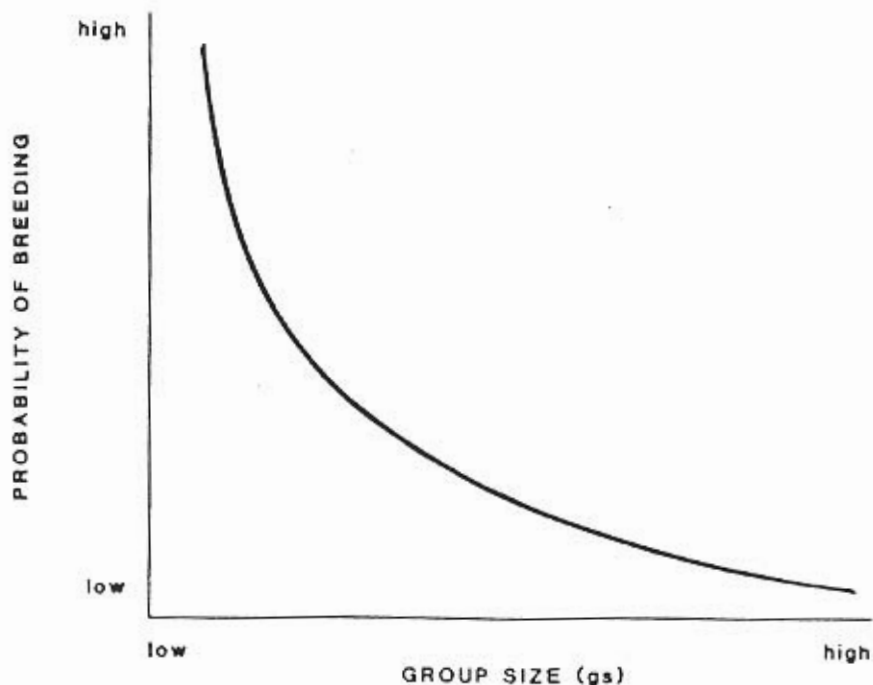
$$(gs)_{max} = \frac{R_T - xn}{r} + x \tag{11}$$

Fig. 2. The relationship between group size and the probability of reproduction in the social group.

If breeding males and females have different resource requirements and n is the minimum amount of resource needed to support one breeding female, while q is the minimum amount of resource needed to support one breeding male, and x is the number of breeding females, while w is the number of breeding males, then the maximum group size becomes

$$(gs)_{max} = \frac{R_T - (xn + wq)}{r} + (x + w) \qquad (12)$$

As the number of breeders increases so that the resource is more equitably distributed among the group members, equation (12) approaches the maximum group size predicted by equation (7).

VI. SOCIAL DYNAMICS: A DYNAMIC EQUILIBRIUM MODEL

So far, in the social equilibrium model, we have not taken into account what happens to group size with small and continuous changes in aggression. This can be modeled with a system of linear differential equations

$$\frac{dB}{da} = kU + 2l\,(N-B) \tag{13}$$

$$\frac{dU}{da} = 2l\,(N-B) - 2mU$$

where B is the number of breeding individuals, U is the number of non-breeding individuals, and N is the number of individuals that the resources can support if all of the individuals are completely solitary. In this system of equations, k, l, and m are numerical coefficients that are determined empirically for different species and different resources. Specifically, l represents the proportionality between the rate of increase of the number of breeding individuals when all animals are solitary and the increase in the number of individuals over N due to decreased aggression. The influence, as aggression decreases, of the increase of non-breeding individuals on the number of breeding individuals is represented by k. The coefficient m, assumed here to be small, represents a possible tendency of the non-breeding individuals to assume dominance of the social group. For most species, m would be equal to 0. The coefficients k, l, and m are assumed to be nonnegative.

