

# 1. Socioecology: Origins and Trends

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UNDERSTANDING why species differ in their social behavior has fascinated biologists for years. Yet the search for explanations has never been more vigorous than it is now. In the past decade theories of the way evolutionary forces affect social behavior have been developed and tested in substantially greater detail than ever before. In the same period there has been a significant increase in our knowledge of the social behavior of wild animals. These developments have paved the way for two kinds of advances in our understanding of social behavior.

First, diverse patterns of behavior, from foraging to mating, are being understood in terms of their individual selective benefits. General rules are emerging that cut across different species and tie behavior to fundamental principles of evolutionary theory. Some rules are concerned with adaptations to the nonsocial environment, while others are related solely to the social strategies of conspecifics. Excellent reviews of these rules are available, particularly in Krebs and Davies' *Behavioural Ecology* (1984), where selected rules are applied to a wide variety of species. These examples show many elegant matches between theory and data, and thereby promise a remarkably tidy future for the analysis of social behavior.

Second, the adaptive significance of whole social systems is being dissected, analyzed, and understood in relation to environmental pressures. Remarkably, however, no recent book has systematically compared social systems as wholes. It is therefore often difficult to appreciate how different components of the system fit together, or why similar principles yield different results in different species. Nor is it yet clear what the major principles of grouping are in the vertebrates, or the extent to which they vary in different taxa. Accordingly, the present collection reviews the relationships between ecology and social behavior in a variety of birds and mammals. By comparing social ecology in different species groups, this book is intended to contribute to understanding the broad patterns of higher vertebrate social evolution.

The first pieces to the puzzle were discovered by John Crook over twenty-five years ago. Crook began in the late 1950s by comparing the behavior of different species of African weavers, birds that occupy a variety of habitats

from primary rain forest to grassland savannah. He collected data on habitats, diets, nesting habits, and group sizes of approximately one hundred species, and found strong superficial correlations between ecology and social organization (Crook, 1964, 1970). This was exciting because it suggested that if the right variables were found, and if appropriate groups of species were compared, then the ways in which environments shape social systems could be identified. After a flurry of activity, the comparative method faltered. At this time social systems were described not in terms of the types and strength of social interactions, but in terms of the outcome of these interactions. Correlations between the outcomes, such as group size, dispersion pattern, mating system, and ecology, were of little use in showing how environments shaped social structure. What the comparative approach needed was a good theory. It got two: one from the social theorists and one from the ecologists.

The twin pillars of the modern theory of social behavior are the principles of individualistic reproductive maximization (G. C. Williams, 1966) and kin selection (W. D. Hamilton, 1964). With the development of these principles, animals came to be viewed as individuals who were armed with many behavioral options in their struggle for maximizing either their own reproduction, or that of their relatives. Extensions of the theory showed which options were better than others, in particular circumstances. By analyzing the behavior of individuals, the foundations for a comprehensive theory of social behavior were laid. Perhaps the most striking insight was that of Trivers (1972). He proposed a relationship between parental investment and sexual competition. He argued that when one sex invests more in the rearing of offspring than the other, members of the latter will compete for members of the former. The implication was simple: the sexes tend to invest their reproductive effort differently. When females invest heavily in parenting, males should invest heavily in mating, and vice versa.

The comparative method got an additional theoretical boost from the ecologists as well. Orians, Verner, and Willson analyzed polygamy and monogamy in red-winged blackbirds and proposed a general model for the evolution of polygyny (Orians, 1969). Like Trivers's theory, it was based on the idea that ecology influenced each sex differently. It suggested that when ecological conditions were just right, some males could defend large amounts of resources that females required. The model required that the habitat be divided into patches of vastly different qualities. When this occurred, many females could rear chicks in the best areas, whereas in the less rich areas, only one could succeed. In their model females, by attempting to maximize their reproduction, showed how they could induce the coexistence of both polygyny and monogamy in a population.

