Resources and the Evolution of Social Behavior

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CHAPTER 8

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1 INTRODUCTION

Although there are perhaps one million species of animals in the world, relatively few are social (Wilson, 1975a). Even among some groups of animals that are well known for their sociality, there are closely related species that are not social. The ants and honeybees in the insect order Hymenoptera are recognized as having a complex form of sociality, but other species of Hymenoptera are not social. The parasitic wasps are generally not social. Wasps in families closely related to the ants are not social. Wild bee species that are related to the social bees are solitary. Similar situations can be found among other animal groups. Some are social, others are not. We may then ask the question. why are so few animals social? In attempting to answer this question, we must also ask the question. how did sociality evolve?

Attempts to explain sociality can be classified into descriptive models and evolutionary models. Descriptive models attempt to infer a pathway for the development of social behavior from successive stages of sociality found among different animal groups. The familial and the parasocial pathways (Vehrencamp, 1979; Lin and Michener, 1972) are examples of descriptive models. The stages of the familial pathway (Vehrencamp, 1979; Wilson, 1975a) are solitary, subsocial, intermediate subsocial, and eusocial. In the solitary stage, the adults merely come together for the purposes of breeding. The male leaves or dies immediately after mating, and the female provides no parental care for the offspring. In the subsocial stage, the adults mate, and one or both parents care for the young for a certain length of time, so that the generations overlap. The young usually leave the care of the parents before the onset of sexual maturity. In the intermediate subsocial stage, there is also extended parental care, and the group members of at least two generations cooperate in a variety of activities such as foraging and defense. In the eusocial stage, there are the overlapping generations, extended parental care, and cooperation in a variety of tasks, but also there is a reproductive division of labor, with some individuals producing offspring while others do not breed. Since it is based on the premise of increasing parental care, as well as increasing levels of cooperation, the familial pathway is primarily applicable to situations in which relatives, parents and offspring, cooperate with one another.

Various stages of sociality along the familial pathway have been ascribed to a variety of animal groups. Among the mammals, the primates, carnivores,
cervids, and squirrels provide examples of different familial stages of sociality (Wilson, 1975a). The naked mole rat, the one mammal that seems to have a totally eusocial stage, probably belongs within this pathway (Jarvis, 1981). In the birds, species that have helpers (Woolfenden, 1976; Zahavi, 1976) belong to the familial pathway. Among the insects, the ants, termites, and many of the bees are believed to represent stages of the familial pathway (Wilson, 1971).

The parasocial pathway is based on the premise that cooperation in groups evolves through aggregations of unrelated individuals, rather than by aggregations of offspring through increased parental care (Lin and Michener, 1972). The stages of the parasocial pathway are as follows (Vehrencamp, 1979): solitary, communal, quasiasocial, semiasocial, and eusocial. The solitary stage is the same as in the familial pathway. Adults come together to breed. In the communal stage adults of the same generation form noncooperative aggregations, often centering around some resource such as limited nest sites or clumped food. The quasiasocial stage involves cooperation among the individuals in the aggregation. Such cooperation may involve communal nest construction, foraging, or defense against predators. The semiasocial stage involves cooperation, and also a reproductive division of labor. Up until this point, having two or more generations overlapping in the group is not a necessary condition. In the eusocial stage, however, just as in the familial pathway, two or more generations must be present— as well as cooperation and a reproductive division of labor.

Examples of the parasocial pathway are somewhat sparser than examples of the familial pathway. Among the mammals, some antelope (Jarman, 1971), pinnipeds (Bartholomew, 1970), and bats (Bradbury, 1977) aggregate. Some bats form stable colonies of unrelated females (McCracken and Bradbury, 1977; Bradbury and Vehrencamp, 1976, 1977), and some buffalo form groups that have antipredator defenses (Sinclair, 1977). Among the birds, a number of species form aggregations. These may have the function of allowing the birds to exploit limited nesting sites (Lack, 1968), exploit patchily distributed food (Krebs, 1974), or provide a passive defense against predators (Page and Whitacre, 1975). In a few species unrelated helpers cooperate with breeding individuals (Gaston, 1973; Fry, 1972). In the ants, several females contribute eggs to a communally built nest (Vehrencamp, 1978). Among the insects, the vespid wasps are examples of stages in the parasocial pathway (Wilson, 1971).

Both the familial pathway and the parasocial pathway describe several stages in the evolution of sociality, but do not really address the "why" of social behavior. Both models stress cooperation, with the cooperation based on parental care and parent-offspring association in the familial pathway, and on aggregations of unrelated individuals in the parasocial pathway. The essential question of why the cooperation develops is not addressed. Many other animal species that are related to the ones cited above have not developed any stage of sociality, and remain solitary.
Evolutionary models of sociality attempt to answer the "why" question. Most of the evolutionary models have emphasized aspects of population genetics, following the elegant arguments of Hamilton (1964) on the evolution of sterile workers among the bees and wasps. Hamilton suggested that the haplodiploid system of the Hymenoptera plays a large role in the evolution of sociality. In the Hymenoptera, males are haploid with N chromosomes, whereas females are diploid with 2N chromosomes. A female can choose whether or not to fertilize an egg from sperm stored in her spermatheca. If she does not fertilize the egg, the egg develops parthenogenetically into a male with a haploid set of chromosomes (Slobodchikoff and Daly, 1971).

