

20. Social Evolution in Birds and Mammals

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ONE AIM of this book is to examine the extent to which social evolution in different taxonomic groups can be understood through a series of common principles. At the most general level the same fundamental rules presumably relate ecology and social organization in all animals: social behavior evolves as an adaptation to maximize fitness, given a particular set of ecological pressures. However, the precise way in which ecological pressures generate social organization in different taxa is not yet firmly known. Furthermore, the problem of understanding socio-ecological principles has in some respects been made more difficult than it was twenty years ago by the discovery of marked differences in social relationships in many species with gross similarities in their grouping patterns (e.g., Dunbar, Chapter 15). Long-term social relationships based on individual recognition are particularly prevalent in birds and mammals compared to other animals (Wrangham, 1983), probably partly because species in these taxa have relatively advanced cognitive abilities. This means that in these groups socio-ecological studies must go beyond an analysis of grouping patterns to explain patterns of competitive and cooperative relationships. In this chapter, therefore, we consider how the analysis of social systems to date has paved the way for a unified theory of social evolution capable of explaining social relationships both between and within the sexes. Such a theory needs to specify which behavioral variables are most directly subject to ecological pressures, and what ecological or other pressures are most influential in social evolution. These problems are discussed in turn, illustrated with case studies from this volume. In the final section we examine briefly some general problems raised by the comparative approach taken throughout the book.

BEHAVIORAL VARIABLES AND SOCIAL RELATIONSHIPS

The classical socio-ecological method is to analyze the ecological basis of grouping patterns without paying attention to the types of social relationships within or between groups. Historically this was a natural starting point because grouping patterns were documented before social relationships. For the same reason it continues to be a useful method when species are first studied because it provides correlations with heuristic value. For instance,

Leighton found that larger species of hornbills tend to live in smaller groups (Chapter 6). Although different species of hornbills eat similar foods, he showed that larger species eat more from a given patch. Since group size is presumably constrained by food dispersal, species differences in body size appear to be ultimately responsible for differences in group size. This is a helpful idea because it suggests an explanation for the species distribution of helpers, which occur only in the smaller species living in the larger groups: helping may be inhibited in the larger species because their group size is constrained by feeding pressures, putting a new twist on the theory that the distribution of helpers is best explained by the availability of breeding opportunities (Emlen, 1984) as was shown to be the case in jackals (Moehlman, Chapter 4), and scrub jays (Woolfenden and Fitzpatrick, Chapter 5). Among hornbills, species differences in body size may be ultimately responsible for the distribution of helping.

Valuable though this type of analysis is, it has limited power because it does not consider the nature of social relationships. Helpers tend to be males in some species (most birds, e.g., Florida scrub jays: Woolfenden and Fitzpatrick, Chapter 5), and can be either sex in others (canids: Moehlman, Chapter 4). Indeed, in some species the sexual distribution of helping can vary between populations, as occurs in bicolor wrens *Campylorhynchus griseus* (Austad and Rabenold, 1985). Again, male helpers do more work than females in many species, such as Florida scrub jays (Woolfenden and Fitzpatrick, Chapter 5), but less than females in acorn woodpeckers *Melanerpes formicivorus* (Koenig et al., 1983). The reasons for this variability between and within species are not understood (Koenig et al., 1983), but it means that an analysis of grouping patterns on its own is insufficient to explaining social relationships. Accordingly, other effects of ecology must be included in order to understand the full system.

Consideration of ecological influences that might explain social relationships can sometimes lead to new explanations for the pattern of grouping. For example, many nocturnal primates forage alone within individual territories. Their solitariness is sometimes ascribed to their antipredator tactics, because these are cryptic animals that would probably be more easily detected by predators if they foraged in groups (Clutton-Brock and Harvey, 1977; Schaik and van Hooff, 1983). Foraging alone, however, does not require exclusive, nonoverlapping home ranges. To account for territoriality in these species an additional explanation is needed. Territoriality in many birds and in nocturnal primates has been explained as occurring because food resources are economically defendable by lone individuals (e.g., Hladik, 1975). If this is shown to be the case for the nocturnal primates, it will account not only for territoriality but also for solitariness. Hence, it is not yet clear if the explanation in terms of predator avoidance (which has not been tested) is needed.

A similar example is provided by Packer (Chapter 19). The traditional explanation for lions living in social groups is that it makes cooperative hunting possible. Although this explains the grouping pattern, it does not explain why females form semi-closed groups that defend their carcasses from other groups. Packer argues that lions differ from other cats in having frequent access to easily locatable and defensible resources (large carcasses), and that the need for allies to help in defending those resources can explain why females form large closed groups. In this case Packer shows that the original explanation of the grouping pattern is not only unnecessary, but appears to be wrong: group hunting does not appear to be as efficient as previously thought. The need for joint defense of resources therefore seems to explain both the kinds of social relationships that are formed, and the fact that lions hunt in groups. A similar example is provided by Wrangham's (1980) analysis of primate groups, where it is suggested that the need for allies in defense of high-quality food patches generates semi-closed groups of females with cooperative relationships. It is therefore no longer clear whether predator pressure contributes significantly to explaining species differences in primate grouping, as has often been argued (Crook, 1970; Alexander, 1974; Schaik and van Hooff, 1983).