At this period, both social theorists and the ecologists were expanding their theories and attempting to account for the evolution of mating systems

other than polygyny. A major breakthrough occurred when Maynard Smith (1977) viewed the mating system problem as a game in which the optimal behavior of one parent depended on the behavior of the other. He argued that whether or not one parent should withhold parental care depends on how likely the other parent is to continue caring for the offspring. Since the parents' interests were similar, but not identical, Maynard Smith's idea was to search for a pair of strategies, one for the male and one for the female, which, when performed together, produced an 'evolutionarily stable strategy,' or ESS. Such a strategy would occur when it would not pay a male to depart from his strategy as long as the female continued to follow hers, and it would not pay the female to depart from her strategy as long as the male continued to follow his. The elegance of this approach was that all the pairwise options of: 1) both male and female care; 2) female care, male desert; 3) male care, female desert; and 4) both male and female desert, can be pitted against each other in a thought experiment and compared. Thus, the model offered the hope of determining the conditions that favored monogamy, polygyny, polyandry, and promiscuity, the four basic mating systems. Whether there is to be parental care and, if so, which parent is to provide it depends on the relative effectiveness of uni- or biparental care, the likelihood of a deserting partner finding an additional mate, and the extent to which a female's ability to provide care reduces her ability to produce future offspring. By estimating these parameters, the favored mating system can be predicted.

The model has many powerful features. First, it emphasizes sexual asymmetries, and focuses attention on a limited number of measurable variables that ultimately are associated with reproductive energetics. Second, it demonstrates that when selection favors only uniparental care, whether it is provided by the male or the female often depends on historical conditions and how they set the parameter values. This should provide powerful support to the comparative approach. The only problem with the model is its misuse by some in narrowing, rather than expanding the scope of the problem. Focusing on mating systems and their environmental determinants only provides a first step toward understanding a social system where social relationships other than those between males and females must be explained. Although a limited set of variables can adequately account for the evolution of each broad class of mating system, the problem will grow as explanations on a finer scale are required. The present reduction of dimension only becomes a problem if field workers limit their observations of natural systems to just this simple set of variables. If this were to happen, valuable insights would be lost.

While the social theorists were elaborating general rules for the evolution of the major mating systems, ecologists were expanding Orians' principle to account for the complex systems found in species other than blackbirds.

✓ Emlen and Oring (1977) proposed that the potential for polygyny depended on both the spatial and temporal distribution of members of the limiting sex. For example, an even, scattered distribution of females makes it unlikely that one male will control more females than others. But when females live in groups, or as Orians suggested, the resources they need occur in patches, then some males will have the opportunity ultimately to control large numbers of females. Under these conditions the potential for polygyny is high. Whether it is realized depends on other factors, such as the degree to which females synchronize their reproductive behavior. If all females are receptive at exactly the same time, then males have little chance of mating with more than one female, and the polygyny potential is lost.

For the first time, a general theory of mating systems was emerging, but what it lacked was an understanding of how ecology shaped female reproductive interests. For Emlen and Oring, female distributions were given. But reliance on this assumption was eliminated by studies on antelope (Jarman, 1974) and bats (Bradbury and Vehrencamp, 1977a, b). Both studies showed that female distributions were finely tuned to the environment and depended on the needs of females to seek food and safety from predators. For antelope females, Jarman argued that diet was determined by body size; small females needed high-quality forage, whereas large females needed large quantities of low-quality food. And he showed that because high-quality items were more widely dispersed than low-quality items, smaller females were forced to live more solitary lives than larger females. As a consequence, he concluded that monogamy was the typical mating system of the smaller antelope, whereas polygyny, in its various guises, was to be the norm for the larger ones.

✓ As Jarman's (1974) study shows, a framework is now in place for examining how ecology shapes certain intra- and intersexual relationships. Of course the framework will be strengthened as the ESS approach is applied to more types of competitive and cooperative interactions among social animals. But even in its simplest form, the model expects first, that female behavior—and this includes their social relationships—will be adapted primarily to meeting demands imposed by the physical environment. This is because the reproductive rate of females will normally be raised, or lowered, more predictably by their success in meeting these demands than by their success in other endeavors such as finding, or choosing among, mates. ✓ Second, it expects that male strategies are adapted primarily to competing for mating opportunities, because male fitness is more closely tied to mating success than to the acquisition of other resources. Taken together, they imply that to understand the ecological basis of social organization, it is imperative to understand separately the ecological and, as the ESS approach shows, social pressures operating on each sex.