Hamilton suggested that in normal diploid systems parents and offspring, and also two siblings, are related to each other, on the average, by one-half of their genes. However, because of the haplodiploid system of the Hymenoptera, a mother and her daughter are still related by one-half, but two sisters are related to each other by three-quarters. Hamilton reasoned that such a high level of relatedness would promote cooperation among sisters, and the system would evolve toward a preponderance of cooperating females. The relatedness argument has been the basis for the concept of the selfish gene (Dawkins, 1976), with the assumption that genes promote behavior ensuring the production of more copies of those genes. Since relatives are more likely to have copies of the same genes than are strangers, the inclusive fitness (the fitness of the animal and its relatives) is expected to be important by these arguments.

Unfortunately, although Hamilton's inclusive fitness arguments are elegant, they do not explain sociality in the general case. All of the Hymenoptera are haplodiploid, but only a few species are social. Although suggestions have been made that inbreeding (Hamilton, 1972) or genetic linkage (Lacy, 1980) would increase the relatedness of termite siblings, none of the termites is haplodiploid, yet they are social. Even among the social honeybees, queens may mate with a number of males, lowering the genetic relatedness between sisters having the same mother but different fathers (Page and Metcalf, 1982). Also, the haplodiploid argument does not explain the behavior of slave ants, who cooperate with their masters but are not related to them (Wilson, 1975b). In both ants and honeybees, transfers of large numbers of individuals from one colony to another are known (Wilson, 1971). The individuals transferring to a new colony are unlikely to be sisters, yet they cooperate with the resident colony members.

Other evolutionary models attempt to isolate the conditions under which cooperation can develop. A model by Baylis and Halpin (1982) suggests three circumstances in which animals can develop cooperation: aggregations, gamete transfer, and parturition. All three circumstances have the potential for bringing animals into close proximity with one another, setting up the conditions necessary for the development of cooperative behavior. The assumption is that once animals are brought into close proximity, they can evolve social behaviors. However, some animals do not evolve social
behaviors under those circumstances, so proximity is clearly a necessary condition, but not a sufficient condition in itself.

2 A RESOURCE-BASE MODEL OF SOCIALITY

I would like to propose an evolutionary model of sociality that also contains some elements of descriptive models. I suggest that sociality develops in response to an unequal distribution of resources, a need to defend those resources, and an inability to exploit those resources except as a group. These, I suggest, are the ultimate factors causing sociality. Proximate mechanisms in this model, corresponding to the evolutionary stages of the descriptive models, are (1) habitat variability and mating systems; (2) cooperation and aggression; (3) group size and dominance; and (4) division of labor in resource extraction.

3 HABITAT VARIABILITY AND MATING SYSTEMS

Let us suppose that in a variable habitat, resources are patchily distributed, with some patches having high-quality resources and others having low-quality resources. As a further constraint, let us suppose that a criterion of low-quality patches is a uniform distribution, within the patch, of a subset of the necessary resources, whereas high-quality patches have within them a variable distribution of a subset of resources. For example, an animal feeding on dietary items A, B, C, D, and E may find items A, B, and C uniformly distributed in a low-quality patch, and in a high-quality patch may find items A–E, but with each item dumped into a subpatch, and the subpatches randomly distributed within the high-quality patch. I predict that low-quality uniform patches will support monogamous animals, whereas high-quality variable-distribution patches will support polygynous animals (Fig. 1).

The reasons for this prediction are as follows. High-quality patches should have higher carrying capacities and should be able to support more animals. If a high-quality patch has a uniform distribution of resources, animals occupying the patch have two alternatives. One is to shrink their use area of the patch to one that can be defended or exploited by a single, or at most two, animals. The other is to collect a polygynous group of animals. Because of the potential costs of interanimal aggression (see below), I predict that under these circumstances the animals will remain solitary. If a high-quality patch has unequally distributed resources, the animal has the same two choices discussed above. Shrinking its use area to one that can be defended or exploited by one or two animals may leave those animals without access to one or more resources. The alternative is to form a group of animals that
could collectively function in defending or exploiting all the resources of the patch.

At least in the beginning stages of group formation, I predict that such animal assemblages would be polygynous groups, rather than groups with an equal number of males and females. This is because of the costs of aggression between males competing for females. As Trivers (1972) has shown, females that have a large investment in the mating and postmating process (e.g., larger egg, postparturition costs) would tend to be choosy in mating with males. Such female choice leads to a large variance in male reproductive success, causing intermale competition. In the beginning stages of group formation, such intermale competition would prevent a male from tolerating another breeding male within the group. However, if the relative investment of males and females into the mating and postmating process does not follow this pattern, the above condition would not be expected to hold.

A model somewhat similar to the above one was proposed by Wittenberger (1979). In his model, Wittenberger considered the relationship between environmental quality and female fitness, in a variant of the Verner-Willson-Orians polygyny threshold model (Orians, 1969; Verner and Willson, 1966). Wittenberger and also Altmann et al. (1977) suggest that female cooperation may be an important component of the polygyny threshold model, and that monogamous females should have a higher fitness than polygynous ones when females compete for resources, but polygynous females should have a higher individual fitness when females cooperate (Altmann et al., 1977). In low-quality territories, Wittenberger suggests that competition...
would counteract the effects of cooperation so that monogamous females have a higher fitness. whereas in high-quality territories the negative effects of competition would be less important than the positive benefit of cooperation.