In order for the model to correspond to biological reality, certain relationships among the coefficients must hold, namely

$$(1 - m)^2 - 2lk > 0.$$

In addition, to solve for the system of equations, certain boundary conditions must be assumed. Although the number of breeding individuals in a social group seldom is less than one, we may for mathematical convenience set $B(0) = 0$. The effect of setting $B(0) = 1$, while more realistic biologically, complicates the mathematics without having any appreciable effect on the solutions. The number of non-breeding individuals in social groups is conditioned by the resources, and this is represented by the parameter u.

With these conditions, elementary methods result in the following solution to equations (13)

$$B(a) = N - \frac{1}{2}\left(N - \frac{ku+N(1-m)}{\beta}\right)e^{-(\alpha-\beta)a} - \frac{1}{2}\left(N + \frac{ku+N(1-m)}{\beta}\right)e^{-(\alpha+\beta)a}$$

$$U(a) = \frac{1}{2}\left(U + \frac{2(U+N)}{\beta}\right)e^{-(\alpha-\beta)a} + \frac{1}{2}\left(U - \frac{2l(U+N)}{\beta}\right)e^{-(\alpha+\beta)a}$$

where, for convenience, we have set $\alpha = l + m$ and $\beta = ((1 - m)^2 - 2lk)^{1/2}$. Note that $\beta < \alpha$. The important features of the solution can be determined from the graphs of U (a) and B (a) (Fig. 3).

The graphs of U (a) and B (a) show that as aggression increases the number of breeding individuals approaches N and the number of non-breeding individuals approaches 0. Another feature of the solution is that as aggression decreases (i.e., as cooperation increases), the number
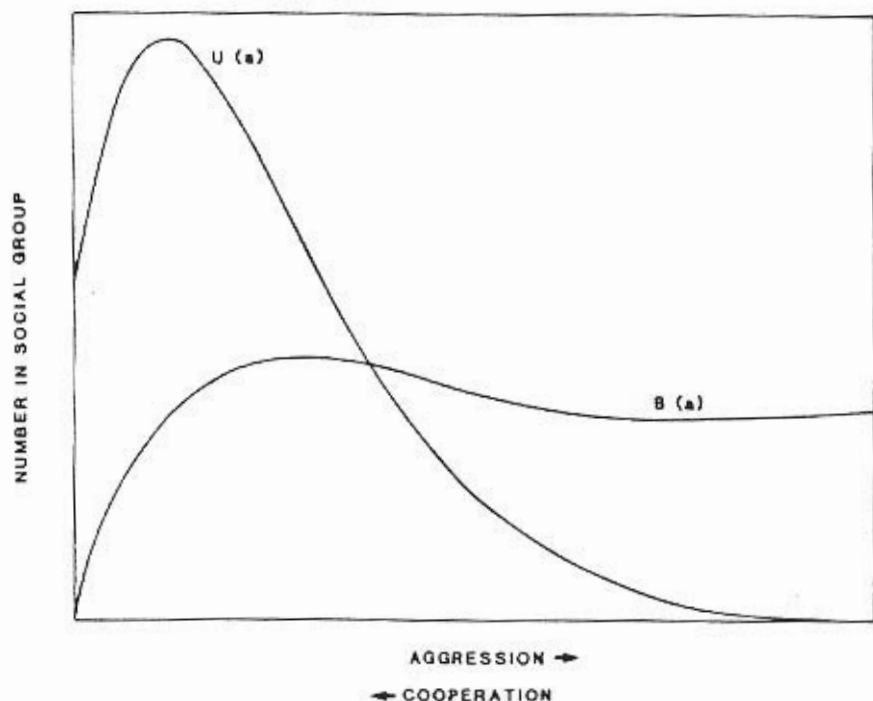
Fig. 3. Graphical representation of the predictions of the dynamic equilibrium model for a given resource level. B represents the number of breeding individuals, while U represents the number of nonbreeding individuals.

of non-breeding individuals rises dramatically, while the number of breeding individuals decreases. This is the same result predicted by the sociality equilibrium model. At the highest levels of cooperation (or the lowest levels of aggression) there are extremely few breeding individuals, with a preponderance of non-breeding individuals. This is similar to the situation that is seen among many of the eusocial Hymenoptera.