These examples imply that explanations derived solely for grouping patterns should be treated cautiously until social relationships have been accounted for also. Furthermore, it is important to note that in species with long-term social relationships, it is the relationships themselves that need to be explained, rather than merely the interactions, which can be cooperative or competitive. The distinction between social interactions and social relationships is critical because the costs and benefits of a given interaction are strongly influenced by the relationship within which it occurs. For example, an escalated fight started by competition over a trivial resource may be inexplicable unless one knows that a long-term dominance relationship is at stake (deWaal, 1983). Similarly, mutualistic relationships involving delayed reciprocity may look altruistic when viewed merely as interactions; and cooperative relationships may include agonistic components, which, if viewed as isolated interactions, may make them seem to be competitive. Often, therefore, the occurrence of particular types of social interactions cannot be explained without reference to other types of social interactions.

Recognition of the importance of analyzing social interactions in the context of long-term social relationships raises two questions. First, how should social relationships be described and classified? Second, which kinds of social relationship are most important for understanding the influence of ecology on social organization? The classification of social relationships is still at an early stage, but there is evidence that the overall patterns of social relationships are not necessarily well correlated with each other in different species even where some aspects are strikingly similar. For in-

stance, female lions and female vervet monkeys *Cercopithecus aethiops* are similar in forming cooperative relationships to defend resources against other groups. Yet they appear to differ because intragroup dominance interactions among females, especially those involving alliances, occur more frequently in vervets than in lions (Wrangham, 1983). This kind of difference between intergroup and intragroup relationships, which also occurs between terrestrial and arboreal cercopithecines (Gouzoules, 1984), is important because it indicates that social networks must be described in terms of all four axes of interindividual interaction (cooperation, competition, spite, and altruism, W. D. Hamilton, 1964) rather than merely with respect to one of these.

Nevertheless, there are two ways in which an ecological analysis of social organization benefits from a focus on a limited set of social relationships. First, since the most fundamental problem in social evolution is understanding why animals act altruistically, cooperative and altruistic elements of social relationships are especially important. Intense forms of competition within semi-closed groups are not explicable without an account of the social glue responsible for the existence of the group in the first place.

Second, social relationships among breeding adults are critical because they have the most immediate effect on fitness, and are therefore the ones subject to the most intense selection pressures. Socio-ecological studies have often focused on mating relationships rather than including a specific analysis of relationships within sexes. This is because socio-ecology began and has been continued most forcefully among birds (Orians, 1961; Vehrencamp and Bradbury, 1984). A focus on intersexual aspects of mating relationships is appropriate in birds because cooperation among breeding adults of the same sex is rare, so that differences among species' social systems can be accounted for to a large extent in terms of male-female relationships.

In a few birds and many mammals, however, mating relationships are not the only, or even the major, source of variation in social systems. In birds, for example, the occurrence of helpers is not predicted by the type of mating system: monogamous pairs may or may not have helpers. Many mammals are polygynous, but the range of relationships within each sex is enormous and poorly correlated with mating types. This is most clearly illustrated when a variety of single male, multifemale mating systems (harems) are compared (Rubenstein, Chapter 13 and below). As in the case of ecological explanations of grouping patterns, therefore, this means that the social system cannot be accounted for purely in terms of the mating system.

This principle is not new, of course. It is responsible, for instance, for the distinction between resource defense polygyny (where female-female relationships are unimportant) and female defense polygyny (where the system depends critically on female sociality) (Emlen and Oring, 1977). There is still, however, a strong emphasis on mating relationships in the social ecol-

ogy literature (cf. Vehrencamp and Bradbury, 1984). We regard explicit recognition of the need to analyze relationships both between and within sexes, as exemplified in this book, as a necessary precursor to a general theory of social ecology. Furthermore, as described in the introduction, the impact of ecological factors is generally expected to be greatest on female relationships and distribution, setting up the conditions which lead by a series of feedback loops to the eventual social system. This is diagrammed in Figure 13.1.

SOURCES OF SOCIALITY

In a global review of the origins of animal sociality, Alexander (1974) argued that the ecological factors favoring the evolution of social groups (as opposed to aggregations) fall into two main classes, predation pressure and resource distribution. The essence of the argument is that grouping invariably confers disadvantages in terms of increased competition and disease. Even where the resource distribution allows animals to form groups at low cost, therefore, positive benefits must exist to outweigh these inevitable costs. With rare exceptions (such as hyraxes huddling for warmth) all such benefits come from either escaping predators or acquiring resources. The major exception was the case of human groups, which were supposed to be favored as a response to the aggression of neighbors. In this case conspecifics were supposed to have analogous effects to predators, leading to the formation of groups despite their inherent disadvantages.

The idea that predation and resource distribution are the two principal factors responsible for variation in social behavior is widely accepted, and the preceding chapters give numerous examples of their effects. These chapters also support, however, the idea that it is useful to recognize a third major category of factors responsible for the formation of social groups, namely intraspecific competition. Intraspecific competition is routinely argued to have effects on social grouping, but it has not previously been elevated to the rank of a common cause of gregarious life. This is perhaps partly because it is a less independent variable than predation pressure or resource distribution. In fact, its intensity often reflects the strength of these ecological forces. It appears to us, however, to merit equal treatment with the two classical factors as a major source of sociality. Like predation and resource distribution, the effects of intraspecific competition are expressed in different ways in different species, are mediated by ecological constraints, and can account for the evolution of complex social groups even when no other factors favor grouping. This means that investigations of animal sociality should routinely examine all three influences. To substantiate these arguments we consider the three factors in turn. We examine both their effects on sociality and the ways their effects interact with each other.