My model does not depend on competition, and it predicts that resource quality and distribution affect both male and female fitness. The conditions for maximizing male and female fitness are not necessarily the same. Downhower and Armitage (1971) showed that among the yellow-bellied marmots, the average female fitness was highest in monogamous groups, whereas the average male fitness was highest in polygynous groups. Svendsen (1974) has pointed out that three kinds of females occur in marmot societies: aggressive, social, and avoiders. Aggressive females tend to live as solitary individuals or monogamous pairs, and have the highest fitness when they are monogamous. Social females tend to live in social groups and have their highest fitness in a larger group. Avoider females tend to live by themselves at peripheral burrows. Armitage (1977) has suggested that these relationships can be complicated by the population density, the age-sex structure of the population, and the number of years that residents have lived together. Since the quality of marmot territories is highly variable (Anderson et al., 1976), the Downhower and Armitage (1971) results do not provide a specific test of the relationship among fitness, mating system, and habitat quality.

3.1 A Test of the Model: Gunnison’s Prairie Dogs

Prairie dogs offer an excellent test of the habitat variability—mating system model. Blacktailed and Gunnison’s prairie dogs are social, colonial animals that feed on plants and defend territories (King, 1955; Fitzgerald and Lechleitner, 1974). The territories are defended by cooperative groups involving one or more males and one or more females (King, 1955). Cooperative behavior also extends to the use of alarm calls, warning other prairie dogs of the approach of predators (Slobodchikoff and Coast, 1980). The behavior of the blacktailed prairie dog, Cynomys ludovicianus, has been studied extensively by King (1955) and Hoogland (1977, 1979).

Our work has concentrated on the Gunnison’s prairie dog, Cynomys gunnisoni. This prairie dog lives in colonial groups in Arizona, New Mexico, Colorado, and Utah (Hall and Kelson, 1959). The towns or colonies tend to have fewer animals than the blacktailed prairie dog towns (Fitzgerald and Lechleitner, 1974). Plant species diversity and habitat variability are high both between towns and within towns (Shalaway, 1976).

To test the model, my associates Ken Paige, Mike Schwartz and I manipulated the resources within a single town. The town is located on the grounds of the Museum of Northern Arizona. Three other towns are within 2 km. Our manipulations have been confined to only a single town because the variability in plant species present and plant abundances between even adjacent towns is extreme, precluding the comparison of treatment effects.
involving manipulation of the same plant species in different towns. Experimental manipulations were carried out from May to September 1982.

Experimental procedures involved observation, removal, and supplementation of resources to create more uniform territories. The town was divided into a 120 x 80-m² grid, with stakes placed at 10-m intervals. Prairie dogs were live-trapped, marked with Lady Clairil hair dye, and released. The behavior and movements of the animals were observed with a spotting scope from a 4-m high observation tower positioned at one edge of the grid. Movements and aggressive interactions were noted daily, allowing feeding territories to be mapped. Observations were made from a blind on the tower. The animals were observed under normal conditions until 12 July, when the field was mowed with a tractor-mower, and the plants were mulched into the ground. Two weeks later, each territory was supplemented with 800 g (5600 kcal) of unshelled sunflower seeds, placed in the territory center. Sunflower seeds are part of the normal diet of these prairie dogs (Shalaway, 1976), and have a caloric value of 7 kcal/g, unlike the green forbs and grasses comprising the rest of the diet that have caloric values of 3-4 kcal/g. Plant diversity and distribution were sampled with line transects in each territory every 2 weeks.

The prairie dogs established feeding territories, which they actively defended against intruders (Table 1). Although some territories had only a single male and a single female, most territories early in the season had at least one male and more than one female (Table 2). The territories were very variable in the caloric content of food plants, that is, the actual plants utilized by the animals for food (Table 3). As the resources increased in terms of the quantity of available energy (Table 3), the feeding territories

Table 1. Response of Mean Territory Size of Prairie Dogs to Experimental Treatment of Resources

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Date</th>
<th>Mean Territory Size (m²)</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>May 14-31</td>
<td>824</td>
<td>F = 2.41</td>
</tr>
<tr>
<td>None</td>
<td>June 1-July 2</td>
<td>231</td>
<td>F = 1.10, NS</td>
</tr>
<tr>
<td>None</td>
<td>June 1-July 2</td>
<td>212</td>
<td>F = 1.10, NS</td>
</tr>
<tr>
<td>Mowed</td>
<td>July 13-19</td>
<td>603</td>
<td>F = 0.01</td>
</tr>
<tr>
<td>Mowed</td>
<td>July 13-19</td>
<td>548</td>
<td>F = 1.10, NS</td>
</tr>
<tr>
<td>Seeds</td>
<td>July 21-August 5</td>
<td>439</td>
<td>F = 1.12, NS</td>
</tr>
<tr>
<td>Seeds</td>
<td>July 21-August 5</td>
<td>356</td>
<td>F = 2.03</td>
</tr>
<tr>
<td>Seeds</td>
<td>August 6-17</td>
<td>245</td>
<td>F = 1.15, NS</td>
</tr>
<tr>
<td>Mowed</td>
<td>July 13-19</td>
<td>600</td>
<td>F = 0.01</td>
</tr>
<tr>
<td>Seeds</td>
<td>August 6-17</td>
<td>268</td>
<td>F = 1.10, NS</td>
</tr>
</tbody>
</table>

* Significant at p < 0.05
contracted in size (Table 1), and on the average there were more animals per territory (Table 2).