VII. A GAME THEORETIC MODEL OF SOCIALITY

If we assume that resources are unequally distributed among dominants and subordinates, then we can develop a game theoretic model of the resource conditions under which animals should form social groups. This model is a non-zero-sum game that is based on bargaining solutions (Bartos 1967).

In this approach, let us make some assumptions about the social group: (1) both dominants and subordinates can breed; (2) dominants are

better at finding, defending, extracting or utilizing resources than are
subordinates; (3) dominants can have more offspring in a social group
containing subordinates than they can have by themselves as solitary in-
dividuals; (4) subordinates may have fewer offspring immediately in the
social group but have some expectation of becoming dominants; and (5)
subordinates can share access to resources with the dominants in the so-
cial group. Thus, in our assumptions, both the dominants and subordi-
nates can derive some benefit from the social group, to different de-
grees.

Now let us construct a payoff matrix. We will assume that the
maximum payoff or loss is +5 or -5. In Case 1, the resources can be
shared. We have then four strategies (Table II).

In Strategy A, the dominants (Ds) are willing to share their access
to the resource. In the process of sharing, the dominants give up some
of the resource for the promise of increased reproductive success. The
payoff to the dominants falls to +2. Because the dominants are willing
to share, the payoff to the subordinates is the maximum of +5.

In Strategy B, the dominants are willing to share, but the subordi-
nates take some of the resource and leave, not staying to participate in
the social group. Here both the dominants and subordinates lose, the
subordinates because they give up their access to future resources that
the dominants may find, and the dominants because they have shared
some of their resource without attracting any subordinates to the social
group.

In Strategy C, the dominants do not share their resources, but the
subordinates stay anyway. The maximal payoff of +5 goes to the domi-
nants, and the maximal loss of -5 goes to the subordinates.

In Strategy D, the dominants do not share, and the subordinates do
not stay. Here there is neither a gain nor a loss to either group, and the
payoff to both is 0.

A geometrical analysis of the payoff space (Fig. 4) shows the payoff
matrix plotted with respect to the payoffs to both the dominants and
subordinates. The equilibrium point V* is a positive payoff for both the
dominants and the subordinates. This equilibrium point, however, shows
that neither the dominants nor the subordinates gain as much from par-
ticipation in the social group as predicted by Strategy A. The conse

Table II. Payoff Matrix for Dominants (Ds) and Subordinates (Ss) under
Conditions of Resources Sufficient to Share

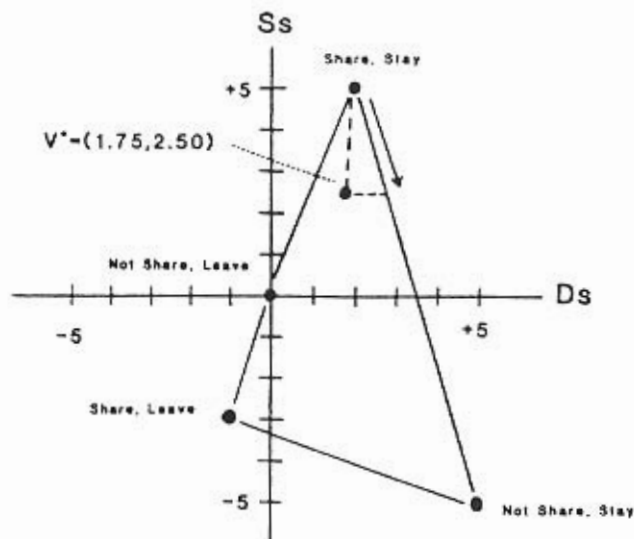|		Ds	Ss
Strategy A:	Ds share, Ss stay	+2	+5
Strategy B:	Ds share, Ss leave	-1	-3
Strategy C:	Ds not share, Ss stay	+5	-5
Strategy D:	Ds not share, Ss leave	0	0

Fig. 4. *Graphical representation of the game theory payoff matrix under the conditions that the resources are sufficient to share.*

quence of this is that there is some latitude for the dominants to withhold sharing the resources without having the subordinates leave the social group (the arrow in Fig. 4 shows the extent to which the dominants can withhold resources without an appreciable change to the equilibrium payoff of the subordinates). The subordinates, on the other hand, can increase their access to the resources to some extent without any serious change in the equilibrium payoff for the dominants. This predicts a constant conflict situation within the social group, where the dominants are trying to skim on sharing with the subordinates, and the subordinates are trying to get more resources out of the dominants.