Although only a beginning, the model contains some very basic ideas whose usefulness must be evaluated. With the recent proliferation of long-term field studies, there is sufficient data to apply these ideas to many different species with different ecologies and different phylogenetic histories. The collection of essays in this volume represents such an application, and one that succeeds in refining the old ideas and defining new problems.

We deliberately limited the scope of the analysis to birds and mammals, the main reason being that the complexity and individualistic nature of the social relationships exhibited by these groups poses the greatest challenge for the existing framework. The birds and mammals also exhibit the full range of standard mating systems, and comprise a sufficiently large number of different taxonomic groups. This has allowed us to maintain diversity, without spreading ourselves taxonomically so thin that no generalizations could be made. Moreover, for the first time, the long-term studies necessary for interpreting changes in social relationships of such long-lived animals are numerous enough to be evaluated.

The book is divided into two parts—Monogamous Variations and Polygynous Patterns. As is the case in the world at large, most of the avian studies are found in the former section and most of the mammalian studies are found in the latter. But as these studies show, similarities in the ecological bases underlying the evolution of the social systems of each type is surprisingly low.

The book begins with studies on the monogamous theme, in particular with Oring's study of facultative polyandry in spotted sandpipers. Of all the mating systems, polyandry is perhaps the least well understood. Few correlations with habitat type have been found, and when contrasted with monogamous systems, polyandry emerges from most studies as favoring females, but not males (Verhencamp and Bradbury, 1984). As our general framework suggests, such an analysis, if true, would certainly not be evolutionarily stable. Oring's analysis suggests that, at least for sandpipers, ecology plays an important role, and that both males and females benefit. According to Oring, sandpipers nest in areas where nest predation is extremely high, except on some islands. In these isolated places, the density of birds rises and because of intense female competition, some are excluded. Conversely, some secondary males are included. For males and females that breed the benefits are higher than they would be by breeding monogamously in less safe areas. Given that most polyandrous birds nest in open and defenseless areas, predation might be a critical variable for these other species as well.

Predation is clearly the major selective agent in the moorhen, a bird that usually mates monogamously, but occasionally exhibits polyandry. Petrie, in Chapter 3, has been able to show that nest failure resulting from predation

places pressures on males to compete for territories comprising dense stands of aquatic vegetation. Yet females do not seem to choose mates on the basis of territory quality. Instead, they seem to choose males that are disproportionately fat. Petrie resolves this paradox by demonstrating that males perform most of the nest-guarding functions while females feed. With such a high likelihood of nest failure, it seems to be critical that a female stay well provisioned so she can lay replacement eggs, and that a male start the season with enormous fat reserves so he can incubate eggs laid late in the season. As in Oring's sandpipers, the threat of predation seems to establish a situation in which female behavior controls that of males. But in the moorhen the control is only partial, as males are simultaneously driven to compete for the safest territories. Nevertheless, in this monogamous society the division of posthatching parental labor is far from equal.

When it comes to examining the ecological adaptations underlying monogamy, few groups of animals provide a better basis for comparison than the canidae. All are monogamous, but the larger members of the family show polyandrous tendencies, whereas the smaller ones lean toward polygyny. In Chapter 4, Moehlman uses an insightful life history analysis to make ecological sense of this trend. She shows that larger species tend to invest disproportionately more in reproduction than smaller species, but they do so by making disproportionately larger litters containing relatively smaller young. Consequently, the young of large species need more postpartum care, and at a time when the mother has already invested heavily. Obviously, assistance is needed, but who should help? Moehlman shows that for large species, as typified by wild dogs, potential competition among many breeding females for the spoils of cooperative male hunting leads to enforced dispersal of all but one. As a result, a male-biased sex ratio sets the stage for polyandry. She also shows that virtually the converse occurs in the small species. Competition among females is much lower and the need for assistance in raising young can be met by the male. Using data on foxes, Moehlman shows that when food abundance increases, female densities increase, a condition that enables some males to mate polygynously. According to this line of reasoning, the species in the middle of the size range should be the most monogamous. Food is not as plentiful so the male will be necessary. As Moehlman's studies on jackals illustrate, helpers are the younger of previous litters, and members of both sexes contribute about equally to the rearing of their young siblings. But as they age, the threat of competition with their parents leads to their dispersal in search of their own breeding territories.