The experimental manipulation of removing the plant resources caused both an increase in the size of the feeding territory and a decrease in the number of animals per territory. Most territories became monogamous, in the sense that they were occupied by a single male and a single female (Table 2). Supplementing the territories with a single food resource (sunflower seeds) caused a contraction in the size of the territory to approximately the pretreatment levels, but did not create a corresponding increase in the number of animals occupying the territory.

These results suggest that although the energetic content of the resources influences the size of the feeding territory, energy alone does not necessarily influence the formation of monogamous or polygynous groups of prairie dogs. Since the groups remained monogamous when the energetic content of the territories was boosted with a uniform resource, I suggest that an

<table>
<thead>
<tr>
<th>Time (Treatment)</th>
<th>( \bar{x} )</th>
<th>( s )</th>
<th>n</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>May (mowed)</td>
<td>2.5</td>
<td>0.84</td>
<td>6</td>
<td>NS</td>
</tr>
<tr>
<td>June (mowed)</td>
<td>2.8</td>
<td>0.92</td>
<td>6</td>
<td>NS</td>
</tr>
<tr>
<td>Early July (mowed)</td>
<td>1.8</td>
<td>0.99</td>
<td>8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Late July-early August (seeds)</td>
<td>2.0</td>
<td>0.53</td>
<td>8</td>
<td>NS</td>
</tr>
<tr>
<td>Mid-August (seeds)</td>
<td>1.9</td>
<td>0.69</td>
<td>7</td>
<td>NS</td>
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</tbody>
</table>

<table>
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<tr>
<th>Territory</th>
<th>28 May 1982</th>
<th>10 July 1982</th>
<th>14 September 1982</th>
</tr>
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<tbody>
<tr>
<td>80-70</td>
<td>431</td>
<td>727</td>
<td>1038</td>
</tr>
<tr>
<td>154</td>
<td>263</td>
<td>354</td>
<td>3607</td>
</tr>
<tr>
<td>7</td>
<td>23</td>
<td>1532</td>
<td>2584</td>
</tr>
<tr>
<td>20</td>
<td>118</td>
<td>759</td>
<td>8617</td>
</tr>
<tr>
<td>70</td>
<td>—</td>
<td>2097</td>
<td>3607</td>
</tr>
<tr>
<td>5</td>
<td>347</td>
<td>1364</td>
<td>421</td>
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<td>17</td>
<td>411</td>
<td>1520</td>
<td>1038</td>
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<tr>
<td>38</td>
<td>—</td>
<td>691</td>
<td>3222</td>
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<td>72</td>
<td>—</td>
<td>3719</td>
<td>205</td>
</tr>
<tr>
<td>12</td>
<td>402</td>
<td>987</td>
<td>387</td>
</tr>
<tr>
<td>90</td>
<td>796</td>
<td>441</td>
<td>387</td>
</tr>
</tbody>
</table>

* Values are in kcal/ft².
important component of group formation in the prairie dogs is the presence of a diversity of resources, perhaps due to constraints of nutrition and water balance. Prairie dog towns characteristically have the food resources very patchily distributed (Shalaway, 1976).

The above data suggest that Gunnison's prairie dogs respond to both the quantity of their resources and the distribution of the resources. When the resources are abundant, diverse, and patchily distributed, the prairie dogs form polygynous groups. When the resources are uniform, the animals form monogamous groups. At present, data on relative fitnesses on the territories are not yet available. If, however, the prairie dogs are responding in a way that would maximize their fitness, these results suggest that group formation in prairie dogs follows the predictions of the model.

This pattern may reflect a general trend in prairie dog sociality. The black-tailed prairie dog, *Cynomys ludovicianus*, lives in territories that are highly variable in patch quality (Halpin, personal communication; Kelso, 1938), and the predominant mating system is polygyny (King, 1955). The whitetailed prairie dog, *Cynomys leucurus*, lives in fairly uniform, low-quality patches, and its predominant mating system is monogamy (Clark et al., 1971).

### 3.2 Evidence from Other Animal Groups

The same relationship between resource quality and group formation also seems to hold true in the case of marmots (which are closely related to the prairie dogs). Yellow-bellied marmots, *Marmota flaviventris*, have a variable social system (Armitage, 1977), unlike the more solitary eastern woodchucks, *Marmota monax* (Barash, 1974a). The resource patches used by the yellow-bellied marmots are extremely variable (Andersen et al., 1976) and most territorial groups of yellow-bellied marmots are polygynous. The eastern woodchuck tends to live semicolonially in a more uniform habitat and is mostly monogamous (Merriam, 1971). The Olympic and arctic marmots live in rather uniform, poor habitats in family groups of one male, two females, and the young. But, only one female bears young per year, so the system is functionally monogamous (Barash, 1974a).