In Case 2, where resources are insufficient for sharing, we have a different set of predictions. As before we construct a payoff matrix (Table III), where strategies C and D are the

Table III. Payoff Matrix for Dominants (Ds) and Subordinates (Ss) under Conditions of Resources insufficient to Share

		Ds	Ss
Strategy A:	Ds share, Ss stay	-2	+1
Strategy B:	Ds share, Ss leave	-5	+3
Strategy C:	Ds not share, Ss stay	+5	-5
Strategy D:	Ds not share, Ss leave	0	0

same as before, but strategies A and B are now different. In Strategy A, if the dominants share, they lose a part of the resource that they need for maintenance, while the subordinates, by staying, gain a little, although the amount gained is not very much since the resource is not abundant. In Strategy B, the dominants lose the maximum by sharing, since the resource is not abundant.

Under these conditions, the equilibrium point V^* is at $(0,0)$, or the point where dominants should not share and the subordinates should leave. However, two interesting results can be seen. One is that both the subordinates and the dominants can improve their payoff by sharing and staying if resources become more abundant (see the direction of the arrow at share, stay, Fig. 5). The other result is that dominants can improve their negative payoff slightly in Strategy B, even if the subordinates leave (see the direction of the arrow in share, leave, Fig. 5). However, the subordinates get a lower payoff by staying at this point rather than leaving. There is, thus, a basic conflict in the initial conditions for sociality, where the dominants may be willing to share but the subordinates may be willing to take but not stay. As can be seen from Case 1, this conflict can be resolved where resources are abundant, but this conflict can prevent the formation of social groups where resources are sparse.
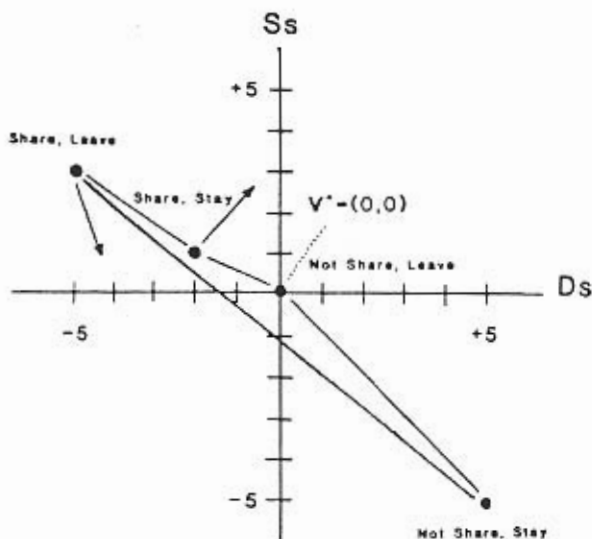

Fig. 5. Graphical representation of the game theory payoff matrix under the conditions that the resources are not sufficient to share.

VIII. REPRODUCTIVE DOMINANCE AND REPRODUCTIVE EXPECTATION

The sociality equilibrium model shows that once social groups form, they may be maintained even though the resource may not be sufficient for all individuals to breed. We may then ask the question: What prevents animals from leaving the social group under these conditions? To answer this question, we will develop a model of reproductive expectation. This model deals with the expectation of reproducing in a social group versus the expectation of reproducing as a solitary individual.

The assumptions of the reproductive expectation model are: (1) only one female breeds in the social group; (2) if a breeding female dies, another female enters the group in a non-breeding, subordinate position; (3) the mortality rate for all females is the same; and (4) the social group produces more offspring than solitary animals.