Predator Pressure

High predation risk is normally argued to favor large groups, although in species relying on cryptic behavior to avoid predators it favors solitariness (Pulliam and Caraco, 1984). There are many mechanisms by which individuals achieve greater safety in groups, and their importance varies between species. Their effects on social relationships also vary. For instance, three types of mating systems are attributed to predation in this volume: polygyny, monogamy, and polyandry.

First, Robinson (Chapter 9) showed that fledging success in yellow-rumped caciques depends on the degree of protection from mammalian predators. Safe nesting sites occur in small, uncommon patches where coloniality is therefore favored. Yellow-rumped caciques cooperate in mobbing predators, but there is no evidence of differentiated social relationships between pairs. Predation has a strong indirect effect on mating relationships, however, because it forces females to cluster. This means that clumps of females are economically defendable by males, leading to polygyny.

In other species where predation favors groups, the result need not be polygyny, because one female may monopolize breeding by suppressing the reproductive effort of other females. This leads either to monogamy or polyandry. Thus in dwarf mongooses there is good evidence that individuals need to be in large groups in order to have a reasonable probability of survival. Rood (Chapter 7) showed that adult mortality is lower in large packs, despite a high rate of successful predator attacks (Rasa, 1983a). Elaborate antipredator behavior has also been described. The implication is that unmated adults choose to help rather than breed alone because breeding in small groups would bring a high risk of death. The only mammals in which nonbreeding adults are helpers also have reproductive suppression of females by a dominant female (carnivores: Emlen, 1984; Moehlman, Chapter 4; tamarins: Terborgh and Wilson Goldizen, 1985). This suggests that female–female competition is a critical feature for the development of helping, presumably because it constrains breeding opportunities.

Female–female competition appears to be equally important in the development of some forms of polyandry, in which the ecological basis is not yet generally understood (Erckmann, 1983). The chapters by Oring and Lank (Chapter 2) on spotted sandpipers and by Petrie (Chapter 3) on moorhens offer two examples. In both cases polyandrous relationships appear to be favored partly by a high predation risk, as is often suspected for polyandrous birds (Emlen and Oring, 1977). In Petrie's moorhens most pairs are monogamous, but there is a potential for polyandry because female egg production rate is not apparently limited by food availability, and the chicks are precocial. The fact that entire clutches are often lost means that it pays females to spread their eggs in many baskets and to be polyandrous provided that excess males in good condition are available to aid incubation. The same is

true of spotted sandpipers, where again a low rate of polyandry is sometimes found. In Oring and Lank's study, however, the relationship between predation and polyandry is taken a step further, because populations that are exposed to high rates of predation are forced, like yellow-rumped caciques and dwarf mongooses, to live in dense clumps. Unlike caciques, female spotted sandpipers both nest and forage within individually defended areas. Female exclusion then sets a limit on the number of breeding females, similar to dwarf mongooses, and by skewing the sex ratio increases the incidence of polyandry. It is not yet clear what determines why females are able to defend an area sufficient for two nests, or why males do not exclude other males, but the association between a high predation rate, increased nest density, and increased frequency of polyandry is convincing.

In yellow-rumped caciques and dwarf mongooses, high risks of predation are argued to generate larger groups than would otherwise be favored. The same effect of predation is proposed for gelada baboons by Dunbar (Chapter 15), who shows that low-ranking females experience low reproductive rates, probably as a result of harassment by dominant females. Accordingly, there must be a compensating advantage for sociality. The fact that geladas form larger groups in more dangerous areas supports the idea that the benefits come from reduced costs of predation.

Predation has been argued to explain sociality not only in gelada baboons but also in many other group-living primates, where resource dispersal appears to impose constraints on the size of groups that form, and here the effects of ecological constraints on grouping look important (Crook, 1972; Schaik and van Hooff, 1983). Terborgh (1983), for example, showed how group size varies with food types in South American monkeys. Species dependent on large, concentrated resources, such as squirrel monkeys *Saimiri sciureus*, can afford to live in large groups, whereas those eating small, evenly distributed resources, such as tamarins *Saguinus* sp., are forced to live in small groups. Whether predation is indeed a universal impetus for sociality is a matter of debate (Cheney and Wrangham, 1986), but the importance of species differences in ecology as a constraint on grouping is widely accepted.

Although these examples illustrate how predator pressure can favor grouping in different ways depending on other pressures, models have yet to be developed to explain the kinds of social networks which different antipredator tactics generate within groups. Where antipredator tactics depend on cooperation, closed groups may be more likely, whereas if they depend on dilution, open and flexible groups might be expected (Helfman, 1984; Wrangham, 1982). This is a particularly important problem for understanding the effects of predation on primate groups, since social relationships differ extensively in species with similar group size and composition. In antelope little is yet known about female social relationships, and it is possible

that the effect of predator pressure is commonly restricted to a general tendency for gregariousness, rather than for structured social relationships between females (Gosling, Chapter 12; Rubenstein, Chapter 13).