Similar shifts from monogamy to polygyny as a function of resource distribution can be seen among the African antelope. Jarman (1974) classified antelope into five social groups, depending on the type of habitat they lived in. Class A consists of the duikers and the dik-diks, animals with small body size. They are monogamous, feed selectively, and stay in one vegetation type. They take items such as flowers, twig tips, fruits, and seed pods, food that is relatively uniformly distributed in space and time. Class B consists of redbucks, gerenuks, and lesser kudus, which are polygynous, have a group size of three to six, with at least two or more adult females in a group. They feed on a range of grass species or browse, remaining in one or several vegetation types and one home range throughout the year. Their food tends to be somewhat clumped spatiotemporally. Class C includes the waterbucks,
kobs, gazelles, and impalas, which are polygynous and have a group size of six to sixty. They feed on a range of grasses and browse rather selectively. Their diet changes seasonally, as does their preference for vegetation type, caused by even more clumping of resources spatiotemporally. Class D involves the wildebeests and topis, which are polygynous and have a group size of six to several hundred thousand. They feed on grasses, and select specific plant parts or growth stages, leading to even greater spatiotemporal clumping. Class E consists of buffalo and elands. They are polygynous, feed on a wide range of grasses or browse, and move seasonally. Their diets are diverse and the patches vary spatiotemporally.

Other animals form larger or smaller groups in response to abundance and distribution of resources. Coyotes form packs of several animals when large prey such as elk are available. Otherwise, they hunt as solitary animals (Bekoff and Wells, 1981). When the coyotes form groups, helpers are present that assist in territorial and food defense (Bekoff and Wells, 1982). Acorn woodpeckers seem to have a similar response to resource levels (Stacey and Bock, 1978). Some woodpeckers within a population form social, cooperative groups that store acorns in caches, and collectively utilize and defend the stored acorns. Other woodpeckers in the same population live as temporary monogamous pairs that do not store acorns. These pairs migrate during the winter, whereas the social groups do not. Monogamous individuals seem to be less efficient than groups at harvesting acorns. Primate studies (Clutton-Brock and Harvey, 1977: Milton and May, 1976; Southwick and Siddiqi, 1974) relating ecology to social organization generally suggest that monogamy occurs in patches with uniformly distributed resources, whereas polygyny occurs in patchy resource distributions. Monogamous species tend to occupy large home ranges (Clutton-Brock and Harvey, 1977). Baboon groups tend to be larger when resources have high densities but very patchy distributions (Altmann, 1974).

**4 COOPERATION AND AGGRESSION**

If animals are to join groups in order to exploit or defend essential resources, the animals must be able to cooperate with one another. Noncooperative aggregation may be important to some animals such as colonial sea birds (Lack, 1968) for exploiting limiting nesting sites, but without cooperation the evolution of social behavior is not possible. Cooperation in turn requires limiting or controlling aggressive interactions within the group, so that the animals are relatively free to pursue other activities in reasonably close proximity to other members of their group. This means the development of mechanisms that allow a curtailment of personal space and other aggressive tendencies that may result in noncooperation and group disintegration. In this section I would like to consider how cooperation may arise, and the general relationship between cooperation and aggression in social groups.
4.1 A Game-Theoretic Approach to Cooperation

One promising approach to the question of cooperation has been a game-theoretic one. Game theory has been applied to biological problems in a number of contexts, principally in an analysis of the strategies of aggressive behavior (Maynard Smith and Price, 1973). A basic component of the approach is a payoff matrix that expresses what each player is expected to win by pursuing a given strategy. If a player pursues a single strategy, this is known as a pure strategy. If the player uses more than one strategy based on a certain probability or expectation of winning, this is called a mixed strategy. In a game, a player usually can play a pure or a mixed strategy that consistently provides the highest payoff for the conditions of the game. In other words, for the particular game, no other strategy will yield better results (Maynard Smith, 1982). Maynard Smith and Price (1973) originally considered that an animal would be genetically programmed to play a particular strategy, and defined an evolutionary stable strategy (ESS) as a strategy that cannot be beaten by a mutant playing another strategy. In behavioral terms, animals are rarely genetically programmed to play only one particular strategy, but an analogous situation occurs. The animal could play a behaviorally stable strategy (BSS) that cannot be beaten by another animal playing another strategy. Game theory analysis often involves equilibrium points, most notably the Pareto equilibrium and the Nash equilibrium. The other authors on social behavior in this volume also deal extensively with a game-theoretic approach.

Axelrod and Hamilton (1981) have formalized some of the requirements for cooperation, using a game-theoretic approach. Figure 2 shows a payoff matrix for a game situation called the Prisoner's Dilemma (Rapoport and Chammah, 1965). In this game, the Prisoner (Player 1) has several choices. One choice is to play C (cooperation), and if Player 2 also plays C, that is, if they mutually cooperate, Player 1 receives a payoff of 3, in arbitrary units. On the other hand, if Player 1 plays C and Player 2 plays D (defection), Player 1 receives a payoff of 0, the "sucker's payoff." Player 1 can get the highest payoff in this game by playing D when Player 2 plays C. As part of the Dilemma, Player 1 receives a payoff of only 1 if both players play D.