We can now define the following terms:

N_s = the number of offspring of a solitary female
N_c = the number of offspring produced by the social group
p = the probability of survival of an individual female
n = the number of animals in the social group

Then the reproductive expectation of a solitary female (E_s) will be

$$E_s = p\, N_s \tag{14}$$

and the reproductive expectation of a social female (E_c) will be

$$E_c = N_c \frac{1}{n-j}\, p\,(1-p)^j \tag{15}$$

where j is an index of the number of females. Formula (15) can be approximated by the following:

$$E_c = \frac{N_c}{n}\left[p + \frac{n}{n-1}(1-p)\right] \tag{16}$$

The results can be seen in Fig. 6, where the reproductive expectations of both the solitary and social group can be seen, with m_c the slope of the social group reproductive expectation, and m_s the slope of the solitary female reproductive expectation. In terms of reproductive expectation, there will be evolutionary pressure to form groups if

$$\frac{E_c}{E_s} > 1 \tag{17}$$

or if the reproductive expectation of the social group is greater than the reproductive expectation of a solitary individual. If this condition can be satisfied, then a female should stay in the social group, even if she has a low probability of actually breeding.

Let us consider a numerical example. Let us assume that we have a colony of wasps that consists of five females. Of these, only one reproduces at any given time. The probability of survival of an individual wasp, either in the colony or as a solitary individual, is $p = 4/5$. Let us
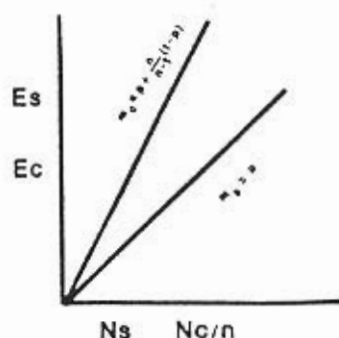
Fig. 6. Reproductive expectations for a solitary individual and for a social group of individuals, assuming that only a single individual in the social group breeds, and all the remaining individuals are nonbreeders.

contrast the reproductive expectation of a wasp in the social group with a wasp that lives as a solitary individual. Elementary algebra shows that

$$\frac{N_c}{N_s} > \frac{20\ p}{5 - p} = 3.8$$

Thus, a social group of five females must produce at least 3.8 times more offspring than a solitary female in order to have a reproductive expectation, per capita, that is higher than the reproductive expectation of a solitary female. However, if the social group can accomplish this through increased parental care and offspring survival, then a female should stay in the social group even if she does not ever reproduce. The important key is that she should have some probability of becoming a reproductive female. This appears to be true in most of the social Hymenoptera and Isoptera, which have large numbers of worker individuals that never reproduce. Each of these worker individuals has some initial probability of becoming reproductive, and consequently each individual has some reproductive expectation within the social group (Slobodchikoff 1984).

IX.   SUMMARY: SOCIAL DYNAMICS AND EVOLUTION

The dynamics of social behavior can be viewed as an interaction between resources and individuals seeking to exploit those resources. Through cooperation, the group is able to collectively exploit or defend resources that each animal individually would not be able to exploit or defend.

We suggest that this interaction between resources and individuals can occur independently of the relatedness of individuals in the group (sensu Hamilton 1964). As we argued earlier, many other species of

Hymenoptera have the same haplodiploid system of sex determination as the honeybees, and so should theoretically have the same levels of genetic relatedness among sisters as worker honeybees, yet most of these species are not social. Electrophoretic analysis of worker ants fails to substantiate a high degree of genetic relatedness among workers in some nests. For example, the Australian desert ant *Rhytidopondera mayri* has relatedness levels of 0.1-0.2 among workers, rather than the 0.75 predicted by Hamilton (Crozier et al. 1984). Similarly, polygyne or multiple queen colonies of the fire ant *Solenopsis invicta* have a relatedness near zero among both the workers and the queens (Ross and Fletcher 1985). The same situation is found among *Polistes exclemans* social wasps, where the relatedness between workers and the brood that they raise is quite low (Strassmann 1985). Even among the honeybees, queens can mate with multiple males, leading to a greatly lowered relatedness among workers (Page and Metcalf 1982).

