

Chapter 1

ECOLOGICAL TRADE-OFFS AND SOCIAL BEHAVIOR

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- I. COST-BENEFIT ANALYSES AND THE ORIGIN AND MAINTENANCE OF SOCIAL BEHAVIOR

Recent discussions regarding the origin and maintenance of social behavior are often based on conflicting, or at least confusing, collections of hypotheses and data about the evolution of: (1) groups (colonies or societies); (2) behavior within groups (social behavior); or (3), both (1) and (2). We define a group, with Wilson (1975, p. 585), as "any set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics." We define a society as an interacting group consisting of more individuals than parents and their immediate dependent offspring. In this context, social behavior includes any behavioral interactions among members of social groups. Social behavior, then,

includes any selfish, spiteful, cooperative, or altruistic behavior directed at group members and need not be limited to social species (Hamilton 1964).

At first glance, such discussions of social behavior offer a plethora of potential explanations at odds with themselves. Thus, some treatments have emphasized the importance of ecological factors in the adaptive origin and maintenance of group living and social behavior (e.g., Crook 1965, 1970; Lack 1968). Other treatments have emphasized the importance of kinship in the adaptive shaping of social behavior (e.g., Hamilton 1964; Alexander 1974; Trivers 1985). Still others have emphasized that the groups or social behaviors we currently see may be the result of phylogenetic inertia, i.e., patterns developed in evolutionary time within the phylogeny of the animals in question (Wilson 1975).

These different emphases can be categorized into three classes of hypothesis. The classes are not mutually exclusive and each could have an independent and important influence on explaining the origin or maintenance of sociality in any particular species, population, or group. *Genetic* hypotheses assume that high levels of kinship among group members are necessary and sufficient to explain the kind of society being investigated. *Ecological* hypotheses assume that nongenetic environmental factors are necessary and sufficient to explain an observed social system. Finally, a *phylogenetic* hypothesis assumes that a social system evolved in the context of conditions occurring earlier in the evolutionary history of the lineage in question and does not represent an adaptation to current conditions.

The recent emphasis on genetics stems from the attention generated by Hamilton's (1964) quantification of inclusive fitness, which was intended to explore the effects of kinship on the evolution of altruistic behavior. Hamilton's rule states that altruistic behavior will evolve only when the gain for the beneficiary of a behavior (B , where the beneficiary is a different individual from actor also called donor), multiplied by the probability (r) that the beneficiary and the actor have genes in common, exceeds the cost of that behavior to the actor or donor (C). Costs and benefits here are both positive terms. When the probability of having genes in common (i.e., relatedness) between the actor and the beneficiary is zero, the cost to the actor is often greater than the benefit to the beneficiary. This translates into the classic statement that only when $Br > C$ will altruistic social behavior evolve. This has also been translated into an expectation that relatedness will have profound effects on the evolution of sociality.

For example, Hamilton (1964) originally argued that the social system of honeybees might have arisen, in part, because of haplodiploidy, i.e., because worker bees may be more closely related to each other than they would be to their own progeny. The eusocial Hymenoptera, however, make up a relatively small proportion of species. Most Hymenoptera are not social, although all non-social bee and wasp females have the same probability as the honeybees of being more closely related to sibs than to progeny. Although the actual relatedness among worker honeybees within a hive remains an empirical question and is probably less

than that assumed by Hamilton (Page 1986), the different levels of sociality observed in the Hymenoptera imply that relatedness alone is not a sufficient condition for the evolution of eusociality.

Ecological hypotheses also assume that cost-benefit functions are driving factors in the evolution of sociality, although usually less explicitly than the genetic arguments. As Alexander (1974) noted, there are always costs and potential benefits associated with living and interacting in a group. The implication is that a particular kind of group, or social behavior within a group, will occur only when the benefits to actor (B) exceed the costs to the same actor (C), that is when $B > C$. Note that relatedness is not explicit in this equation. Here the actor and beneficiary are the same individual, and the relatedness in question (the r in Br) is always one (i.e., $r = 1$) and so can be ignored during the calculations.

Most hypotheses of this type suggest that groups originate in order to exploit resources that cannot be exploited as efficiently by solitary individuals (e.g., Crook 1972; Slobodchikoff 1984; Wittenberger and Hunt 1985). They imply that the presence of conspecifics generates a direct and net benefit for an individual joining, or interacting within, a group (e.g., Alexander 1974; Lott 1984; Wittenberger and Hunt 1985). Here, resources are taken to mean any of a variety of factors that can affect fitness: food, space, mates, nonmate social partners, refugia nest sites, climate, and time, to name a few. Since resources can include other animals, social groups also possess the potential benefit of group defense against other animals, particularly predators. Thus, the testing of ecological hypotheses also entails cost-benefit analyses of social groups versus solitary individuals, but without the constraint of relatedness. Unlike the genetic arguments, which have involved extensive theoretical modeling and analysis of kinship, the ecological hypotheses have been explored primarily through studies using the comparative method (e.g., Crook 1965, 1970, 1980; Lack 1968).