These examples demonstrate that the effects of predation on social behavior are often mediated through intervening variables such as whether and how females monopolize resources. The effects of intense predator pressure on social organization are therefore not easily predicted. A further problem is that the effects of predator pressure are not yet sufficiently well understood to explain why they lead sometimes to large groups and in other cases to small groups. For example, the simakobu *Nasalis concolor* is a leaf-eating monkey found only in the Mentawai Islands (Indonesia), where no mammalian or bird predators on monkeys are known to have occurred until 2,000 years ago. Since then some populations have been subject to intense hunting pressure by humans. Populations which are not hunted live at high density and form small polygynous groups, whereas heavily hunted populations live at low density and are monogamous (Watanabe, 1981). Thus in this case the effects of intense predator pressure are opposite to those normally expected for diurnal primates, causing smaller groups than normal. Why this happens is not clear, and will presumably be understood only when the ecological basis of polygyny is known for this species. It reminds us, however, that until the effects of predator pressure are understood better, the tendency for many prey species to live in large groups should not automatically be ascribed to predation.

Resource Distribution

There are numerous ways in which resource distribution shapes social behavior, and it is impossible here to attempt a complete review. We focus instead on the ways in which resource distribution and intraspecific competition interact to generate social systems. They may do so in two kinds of circumstance, when the distribution of resources either merely permits grouping, or actively favors it. Thus resource dispersal may affect either the costs of grouping, or both the costs and benefits.

First, different patterns of resource dispersal cause the costs of grouping to vary widely between species. Evidence that food distribution limits group size to different degrees in closely related species is presented for hornbills (Leighton, Chapter 6), cercopithecine monkeys (Andelman, Chapter 10), horses (Rubenstein, Chapter 13), and great apes (Wrangham, Chapter 16). Within these taxa, species living in smaller or less cohesive groups use food patches at which an increase in group size would apparently lead to a reduction in foraging efficiency. This means that even if animal groups are always disadvantageous, they are more costly for some species than for others. Accordingly, some species should be able to form groups which confer comparatively small benefits, while others should need much larger

compensation. However, in all cases a benefit must be found. The fact that grouping costs are low is not itself adequate to explain the occurrence of permanent groups.

Second, the distribution of resources can favor sociality in both nonbreeding and breeding animals. For nonbreeder sociality, Florida scrub jays provide strong support for the ecological constraints model of helping, because their habitat is sharply defined and offers few vacant territories (Woolfenden and Fitzpatrick, Chapter 5). Among canids also, a shortage of marginal habitat appears to be an important contributor to the costs of novel breeding attempts (Moehlman, Chapter 4), because of costs associated with the rearing of many extremely altricial young and the need for group hunting. In these cases groups occur not because individuals are thereby better able to exploit the habitat, but because intraspecific competition due to habitat limitation constrains breeding opportunities, sometimes in both the parents and the offspring, as Armitage shows in marmots (Chapter 14). The distribution of resources is a critical aspect of the development of groups, because it not only allows groups to occur, but also limits the formation of groups when optimal habitat is limited.

Reproductive opportunities are less clearly limited where breeding adults form groups, but the ecological constraints model may still be applicable. Packer (Chapter 19) shows that the traditional idea that lion groups function to allow cooperative hunting is poorly supported and fails to explain the distribution of felid sociality. He demonstrates that scavenging and high population density are better predictors of sociality. This forces a reexamination of the way ecology and group life are related in lions. Packer suggests that females allow their kin to share the foraging range because the costs of sharing large carcasses are low, whereas the costs of dispersal are high if the habitat is saturated. This argument is clearly analogous to the ecological constraints model proposed by Emlen (1984), because it suggests that the key variable favoring group-living is the high cost of dispersal.

As Packer notes, however, it has yet to be shown that the costs of dispersal are indeed high (or would be if lions were not social). An alternative possibly to the idea that group-living is favored by the high costs of dispersal is that it is favored by the high costs of solitary life, because solitary females are unable to defend carcasses against groups of rivals. According to this hypothesis, grouping can become an evolutionarily stable strategy merely because it imposes high costs on solitary females, while generating lower costs to individuals in groups (Wrangham, 1982). Some support for this idea comes from data on lions in the Kalahari Desert (Owens and Owens, 1984). Subsistence on small prey during the dry season causes females to forage alone in larger home ranges than normal. At these times prides dissolve and females are known to disperse for long distances. By the time the rains begin and the large game return, new prides have formed that include

many nonkin members. Thus, the formation of prides is clearly associated with the presence of large game, whereas there is no evidence that the costs of dispersal are particularly high at that time.

The relative importance of the costs of dispersal or the costs of solitary life in generating group-living is an important issue for many animals (Emlen, 1984). Either way, the lion data suggest that group-living is favored not only by the distribution of resources but also by the effect of intraspecific competitors on resource distribution. Furthermore, in lions an additional pressure from intraspecific competition affects female grouping: female lions benefit from each other's assistance in reducing the rate of infanticide by males (Packer, Chapter 19). Thus, the lion social system includes many complexities not explained by the traditional idea that groups are favored by the benefits of cooperative hunting.