However, the presence of kin may predispose some animals to form social groups. For example, having offspring stay with their parents during a period of parental care provides a pool of ready individuals who can participate in a social group. In yellow-bellied marmots, kin relationships are important in determining the amount of foraging area shared by individual marmots, and spatial overlap is greatest among close kin, but this relationship is modified by other factors such as individual behavior, reproductive state, age of the animals, and the existence of separate burrow systems (Frase and Armitage 1984). Among the vertebrates, kin groups may be a common initial starting point for the formation of social groups. We argue, however, that kinship is neither a necessary nor a sufficient condition for sociality. We suggest that without appropriate resource levels and without the mediating interactions of aggression, kin groups would not be able to form into social, cooperative groups.

The sociality equilibrium models show how aggression can mediate group size for a given level of resources. Aggression has long been recognized as an important component of social systems (Hall 1964). Aggression often has been viewed as an important part of the socialization process of establishing social bonds and dominance hierarchies, either among kin or among non-kin (Bernstein and Gordon 1974; Bernstein and Ehardt 1986). We suggest that a primary function of aggression in social groups is to mediate the group size with respect to the available resources.

From an evolutionary standpoint, the most stable condition for the group should be when the sociality equilibrium is equal to 1. At this point, all the members of the group can breed and there is an equal access to resources by all the members of the group. When the sociality equilibrium is greater than 1, and the resources are abundant, much of the resources can be lost through aggression and the lack of cooperation, and the group can collect more group members. This collection of group members should occur at the expense of the more dominant individuals who at this point have more access to resources than the subordinates. More individuals will collect in the group, however, because the cost to

the dominants of keeping out other potential group members will be greater than the cost that they would face by having competitors within the group use the same resources.

As the sociality equilibrium moves from SE > 1 to SE = 1, the dominants will have to share more of the resources, and the resource then becomes more equitably distributed throughout the group. On the other hand, by sharing more they also do not have to incur the same costs in defending or extracting the resource, since more of the resource defense or extraction is borne by the additional group members. The subordinates at the bottom end of the hierarchy in a social dominance system get access to as much resource when SE = 1 as when SE > 1, so that their access to the resource should be unaffected as SE approaches 1. The dominants can incur a drop in offspring production at this point if their reproductive rate is limited to their increased control of resources, but this loss of offspring production may be balanced by increased cooperation in progeny care within the group as the overall level of cooperation increases. Therefore, actual fitness stays the same or increases for the dominants as SE approaches 1.

As SE drops below 1, reproductive dominance should occur and not all the members of the group will be able to breed. From the standpoint of individual selection, an animal that is unable to breed should not stay in the group unless the probability of finding and breeding in a new group is less than the probability of breeding in the existing group. Under these circumstances, the sociality equilibrium predicts that cooperation should increase and aggression should decrease as the group size increases, and this seems to be the case with the eusocial insects that have an extreme form of reproductive dominance (Wilson 1975). Among these social insects, most species have a small probability at birth of reproducing as adults, and zero probability of joining and breeding in another group. In this respect, some eusocial insect species show incomplete reproductive dominance. Honeybee workers are occasionally able to lay eggs that develop parthenogenetically, because of the haplodiploid system of sex determination, into males. An even more extreme form of reproductive dominance is seen in South African colonies of the ponerine ant, *Opthalmopne berthoudi*, where up to 100 workers in a nest can be inseminated and can produce eggs within the colony. The resulting workers have a low level of relatedness because of the multiple parentage of workers in the colony, but all the workers cooperate in maintaining the colony (Peeters and Crewe 1985). The social equilibrium models predict that this kind of incomplete reproductive dominance is linked to resource levels, and that an increase in resource levels would lead to an increase in the number of reproductive workers.

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