One BSS is D-D, that is, neither animal cooperates, because the costs of consistently playing C to a D are too high (Axelrod and Hamilton, 1981). This may explain from a game-theoretic point of view why so few animals are social. The costs of cooperation may be too high in many circumstances. However, the payoff for C-C may be profitable when a group is necessary for extracting or defending a resource. Then the penalty of noncooperation for an individual animal may be considerably more than the "sucker's payoff" of trying and failing to elicit cooperation. This would be particularly true when interindividual aggression within the group follows a pattern of decline with increasing sociality, for example, intragroup aggression of primates (Bernstein, 1976), lions (Bygoff et al., 1979), and bees (Lin and Mich-
The payoff matrix of the Prisoner's Dilemma. The payoff is expressed in arbitrary units for Player 1. C designates cooperation, D designates defection. Player 1 receives a payoff of T when Player 2 plays D, a payoff of C for C-C, a payoff of D for C-D, and S for D-D. Payoffs are structured so that T pays the most and S pays the least. A necessary condition for the development of cooperation is high individual recognition. (Figure is modified from Axelrod and Hamilton, 1981. Copyright 1981 by the American Association for the Advancement of Science.)

4.2 The Influence of Individual Recognition

Axelrod and Hamilton (1981) show that another BSS is to play C first, and then follow the other player's lead, a tit-for-tat strategy. If Player 2 plays D, then Player 1 plays D; but if Player 2 plays C, then Player 1 continues to play C until Player 2 switches. The prediction of Axelrod and Hamilton is that this strategy would work best when there is individual recognition among animals, and when individuals play the game a number of times against other individuals that they know, so that they can predict the response. Frequent contact between animals may occur initially when home ranges overlap, or when territorial animals meet frequently at boundaries. For example, the home ranges of grey squirrels overlap, and individuals can recognize their neighbors (Thompson, 1978). Neighbor recognition has been described between two species of carnivores (Barash, 1984), as well as for a variety of conspecific birds, mammals (Wilson, 1976), some amphibians (Jaeger, 1981) and ants (Dawson et al., 1979). When such neighbor recognition
occurs, it may take the form of the "dear enemy" response, where animals show less aggression toward neighbors than toward strangers (Wilson, 1975a).

The mechanisms through which animals may recognize other individuals, particularly kin, have been reviewed by Bekoff (1983), who suggested several ways through which such recognition can develop: (1) genetic mechanisms; (2) recognition of phenotypic comparisons; and (3) recognition based on familiarity and spatial association. Genetic mechanisms of identifying related individuals from the same colony have been described for some bees (Breed, 1981; Greenberg, 1979). Recognition by phenotypic comparisons may occur through learning to distinguish the phenotypic differences of other individual animals. Recognition based on familiarity and spatial associations seems to be a common way of identifying individuals (Marler, 1976).

4.3 Philopatry and Cooperation

The above mechanisms for individual recognition obviously are not mutually exclusive, and at least two of the mechanisms may be promoted by philopatry. Philopatry is the tendency of animals of one sex or the other to stay near their parents, or to stay on or near a particular plot of land where they were born. Philopatry is a common phenomenon, with examples known from a number of animal groups (Shields, 1982). The nondispersing sex varies with the animal group. Among the mammals, males tend to disperse while females tend to settle close to their mothers (Waser and Jones, personal communication). In the birds, the females tend to disperse, whereas the males settle close to their father (Vehrencamp, 1979).

Such associations among nondispersing individuals provide the raw materials for the development of individual recognition and cooperation. Kin selection may start off the cooperative process, although it is not a necessary condition for cooperation. An example of a probably kin-selected system of philopatry is that of the ground squirrel (Michener, 1982). The typical pattern is for female juveniles to settle near their mother's territory. The mother may contract her territory or the female juvenile may inherit her mother's territory. While in the early evolutionary stages of this system each animal defends the perimeter of its own territory. The development of cooperation, as in the prairie dogs, allows a shared defense of the perimeter of a common territory. An example of a probably nonkin selected system is that of the neotropical fruit bat, *Phyllostomus hastatus* (McCracken and Bradbury, 1977). Females form cohesive stable groups that cluster in potholes of limestone caves in Trinidad. The female groups maintain relatively exclusive foraging areas, and when they find a rich food source, they vocalize to attract their roost mates. New groups of females are formed by the ousted youngsters from all the harems in the cave. Once a new group is assembled, it stays stable in composition for many years.
4.1 Costs and Benefits of Aggression and Resource Extraction

On a very simple level, the process of forming groups through cooperation can be treated as a cost-benefit analysis. Individual fitness in a group is equal to the benefit from resource extraction minus the cost of aggression (Fig. 3). If the benefit is greater than the cost, the animal should stay in the group. If the cost is greater, the animal should leave. This can be stated more formally by the following equations:

\[ IF_0 = f(RE) \]  \hspace{1cm} (1)
\[ IF_g = f(RE) - f(A) \]  \hspace{1cm} (2)
\[ IF_g = B - C \]  \hspace{1cm} (3)

if \( B < C \), then leave
if \( B > C \), then stay

where \( IF \) is individual fitness, \( RE \) is resource extraction, \( A \) is aggression, \( B \) is benefits, and \( C \) is costs. Equation (1) shows that the individual fitness of a solitary animal \( (IF_0) \) is a function of the ability of the animal to extract resources alone. Whereas Equation (2) shows that the individual fitness of an animal in a group \( (IF_g) \) is a function of its ability to extract resources in a group, minus a function of the costs of aggression in the group. This trans

![Figure 3](image-url)

Figure 3. A hypothetical relationship between sociability and resource extraction (RE) and aggression (A) at low (L) and high (H) levels of RE and A. Dotted line shows how a balance between resource extraction and aggression may influence the degree of sociability.
lates into Equation (3), the individual fitness in a group is related to the benefits minus the costs of being in the group, with the animal staying in the group if the benefits exceed the costs.