In their discussion of human mating systems Flinn and Low (Chapter 11) also propose that resource distribution and intraspecific competition interact to generate certain types of sociality. Unlike Packer's, their chapter takes the basic grouping pattern of humans as given. Humans normally form communities (band, villages, nations, etc.), within which females rear their own offspring with the aid of one or more males. Within populations, mating and investment patterns vary widely and appear to be correlated with resource distribution. The association between the presence or absence of significant material resources and the preferred type of cousin marriage, for example, is difficult to explain in other ways. The relationships proposed by Flinn and Low between resource distribution and competition for mates are clearly far more elaborate than any system in other animals. In part this stems from the fact that females and males (as allies) are resources that can be manipulated and exist regardless of the distribution and abundance of ecological resources. Nevertheless, the underlying principle may be widely applicable: intricate social networks are generated by certain types of intraspecific competition, while the prevalent type of competition is itself determined by the nature and distribution of resources.

Intraspecific Competition

The analyses of felid and human social systems share the view that economic defendability of resources is a key characteristic determining the patterns of social relationship. However, felid and human systems differ because resource distribution is seen as determining social relationships among females in lions, but primarily among males in humans. The factors determining whether females or males (or both sexes) defend resources in different species have not in general been examined, although this is a key issue for understanding not only the basis of different forms of polygyny, but also the kinds of social relationship that occur within sexes (Bradbury and Vehrencamp, 1977a, b; Emlen and Oring, 1977). Emlen and Oring

(1977) argued that "when important resources are unevenly distributed or spatially clumped, certain males can defend areas containing a larger quantity or better quality of resources than others." This is doubtless valid, but it leaves open the question of why females cannot defend such resources in the way argued for males. A general answer, presumably, is that it pays males to defend resources against males where the resources tend to attract more fertile females than the male would be able to mate by alternative strategies; whereas it pays females to defend resources against other females only when they thereby increase their net rate of resolute gain. And since defense of a food resource often severely limits the rate of consumption, females may not generally find it economical to defend food resources. The patterns of resource dispersal that favor each strategy have yet to be established.

The preceding section has shown that ecological influences favoring sociality (either group life or the kinds of social relationships within groups) do not necessarily act alone: they may be mediated by and interact importantly with the pattern of intraspecific competition. In this section, by contrast, we review evidence that, when strong enough, certain forms of intraspecific competition can act alone to promote sociality.

This idea has been proposed for a variety of species. For instance, it applies to monogamous birds without male parental investment, where males sequester females, such as brood-parasitic ducks, cowbirds, and cuckoos, as well as a variety of nonterritorial migratory ducks (Wittenberger and Tilson, 1980; McKinney, Chapter 8). In these species males compete for mating rights to females and subsequently guard them against other males. There need be no advantages in terms of predator avoidance or resource gain. "Male guarding behavior protects females from harassment by unmated males, since harassment and attempted [forced copulation] are both commonplace" (Wittenberger and Tilson, 1980).

In ducks, pair formation occurs well in advance of the breeding season, as McKinney (Chapter 8) describes. An important component is female "inciting" behavior. Males respond to female displays by courtship before they pair, whereas after they are paired they respond to the same display by attacking male rivals. In nonterritorial species males guard the females only until the clutch is laid, at which point the female is sexually uninteresting to other males. Thus in the extreme form of this system the male contributes nothing except defense against other males throughout the period of sexual activity. This defense is necessary only because of male sexual activity, but it is valuable from the female's perspective because it allows her to continue feeding and raising young efficiently. Hence the social system emerges as a consequence of intraspecific competition, with the input of ecological variables reduced to permissiveness.

Wittenberger and Tilson (1980) discussed mate defense monogamy in the context of mating systems theory, and therefore argued that one or other sex is the controlling sex: in this case, males. As McKinney (Chapter 8) shows, however, the system is not imposed on females in a proximate sense. Each female works actively to establish a bond with a male, normally unmated, but not necessarily, if few males are available. (See also Lumpkin, 1983, who argues that prolonged female sexual responsiveness has evolved in a variety of birds because of benefits to the female of attracting a male who guards her against harassment.) The basis of female choice is still uncertain, but male dominance over others appears to be important in a variety of species. Thus it is clear that females behave as if they benefit from the presence of a mate.

In an ultimate sense, nevertheless, the social system can indeed be argued to have evolved as a result of male behavior (cf. Rubenstein, Chapter 13). If no males existed, females can be imagined to feed, lay, and rear their offspring as they do in the presence of males. Mated males are "hired guns," necessary only because guns have been invented.

The hired gun principle has been argued to have effects in other species where resources are undefendable and predation appears unimportant to the development of social relationships. Polygyny in horses (Rubenstein, Chapter 13) and gorillas is explicable because of the benefits of male protection from harassment by other males, as are the communities of chimpanzee and bonobos (Wrangham, Chapter 16). It may be a useful principle that applies to other groups, but has been obscured by searches for direct links between ecology and sociality.

The hired guns need not be male. Matrilineal systems are argued to function as part of a strategy of defense against potential infanticide by other females in yellow-bellied marmots (Armitage, Chapter 14). Parallel arguments are given for matrilineal systems in gelada and lions, except that harassment and competition by other females are viewed as more subtle strategies than infanticide (Dunbar, Chapter 15; Rubenstein, Chapter 13). Armitage stresses this point as he argues that female marmots, ground squirrels, and prairie dogs all repress the reproductive abilities of close kin, but by a variety of ways that fall along this continuum.