Phylogenetic hypotheses are usually proposed as a last resort when extensive estimation of costs and benefits has failed to demonstrate a net benefit in a particular case, or when comparative analysis or experimentation have failed to document the expected type of sociality in a particular case (e.g., Berger this volume). In order to deduce phylogenetic patterns of sociality, the comparative approach has been used, with correlations between social systems and morphological types that are believed to reflect actual phylogeny (e.g., Lin and Michener 1974; Brown 1975). Such phylogenetic arguments suggest that any genetic or ecological factors influencing the adaptive value of sociality have been operative over evolutionary time scales. According to these arguments, extant species are unable to respond to immediate conditions in an adaptive manner. Adaptive arguments about the origin of social systems may be valid, but arguments about the maintenance of sociality do not require adaptative explanations.

To explore the origin and maintenance of groups or sociality within groups, one should investigate all of the factors that can influence the costs and benefits of group living or of particular behaviors within groups. The underlying hypothesis is that only when total benefits

exceed total costs (i.e., when $B > C$), on a per capita basis, will groups or specific social behaviors evolve. For a complete analysis, however, the total benefits and costs need to be partitioned into their direct and indirect components (e.g., Hamilton 1964; Shields 1980; Brown and Brown 1981). Thus, B includes both direct (b_d) and indirect benefits ($b_i r$, where r is the relatedness between actor and those affected positively by his act not including himself) and C includes direct (c_d) and indirect costs ($c_i r$, where r is the relatedness between actor and others which are affected negatively by the same act). Group living or specific types of social behavior are expected to arise only when the per capita combined direct and indirect benefits exceed the per capita combined direct and indirect costs (i.e., when $(b_d + b_i r) > (c_d + c_i r)$).

Under most conditions, selfish, spiteful, and aggressive behaviors are expected to limit group cohesion by increasing the direct and indirect costs of grouping, while cooperative and altruistic behaviors should favor grouping and group cohesion by increasing the direct and indirect benefits associated with group living. Insofar as all indirect effects are influenced by patterns of kinship within groups, kinship will be critical to understanding genetically based sociality. Insofar as most ecological factors disproportionately influence the direct costs and benefits of group living, kinship may be less important, or even irrelevant, in exploring ecologically based sociality.

It is easy to perceive the genetic and ecological arguments as alternative hypotheses. We would caution, however, that it is incorrect to assume that they cannot have operated independently or jointly during the evolution of any social system. For example, it is not difficult to imagine ecological circumstances that originally favored animals living in groups regardless of the relatedness of group members (e.g., a shortage of nest sites). Once members of such a species were regularly living together in groups, however, kinship patterns could be expected to influence the kinds of social behavior displayed among group members according to Hamilton's rule. The end result is that investigators faced with the many *fait accompli's* provided by different extant species (for a review, see Rubenstein and Wrangham 1986) would do best to keep all of the alternatives in mind when interpreting the behavior of their species. It seems most likely to us that genetic, ecological, and phylogenetic factors have all contributed to the origin and maintenance of sociality in specific animal groups. The mix of causative factors at any given time for any given species probably represents a specific solution to a specific set of selection pressures given the historical constraints of its phylogeny.

II. ECOLOGICAL TRADEOFFS AND SOCIAL BEHAVIOR

The chapters in this volume consider some of the ecological tradeoffs that might lead to sociality. While the primary emphasis of these chapters is on a consideration of ecological mechanisms, the chapters also illustrate the interplay between ecology, genetics, and phylogeny.

Several papers treat the general questions of origins and maintenance. Slobodchikoff and Schulz (Ch. 2) suggest that groups will form to collectively exploit resources that cannot be efficiently exploited by solitary individuals. They propose that a proximate mechanism for regulating group size is aggression, and that aggression mediates the quantity and distribution of a particular resource that is available to each individual within the social group. They also suggest that although group size can increase to a point where many individuals within the group do not breed, such an increase can occur in an evolutionary sense only if all the individuals in the group have some expectation or probability of breeding. Giraldeau (Ch. 3) predicts that groups will not be of optimal size, but rather of a size that makes it unattractive for solitary individuals to join the group. This size, which Giraldeau calls the stable group size, varies with kinship patterns and is somewhat less than the maximum group size, where the net benefit in terms of resource extraction per individual in a social group equals the net benefit to a solitary individual. Barlow (Ch. 4) discusses the general terms and conditions necessary for resources to influence social systems. He suggests that mating systems are an important component of resource-determined sociality. Barlow points out that monogamy, perhaps the most simple social system, fits resource models in ways that are similar to the more complex social systems. However, he points out that monogamy in different species has evolved in various ways in response to different selective pressures. Rodman (Ch. 5) addresses a variety of different ecological hypotheses, particularly those that have been used to explain sociality in primates. He points out that there is a need for assessing different alternative hypotheses and assessing the relative complexity of the factors that could be influencing the size of social groups.