The ecological significance of helping in monogamous systems is also examined in the next chapter by Woolfenden and Fitzpatrick in their study of the Florida scrub jay. Their findings provide a striking contrast to the study of jackals, and provide a possible explanation as to why avian males

are more philopatric than their mammalian counterparts. In the scrub jay, the breeding opportunities for newly maturing birds are extremely limited, because the small patches of suitable habitat are saturated. As a consequence, young of both sexes remain at home and help. But unlike the jackals, the fledging success of the parents remains constant after the addition of the first helper, and the behavior of helpers differs depending on sex. Like their adult counterparts, males are primarily responsible for finding food and bringing it to the mother and the young. Moreover, they are likely to remain as helpers longer and disperse shorter distances than females when they finally depart. Woolfenden and Fitzpatrick evaluate most of the standard explanations for these differences in behavior and philopatry and find them wanting. They suggest, instead, that male dominance, which ultimately results from disproportionate male aggressive defense of territories, induces female dispersal. However, since females must also aggressively insert themselves into territorial vacancies, it is not clear that they are less aggressive, or less effective. More work is needed to account for these exciting results. Some of the latest is presented in the next two chapters.

Even if severe habitat saturation favors that young stay at home and help parents defend territories and raise additional young, Leighton shows in Chapter 6 that other environmental features might forestall this outcome. Among hornbills, whether or not the young will have opportunities to disperse to vacant territories depends on body size. For some of the small African species, predation is so high that turnover among adults is rapid. For the larger Asian species, however, the opposite occurs, and the dispersal opportunities of the young are limited. But contrary to expectation, not all the large-bodied hornbills live in groups. Leighton argues that for some species the distribution of important fruit resources prevents economical exploitation once groups are composed of more than two individuals. Large size requires that more food be consumed per day. One solution would be to spend more time feeding and thus increase intake by visiting more patches. But this apparently is not how the largest hornbills behave. This remains an issue that when better understood is likely to bear its own fruit. Rather, hornbills reduce group size so that each patch can be mined more completely on a per capita basis. Thus, food limitation on one hand favors group living by reducing the dispersal options of young. On the other hand, it apparently encourages group dissolution.

Mongoose are some of the smallest carnivores and often behave in ways contrary to our usual stereotypes. In Chapter 7, Rood makes comparisons among a large number of species that differ in body size, diet, habitat, and activity period. Some strikingly broad conclusions result. Virtually all of the smallest species live in groups, feed on insects, and are diurnal, whereas the larger species are solitary, feed on small vertebrates, and are nocturnal. Rood argues that predation is the most important problem faced by mon-

geoses; predatory attacks can be as high as one every six hours, with predator disturbances occurring at a rate of more than one per hour. Yet the nature of the food resource is the force that seems to constrain dispersion pattern. Whereas the small species can protect themselves by traveling in groups during the day because they feed on abundant insects, the large species can not solve their vulnerability problem in this way. Large individuals, by interfering with each other's capture of small vertebrates, are forced to forage alone, and thus at night. But a paradox emerges. If feeding competition among small mongooses is so low, why do dominant females suppress the breeding activity of all other subordinate females, thus inducing them to become helpers? Reproductive suppression is common (see Moehlman, Chapter 2), and will be discussed in greater detail later in marmots (Armitage, Chapter 13) and in baboons (Dunbar, Chapter 14), but in general it usually occurs when females face stiff resource competition. Rood's analysis suggests an alternative answer. Suppression guarantees that the reproductive female will have vigilant helpers. And since survival rates of small groups are so low, reproductively suppressed females may simply be making the best of a bad job, waiting their turn to ascend to the top of a large, long-lived group. More data on the costs and benefits of the various options will be needed before Rood's intriguing hypothesis can be tested.