The classic situation where the behavior of one sex shapes the behavior of the other, independent of resources, occurs among lekking species. As Gibson and Bradbury show in sage grouse (Chapter 17), female movements determine male distributions, and even within leks female choosiness incites males to strut. It is still unclear why leks occur at all. However, in some species they occur only at high population densities (e.g., Uganda kob *Kobus kob*, Leuthold, 1966), or in habitats where predation pressure is extremely high (e.g., topi *Damalisca korrigum*, Gosling, Chapter 12), where

males abandon their normal strategy of territorial defense of food resources. This suggests that ecological pressures have a permissive effect, allowing leks to develop because resources are not defendable.

The effect of female choice in shaping social organization is not limited to leks or mate-guarding groups such as dabbling ducks and gorillas. In the eastern grey kangaroo (Jarman, Chapter 18), females in estrus roam widely advertising themselves to all the males in a neighborhood. Male hierarchies are strictly linear and are based on size. So by roaming over the entire habitat estrus females are virtually assured of mating with the largest and probably oldest males. The advantages of this strategy to females are not clear, but it does seem that they are able to adopt it because there are no stringent ecological pressures forcing them into particular kinds of groups.

These cases stress that intraspecific competition can promote social behavior even in the absence of any classical ecological benefit, just as Alexander (1977) argued for humans. It appears that vulnerability to conspecifics resembles predation risk, resource distribution, and other less common ecological factors in having effects either on its own or in combination with other factors.

EMERGENT CONSIDERATIONS

When a collection of essays focuses on how special features of ecology shape particular social relationships, it is possible to concentrate on details and miss the wood for the trees. In this collection a few important themes recur often enough to warrant further attention.

Biological versus Ecological Determinism

The apparent snug fit between ecology and sociality suggests that most animals come close to achieving optimal solutions to problems posed by nature. In a proximate sense behavior appears to be determined by ecological circumstance. But this should not be taken to imply that there is no genetic control of behavior. As Maynard Smith's (1977) game theory approach has shown, behavioral variation can be maintained in a population by two mechanisms. In one, individuals with different genetic predispositions can coexist at a frequency where each receives equal payoffs. In the other, all members of the population have the same genetic predisposition to adopt a variety of behaviors. As in the previous case, the point of payoff equality establishes the relative frequencies of each behavior. In most of the studies in this volume, behavioral variability appears to be maintained by behavioral flexibility. Thus selection in the past for a particular genetic constitution has freed individuals to behave according to the demands of the environment.

Phylogenetic Constraints

Behavioral flexibility is not infinite. Morphology and physiology often limit a species' behavioral options. For instance, animals without shearing carnassials make poor carnivores. Such limitations are usually the direct result of adaptations to other ecological circumstances, but it should not be assumed that they always are. For instance, within semi-closed groups of birds the pattern of giving aid can show remarkably little discrimination, with different individuals being treated with approximately equal generosity, regardless of kinship or the probability of future reciprocity (e.g., Mexican jays *Aphelocoma ultramarina*: Brown & Brown, 1981a; stripe-backed wrens *Campylorhynchus nuchalis*: Rabenold, 1985). In some social mammals, by contrast, intense discrimination based on kinship or reciprocity is routine (e.g., terrestrial cercopithecines: Hinde, 1983). Even within mammals the degree of differentiation of relationships within groups appears to vary; for instance, coalitions involving competitive elements have been reported more often in primates than in other mammals (Wrangham, 1983). It seems likely that differences in cognitive ability contribute to these taxon-specific differences. In the same way didelphid marsupials appear to have simpler social systems than those of eutherian mammals with similar ecology (Charles-Dominique, 1983). The ability to recognize other individuals and to evaluate probable benefits of particular acts could both be important. If so, the poor cognitive abilities of birds could be responsible for the fact that they form simpler social networks than those of many mammals.

Although this is a reasonable hypothesis, it cannot be properly evaluated until the economics of discriminatory behavior are better understood. For instance, Rabenold (1985) suggested that simple hard-wired behavior programs may be the most effective strategy in group-living birds, assuming that the payoff for a given behavior is highly predictable. Unfortunately, the predictability of payoffs probably depends on the flexibility of the behavior of conspecifics, so that predictability depends in part on the species' cognitive abilities. Nevertheless, it may yet be shown that the spatial and temporal distribution of resources favors greater discrimination in mammals than birds, just as Sherman and Holmes (1985) have indicated that kin recognition abilities in different species of ground squirrels appear to be adapted to the complexity of their social systems. Similarly, ecological hypotheses for species differences should always be investigated before phylogenetic constraints are invoked (Wilson, 1975).

Similarities and Differences in the Socio-Ecology of Birds and Mammals

Phylogenetic constraints may be responsible for some differences between avian and mammalian social systems, such as the degree of differentiation of social relationships. However, many aspects of social organi-

zation are similar in the two taxa. Both birds and mammals, for example, include species with monogamous, polygynous, or polyandrous social relationships; leks and cooperative breeding, indicating that, in general, mating relationships show similar variety in birds and mammals. In some cases where differences are known, it seems likely that they are the result of differences in ecology. For example, there is a higher frequency of territorial monogamy in birds than in mammals (Wittenberger and Tilson, 1980). Although the economics of territorial differences are understood well in only a few species (e.g., sunbirds: Gill and Wolf, 1975), this difference is probably attributable to territories being economically defensible by individuals or pairs more often among birds than among mammals.