Several papers address the relationships between resource abundance, resource distribution, and social behavior. Uetz (Ch. 15) shows that social spiders form groups where prey abundance is high and variance in prey abundance is low. Under conditions where prey are patchily distributed and the variance in prey abundance is high, the daily intake levels of spiders do not support group living, and the spiders living in such habitats are solitary. Using a comparative approach, Gautier et al. (Ch. 14) show that cockroach species living in forest habitats, where food is not abundant and very patchily distributed tend to be non-social. Other cockroach species dwelling in caves, where food is abundant and clumped, tend to have variable social systems, depending on the specific abundance and distribution of the food. These general patterns are found among phylogenetically unrelated species, suggesting that in cockroaches, phylogeny has played a secondary role to ecology in the development of sociality. Heinrich (Ch. 12) shows how sociality is utilized by ravens, which feed on carcasses in the winter. A carcass represents a superabundant and temporary food source, and no single raven can use all the food that is available at any one time. Under these short-term, ephemeral conditions in ecological time, the ravens share information about food sources by calling in other ravens and forming a feeding flock.

Resource abundance and distribution of food and habitat sites can be modified by another resource--climate. Marzluff and Balda (Ch. 11) show how climate affects the abundance of pinyon nut crops. The abundance and distribution of pinyon nut crops in turn influence the social systems of two species of corvids, the pinyon jay and the scrub jay. Both species have to deal with the same set of resources, but the morphological adaptations derived from the phylogeny of the two species mandate different solutions to dealing with the gathering and utilization of pinyon nuts. These different solutions translate into different social systems. Ligon and Ligon (Ch. 10) show that woodhoopoes have a physiological intolerance to low temperatures, and that this intolerance necessitates roosting in groups within cavities for warmth. However, the number of good territories containing good roost cavities that are relatively free from predation is limited, so the birds form alliances of either related or unrelated individuals for the purpose of territory acquisition and maintenance.

Inheritance of resources can be an important feature of the ecological constraints that social animals face. Shields et al. (Ch. 9) show that swallows, faced with environments that vary cryptically in such a way that habitats cannot be immediately assessed, use traditional breeding grounds as an indicator of habitat quality. Shields et al. argue that the decision rule in such cases is: where others have been able to live and breed successfully in the past, so can I. Waser (Ch. 6) points out that banner-tailed kangaroo rats need mounds as refuges, and the supply of mounds is very limited. The chance of successful dispersal by young is low, and the cost of sharing a mound with young is also low. Waser suggests that when resources are non-depreciable, philopatry is likely to occur. Philopatry may be an important precursor to the development of kin-related social behavior in some animal groups. Myles (Ch. 16) argues that in a variety of animal groups it is not the relatedness of individuals that is important, but the tradeoffs involved in dispersal versus the inheritance of some necessary resources. Since in practice kin often inherit resources, many social groups are going to be kin groups. However, Myles argues that inheritance need not be only among kin, and that kin arguments are neither necessary nor sufficient for explaining the formation and maintenance of social groups.

Within a social group, there may be competition for resources. Such social competition is discussed by Pollock and Rissing (Ch. 13), who suggest that subordinates aid dominants in order to remain close to resources that would otherwise be unavailable to them. They argue that such social competition has been an important feature in the origins of a number of social groups, particularly the social Hymenoptera. A game-theoretic model of such social competition is explored by both Pollock and Rissing and Slobodchikoff and Schulz (Ch. 2). A similar view of social competition is suggested by Armitage (Ch. 7), who suggests that among the ground squirrels sociality is both cooperative and competitive, and is aimed at maximizing direct fitness rather than indirect fitness.

Finally, what happens when an investigator manipulates the resources available to a group of genetically unrelated animals and finds that the same social system is maintained? Berger (Ch. 8) shows that some ungulates maintain the same social system, regardless of the distribution and abundance of resources. Berger ascribes this to phylogenetic inertia, the canalizing effect of evolution on the social system of these animals. He also carefully considers, however, all of the difficulties involved in actually determining and measuring the resources that are relevant for manipulation, and shows how difficult it can be to determine that phylogenetic factors have actually insulated a social system from ecological or genetic considerations.

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