5 GROUP SIZE AND DOMINANCE

Group size and dominance are discussed extensively by Caraco and Pulliam in Chapter 10, so the discussion here will center on a few of the relevant details of the relationship among group size, dominance, and the development of sociality.

As animals form groups, the costs and benefits to each animal of being in a group may potentially change with the size of the group. Too few animals in the group may not be able to extract or defend a resource in such a way as to provide sufficient benefit, per individual animal, for being a group. Too many animals may increase the costs of aggression, or deplete the resource. Krebs (1974) shows that heron flocks have a resource extraction curve that peaks at a certain group size, then falls as more flock numbers are added. This leads to the question, asked by Caraco and Pulliam: Is there an optimal group size for animals?

Caraco and Pulliam show that in a group, not all the animals may have the same fitness. Dominance relationships may develop, and the dominants may acquire access to more resources. For example, dominant vespid wasps tend to become reproductive queens more frequently than subordinates (West, 1967). In multiple-queen nests, the dominant vespid wasp queen prevents reproduction of subordinates by eating their eggs, and also forces subordinates to pursue riskier and energetically more expensive tasks (Noonan, 1981). A similar process occurs in bumblebees (Heinrich, 1979). In bird flocks, dominant birds may use subordinates to ensure a better supply of resources (Rohwer, 1977).

As Caraco and Pulliam point out, group size can be considered from the standpoint of Fretwell's (1972) Habitat Selection model. Dominants do better in better-quality habitats. Subordinates do worse, but they can do better in a poorer-quality habitat only if they can become dominant in that habitat. If they switch to the poorer habitat and remain low-ranking subordinates, they do much worse than if they had stayed in their original group. The net result is that the group size would be shifted to maximize the mean fitness of the group, and not necessarily the fitness of the dominants (Fig. 4). An example is the analysis of lion group size by Caraco and Wolf (1975). Although the group size for hunting small prey was determined by the physiological limits of the lions, the group size of lions hunting larger prey was offset in the direction of the mean fitness of the group. Thus, when the lions hunt larger prey that can provide more food per lion than the required physiological minimum, the group size of the hunting females is not at the optimum that would maximize the caloric return. Instead, the group size is
increased, so that each lion receives, on the average, only enough food to satisfy the physiological minimum caloric intake.

I suggest that in a variable, patchy habitat, a social unit will tend to collect group members. If the costs of aggression are high for the dominants to eject newcomers, the group will collect more members. The dominants may be willing to suffer a small drop in fitness by having more group members, rather than face a large drop in fitness by incurring the costs of ejecting joiners. On the other hand, joiners in a colony may stay in the group because of the low probability of surviving as a solitary individual. This may explain the initial stages in the formation of large colonies of termites and honeybees, and does not have to be a kin-selected argument.

5.1 The Probability of Breeding and the Evolution of Castes

If an animal has no probability of breeding as a solitary individual, and a very low probability of breeding in a group, I predict that the animal will join the group. For example, if an animal had the following options:

\[ p(F_a) = 0 \]
\[ p(F_g) = 10^{-7} \]

where the \( p(F_a) \) is a measure of the probability of breeding as a solitary individual, and the \( p(F_g) \) represents the probability of breeding in a group. Selection should favor choosing a group over choosing to be solitary.
This is essentially the choice open to the social insects that have nonreproductive castes. A honeybee, ant, or termite that abandons the nest or hive would not be able to survive to the point of producing viable offspring. At that stage, its fitness is zero. However, a nonreproductive in the social insects has a certain probability, albeit small, during a narrow window in its life-span of becoming a reproductive and reaping enormous benefits in terms of fitness. For example, honeybees become workers or queens as a function of diet, that is, whether they are fed royal jelly throughout their larval life or only for a few days. Each egg potentially can become a queen. In fact, few do so, but the probability of becoming a breeding individual is still present. Even as adult workers, nonreproductive females are capable of occasionally laying male eggs and contributing minutely to their potential fitness (Wilson, 1971). Among the ants and the termites similar windows occur (Wilson, 1971), so that each individual can potentially become a reproductive. Even among the socially more primitive bees and wasps, where queens are often the largest females, larval diet determines to a large extent the size of the individual (Noonan, 1981), and, consequently, the probability of breeding.