Social relationships within sexes, by contrast to mating patterns, appear less diverse in birds than mammals. First, closed foraging groups with more than one breeding female are exceedingly rare in birds but common in mammals. Furthermore, where they occur in birds (e.g., anis, *Crotophaga sulcirostris*: Vehrencamp, 1978), affiliative relationships among breeding females are poorly developed. This is probably related to the fact that within closed groups complete reproductive suppression among females (as opposed to partial reproductive suppression: Wasser and Barash, 1983) is more extensive among birds than among mammals. The localization of breeding effort at a nest-site appears to be partially responsible for the effectiveness of reproductive suppression in birds (Robinson, Chapter 9). Aggressive competition among breeding females is effective at nest-sites, and many mammals that rear altricial young at nest-sites (e.g., dens) also show closed groups with only one breeding female (Emlen, 1984).

Second, competitive relationships among breeding mammals are more highly developed in mammals than birds. Polyandrous mating within cooperative groups has been demonstrated in one bird (acorn woodpeckers: Joste et al., 1985), whereas extensive mate sharing is known in a variety of primates and carnivores (Andelman, Chapter 10; Wrangham, Chapter 16; Moelzman, Chapter 5, and Parker, Chapter 19). Mammals form larger closed groups than birds do. Since in some mammals the number of males per group increases with group size, factors controlling group size may be responsible for the greater elaboration of both female-female and male-male relationships in mammals than birds. Pervasive ecological differences between birds and mammals therefore appear to be important in determining the size and structure of social groups. A systematic comparison of the socio-ecology of the two taxa has not yet been conducted, however.

The Problem with a Name

After the major features of a mating or a social system have been described, a shorthand label is often attached, and the system is placed into one of the many broad, well-established, and conventionally accepted cat-

egories. For example, all mating systems composed of one male and many females are usually termed harems. Yet as many of the chapters in this volume have shown, harems come in a variety of forms, each emerging from a unique set of environmental circumstances. The confusion is great since harems can contain females having affiliative relationships primarily with the male (hamadryas baboons), with both the male and unrelated females (horses), with the male and related females (gelada baboons), or with the male and both types of females (marmots). By lumping these species together the ecological rationale for each set of relationships is obscured. Moreover, even describing these systems as "harems" unwittingly creates the impression that in these groups males control females. As the above studies have shown, this rarely is the case. Similarly, monogamous systems include many variations in social relationships, such as in the division of labor and intersexual dominance (Bossema and Benus, 1985; Wrangham, 1986). The importance of analyzing systems according to the types of social relationship they include, rather than merely by group size and sex ratio, means that categories such as "harem," "monogamy," "polyandry," and other labels that describe principally mating relationships should not be treated as complete.

Different Glues for Different Sexes

The search for the causes of sociality often produces a single benefit that is thought to apply to all members of the society. For example, grouping in wild dogs might be attributed to increased benefits derived from cooperative hunting, or coloniality in caciques might be attributed to reduced vulnerability of nests to predators. But as many of the studies in this volume have shown, the benefits that bind together different classes of individuals within the same society can be very different. Moreover, they are often products of different kinds of glue. As Packer (Chapter 19) suggests, males may band together mutualistically to augment their mating prospects, while females may come together as kin and, by incurring a small cost, may reduce the likelihood of incurring the much greater cost of losing a large carcass to strangers. In addition, at the intersexual level lionesses appear to profit by mutualistically defending cubs against infanticide practiced by newly arriving males. Since different classes of individuals often have different needs, it would not be surprising if subgroups within a society associated for a variety of different reasons. In general, single causes of sociality are most likely to apply where ecological pressures affect both sexes equally, for example, where adult survival is threatened or where the sexes cooperate in obtaining resources. However, these circumstances are not expected to be common, because sex differences in reproductive strategy commonly lead to differences in the importance of particular ecological pressures.

Mating Systems, Intrasexual Cooperation, and Dispersal

One of the most important predictors of the pattern of social relationships within groups is the kinship system. This is not a universal relationship. For instance, in acorn woodpeckers males are more likely to breed in their natal groups than females, but females that stay tend to provide more help than males (Koenig et al., 1983). Generally, however, cooperation appears more extensive among individuals of the sex that tends to stay together as kin. For example, in solitary mammals females tend to be philopatric and have tolerant relationships with female kin, unlike males (Waser and Jones, 1983); in cooperatively breeding birds males are more likely to have kin within groups, and are normally more frequent helpers (Koenig et al., 1983); and in primates the amount of cooperation within sexes is closely correlated with the tendency for kin to live together. For instance, in hamadryas baboons females transfer between groups and males cooperate, while in gelada baboons males transfer between groups and females cooperate (Dunbar, Chapter 15; Struhsaker and Leland, 1979; Wrangham, 1980). This means that an explanation of the pattern of social relationships is tied closely to the problem of explaining dispersal patterns.

Greenwood (1980) proposed that species differences in dispersal patterns were explicable by the mating system. Using the classification of mating systems proposed by Emlen and Oring (1977) and Bradbury and Vehrencamp (1977), Greenwood argued that resource defense systems favor male philopatry and female dispersal, whereas mate defense systems favor female philopatry and male dispersal. Male philopatry was hypothesized to be favored in resource defense systems because it increases the ability of males to acquire resources. In mate defense systems, correspondingly, female philopatry was thought to occur because females invest more heavily in young than males, and therefore benefit by being sedentary. Thus Greenwood (1980) suggested that resource defense mating systems tend to be patrilineal, while mate defense systems tend to be matrilineal.