In Chapter 8, the last of this section, McKinney analyzes the social systems of a group of most unbirdlike birds, the dabbling ducks. Monogamy is the rule, but polygyny is common. Males do not help with parental care, new pair bonds form each year, and females are the more philopatric sex. McKinney shows that the exceptional nature of duck sociality is easier to understand by noting that the young are precocial, and are up and about soon after hatching. The need for biparental care is dramatically reduced, and, as McKinney argues, emancipates males in most species from performing parental duties. The few that stay defend feeding sites, but most leave and attempt mating with other already paired females, or try to get a head start reconditioning themselves for next year's reproductive challenge. But what is the rush? According to McKinney, females begin testing males early in the off-season for mate guarding ability. This is the only way they can reduce the threat of being subjected to forced copulations on the breeding grounds. Judging by the number of similar examples of mate guarding that appear in later chapters, the value of selecting males on the basis of their protective abilities seems to be high and widespread. For the unemancipated female, McKinney marshals strong comparative data showing that returning to a safe nest site favors not only the early testing of males but also female philopatry, early pairing, and an early return to the breeding ground.

As in the ducks, monogamy is uncommon in the blackbirds. Why is this so? This is just one of the many questions that Robinson tackles in Chapter 9 where he compares mating systems in blackbirds. By using the yellow-



rumped cacique as an example, Robinson extracts a set of general rules that he then uses to examine the social systems of other blackbirds. He concludes that in caciques the major factor that controls female distributions and associations is predation. Sites that are safe from mammalian and avian predators are restricted to islands and females compete for access. By clustering and synchronizing nests in these areas, females markedly increase their chances of fledging young. Given that females form colonies, males compete for reproductive control of colonies, with the largest males acquiring rights to the safest ones. What is intriguing is that young males are larger than old males. At this point, it is not clear whether or not reproductive effort causes the age-specific decline in weight. What appears more certain, however, is Robinson's answer to the initial query: coloniality usually leads to polygyny, and when it does not, the role of male parental assistance in the rearing of young turns out to be considerable. Blackbird polygyny rarely takes the forms of resource or harem defense polygyny. Again, the reason appears to be correlated with the colonial habit. Although females nest together, they must forage alone for insects. Thus, Robinson concludes that in order for males to assure their paternity, they are stuck guarding individual females. Thus, polygyny results from a series of matings. But if increasing paternity is certainly important, a new problem arises: Why do some blackbird males, such as red-wings, let their females leave the territory unguarded to forage?

In caciques, the threat of predation forces females to nest together, but the demands of feeding causes them to disperse. For Old World monkeys, the factors causing cohesive groups are still unknown (Wrangham, 1986). Predator pressure is a possible influence but whatever causes group-living, the nature of the food supply is different from that of caciques because it allows most monkeys to travel in permanent foraging groups. Some species of monkeys travel and forage in groups of about thirty individuals, whereas others are limited to feeding in parties of two. In Chapter 10, Anderman shows that group size has a striking effect on the mating system of Old World monkeys. Groups consisting of more than ten females contain many breeding males and exhibit a constant male-female ratio, whereas those consisting of five or fewer females only contain one adult male. At intermediate sizes, both systems occur. Her study examines the ecological determinants of these patterns, but it also raises some serious doubts as to the usefulness of typing species by mating system. She questions whether the findings that harem males in uni-male groups or dominant males in multi-male groups father most of the offspring, which are valid in a few well-documented studies, should serve as models for generalizing about social relationships and reproductive outcomes in both mating systems. Her comparative analysis shows that the degree to which females synchronize their reproductive activity can overturn the old generalizations. When fe-

males are highly synchronized, harem males and dominant males in multi-male groups have their reproductive success reduced because the lower-ranking males adopt novel reproductive strategies. These, in turn, lead to behavioral adjustments by the threatened males and suggest that a coevolutionary arms race is underway. Andelman's analysis shows that a wealth of information is still to be uncovered about male-male relationships, and that the solution will be tied to differences in the coordination of female behavior.