The scenario that I suggest for the evolution of nonreproductive castes is as follows. Initially, individuals form groups, eventually increasing the group size beyond the optimal level. These individuals develop some measure of cooperation among themselves. As a group, they can extract and defend resources much more efficiently than they can as solitary individuals. In the group, dominance relationships arise. Cooperative behavior and a larger group size allow a modification of the immediate habitat for the purpose of food storage and shelter, and the modifications ameliorate the daily physiological stresses placed on each animal in the group. The animals become specialists in cooperative resource extraction, perhaps in response to competition from solitary, nonsocial animals. Although they may be more efficient at resource extraction and defense as a group, their efficiency at performing the entire gamut of tasks required for resource extraction declines, compared with that of solitary animals. Modification of habitat and efficiency of resource extraction reduce the probability of breeding as a solitary individual, so that at this point the animals become locked into a social existence. The dominance relationships allow manipulation of colony members (this is analogous to the manipulation arguments of Alexander (1974)), in such a way that the dominants breed while the subordinates do not. This dominant-subordinate relationship, however, can only be supported if all group members have a chance, however small, of becoming a dominant at some point in their lifetime.

Among many of the social mammals and birds, the earlier stages of this scenario are evident. In the insects, some of the inter intermediate stages leading to eusociality and caste formation can be seen, particularly among the halictid bees (Breed and Gamboa, 1977; Michener and Brothers, 1974; Michener et al., 1971). Mammals and birds have apparently not developed
true nonreproductive castes, with the exception of the naked mole rat, which requires extensive cooperation for modifying its habitat and extracting resources (Jarvis, 1981). Partial nonreproductives in the form of helpers, however, are known in both mammals and birds (Bekoff, 1983; Emlen, 1982a,b).

Perhaps mammals and birds have not evolved social systems with nonreproductive castes because of the interplay of body size, resource partitioning, and competition. May (1978) has shown that generally as body size among taxa decreases, the number of species increases. With more species present, we can assume that there is more subdivision of the available resources in response to competition, that is, more specialization on subsets of resources. Increased body size and fewer species imply a broader partitioning of resources in response to competition. Perhaps because of more broadly partitioned resources, the birds and mammals have not become cooperative specialists at the expense of individual efficiency to the same extent as the social insects.

6 DIVISION OF LABOR IN RESOURCE EXTRACTION

Once social animals cross the threshold and become cooperative specialists, they can extract a set of resources by having individual animals specialize on one resource in the set. This is the basis for flower constancy in honeybees and majoring in bumblebees (Heinrich, 1979). Specialization on one type of resource by each animal in the group can increase the animal's efficiency.

![Figure 5. A hypothetical curve showing the impact of cooperative societies on species diversity of competitors in the immediate habitat. As cooperative sociality develops from left to right, species diversity of competitors decreases. The rapid decrease in species diversity occurs at the stage in which the social group develops cooperative specialists through division of labor in resource extraction.](image)
at collecting that resource. It can also increase the efficiency of the group in extracting the entire set of available resources. At this stage, each individual in the group may not be as good a competitor with a solitary animal over the entire range of resources, but the group, by being composed of specialists, becomes a good competitor with solitary animals at exploiting the entire resource set. This in turn can affect the diversity of species found in the vicinity of eusocial groups (Fig. 5). Such an effect can have a profound impact on the dynamics of communities. Honeybees, for example, can quickly replace a number of wild bee species as major pollinators of some agricultural communities (Wilson, 1971). Ant species can depress the abundance of their closest competitors (Hölldobler and Wilson, 1977).

7 SUMMARY

I suggest that in evolutionary terms, social behavior has developed in response to the distribution and abundance of resources. I develop a hypothesis that proposes four stages in the evolution of sociality: (1) habitat variability and mating systems; (2) cooperation and aggression; (3) group size and dominance; and (4) division of labor in resource extraction. Initial conditions for group formation involve a patchy habitat, ranging from low-quality uniform patches to high-quality patches where subsets of resources are clumped and distributed randomly. I suggest that low-quality uniform patches promote monogamy or solitary, nonsocial behavior, whereas high-quality patches with variable distributions of resource subsets promote polygynous associations that yield more efficient resource extraction and resource defense.

In forming polygynous associations, animals have the opportunity to cooperate with each other. Development of such cooperation may be promoted by individual recognition and philopatry. As cooperation develops, resource extraction or defense increases in efficiency while interanimal aggression within the group decreases.

Within cooperative groups, dominance relationships often develop which have a profound effect on the group size. Development of such dominance relationships allows the group size to increase, since subordinates or joiners often cannot improve their fitness by moving to another group. This tends to increase the group size to a point where each animal in the group receives not the optimal access to resources, but access to the required physiological minimum.

Through cooperation, social groups can modify their immediate surroundings (e.g., build nests) and ameliorate the physiological stress placed on individuals by abiotic factors. At the same time, through cooperation, a social group can become collectively very efficient at extracting resources. Habitat modification and efficiency at resource extraction may affect the probability of breeding of an animal in a social group, to the point where it
becomes unable to reproduce as a solitary animal. At that point, selection may favor the animal's participation in the formation of nonreproductive castes, as long as the animal has even a small probability of being able to reproduce at some point in its life cycle.

Once social groups develop to the point of dividing up the labor of resource extraction, individuals within the group may become specialists on subsets of resources (e.g., the flower constancy of honeybees). As a group of specialists, the social group may then be able to outcompete solitary species that are generalists on a set of resources, and, as such, social species may profoundly affect the diversity of other species in their immediate habitats.

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LITERATURE CITED


Hoogland, J. L. 1977. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys ludovicianus* and *C. leucurus*). Ph.D. dissertation, University of Michigan, Ann Arbor.