It is now clear that there are significant exceptions to these generalizations. Thus among group-living primates, most of the species in which male philopatry occurs show no resource defense by males (mountain gorilla *Gorilla gorilla berengei*, red colobus *Colobus badius*, hamadryas baboons *Papio hamadryas*: Pusey and Packer, 1986; Cheney, 1986). These species suggest that a more complete explanation of dispersal patterns can be obtained by including a consideration of intrasexual relationships. The spirit of Greenwood's argument was that sex biases in philopatry arise if there is a sex bias in the advantage of remaining in or close to the natal range. Greenwood suspected that the mating system would be a good predictor of sex biases in the benefit for philopatry. However, the primate data show that patterns of intergroup dispersal are correlated not with the presence or absence of resource defense, but instead with the tendency for females or

males to cooperate in intrasexual competition (Pusey and Packer, 1986). Thus in mountain gorillas, red colobus, and hamadryas baboons, males within groups form alliances against males in neighboring groups. The fact that they cooperate appears to be more important in determining the benefits of philopatry than whether or not they attempt to defend resources. This observation retains the spirit of Greenwood's argument, while noting that the mating system as such is a less important variable than the way in which males or females compete. As socio-ecologists continue to broaden their analyses from a focus on mating patterns to a systematic consideration of relationships within sexes, it seems likely that more cases like this will emerge.

CONCLUSIONS AND SUMMARY

Although no predictive theory of social evolution exists, a number of general principles seem clear. First, social organization is the result of the interaction between proximate ecological pressures and "culture"—the social traditions already in place and shaped by local and phylogenetic history. Second, ecological pressures can operate rather directly on social relationships, which are formed in different ways depending on sex, breeding status, and other phenotypic attributes. This contrasts with the more traditional view that ecology first determines the size, composition, and dispersion of groups, and then through this context shapes relationships. Third, a suite of ecological pressures—the distribution of critical resources, the defendability of the resources, the intensity of predator pressure, and the intensity and nature of intraspecific competition—provide much of the force behind social evolution.

Unfortunately no crisp generalizations emerge as to how these forces shape social organization. For example, we are still puzzled as to: Why some societies have strong dominance structures whereas others do not (Vehrencamp, 1983); why in some societies the young adopt the rank of their parents, whereas in others they do not (Silk, 1986); and why such different ontogenies lead to differences in juvenile dispersal strategies (Altman, 1980). In part differences in phylogenetic history, which reflects patterns of sexual dimorphism, diet, and vulnerability to predation, as well as differences in demography, which reflects age structure and sex ratios, are responsible. But despite these particularities the following common themes are emerging.

Unravelling the evolution of any social system must begin with an understanding of the roots of female behavior, since the behavior of males is largely adapted to that of females. Finding these roots can be assisted by answering three queries. First, does the distribution of the critical resource (food, water, safe sites) force females to forage, travel, or live alone? If the

resources are sparsely distributed, or intense predation can only be avoided by crypsis, then females will be forced to spend most of their time apart (Gosling, Chapter 12; Jarman, 1974). Second, does the nature of the critical resource facilitate its exclusive defense? If territoriality by lone individuals is economically feasible then females will rarely meet, otherwise they may aggregate when not contesting this critical resource, and a variety of fission-fusion type of social systems may develop (Robinson, Chapter 9; Gosling, Chapter 12; Rubenstein, Chapter 13; Wrangham, Chapter 16).

If females are not forced to forage, travel, or rest alone, then a third query must be answered—does the distribution of the resources or the overall structure of the habitat permit females to aggregate, or force them to do so? Permissive habitats are bountiful ones where resources are distributed fairly evenly, and competition among females is low. In such situations the risks of either predation or male harassment may be so high that females aggregate around males that can provide benefits sufficient to reduce these risks and offset the costs of competition (Rubenstein, Chapter 13; Wrangham, Chapter 16). Since competition for the prime males may be keen, permanent associations may develop. Conversely, in other habitats where resources are distributed in rich but scattered patches competition is intensified and may force females to aggregate, ensuring that others and not oneself, are excluded (Packer, Chapter 19). Even within groups coalitions may form to assist partners in garnering a disproportionate share of the resources that the group already controls (Wrangham, 1980; Dunbar, Chapter 15).

After an understanding of the nature and the determinants of female relationships have emerged, then the effects of these relationships on male behavior can be explored in a similar way. Since competition for elusive reproductive females is so intense, males usually avoid other males when searching for, and obtaining access to reproductive females. But the exceptions are striking (e.g., humans: Flinn and Low, Chapter 11; hamadryas baboons: Dunbar, Chapter 15; chimps: Wrangham, Chapter 16; and lions: Packer, Chapter 19) as is the fact that some also defend directly, or indirectly, one or more females whereas others do not. Moreover, this defense can be as brief as one reproductive episode or as long as a breeding lifetime. Ultimately female distributions and associations limit male options, but the demography of the male population also plays a major role by adjusting the costs of various male strategies. Consequently, the linkage between particular male and female strategies is obscured (e.g., antelope: Gosling, Chapter 12; Old World monkeys: Andelman, Chapter 10). Only with more long-term studies, like those in this volume, will these issues be brought into sharper focus.