Most of the studies in this volume focus on one species and extract general rules linking ecology to social behavior, which are then applied to other closely related species. Another approach would be one that mimics that of Crook's study twenty-five years ago and involves comparing a large number of species and their social systems. But to succeed, it will have to focus on individuals and their reproductive interests. In Chapter 11, Flinn and Low perform such a comparison using the best-studied collection of social systems, those of humans! Human societies provide a wealth of data on relationships. For example, among female-female relationships, distinctions are often made between those of sister-sister, mother-daughter, aunt-niece, grandmother-granddaughter, cousin-cousin, and co-wives. In an ambitious analysis, Flinn and Low examine the ecological and economic settings of societies that span the four major mating systems and find some general relationships. For example, they show that, like most other animals, when ecological resources can be accumulated, polygyny results because some males control more resources than others. And when ecological resources can not be accumulated monogamy often results. But not always, because in humans males usually control a most important resource, females—mates, sisters, and daughters. Flinn and Low show that like all resources, the abundance, distribution, and unpredictability of females affect the strategy of control. But they also show that in human systems, male-male, and, to a lesser and more clandestine extent, female-female relationships influence the distribution of females, and thus the nature of marriage systems. Although we originally intended that this chapter teach biologists about humans, and anthropologists how biologists think, it has gone one step further. It teaches biologists to look at animals with the hand lens of anthropologists.

In addition to human societies, those of antelope are also well studied. In Chapter 12, Gosling examines these societies and shows that despite the myriad of ways in which females forage, move, group, defend themselves against predators, and raise young, there are only a few general mating responses shown by males. He argues that even before males can mate with females, they must establish both dominance over other males and a referent so that their status can easily be recognized by subordinates. Only then can males position themselves to maximize rates of copulation with females.

Gosling suggests that males can either follow females or sit and wait for females to arrive. The best strategy obviously depends on the density and movements of females. By analyzing numerous antelope studies, Gosling concludes that the "following" strategy is favored when food is evenly dispersed and of low density, or when females form groups, whereas the "sit-and-wait" strategy is favored when resources are of high quality and patchily distributed, or when foods needed to meet different seasonal requirements are contagiously distributed. What is perhaps most intriguing about Gosling's analysis is that he finds similarities in male strategies that previous workers have categorized as different. For example, male wanderings and harem holding are categorized as "following" strategies, and seasonal, year-long territories and lek territories are categorized as "sit and wait" strategies. By organizing antelope societies into these novel divisions, some startling insights in male-female relationships emerge.

Whereas antelope social organizations illustrate the role that female behavior plays in shaping male social interactions, the social systems of horses and zebras show that male-male interactions play just as important a role in shaping female social behavior. In Chapter 13, Rubenstein shows that even in the absence of predators, and despite the fact that feeding competition is heightened, unrelated female horses prefer living in cohesive groups. Only under severe conditions where grasslands are very patchy do females break up into temporary aggregations. He asks why should group cohesion be so prevalent, and suggests that the answer is related to male sexual behavior, which is so disruptive that it actually reduces female feeding rates. By associating in groups, and skewing the operational sex ratio, Rubenstein shows that only a few of the best males can defend the groups. By keeping other males away, the harassment levels females experience drop dramatically. Rubenstein also shows that in plain zebras, this strategy of employing males as shields has gone one step further. In these zebras, males without harems form their own cohesive groups. As a counterresponse, previously dispersed harems have come together and pairs of males jointly drive away competitors; alone neither male would have been successful. But perhaps the most fascinating question still remains: Who initiates the movements that bring the harems together? Are the males in control, directly protecting their reproductive interests, or are the females in control, manipulating their hired guns? Some insights into this problem emerge in the next two chapters on other harem living mammals.

The social relationships of another harem mammal, the yellow-bellied marmot, are analyzed in Chapter 14 and they are strikingly different from those of horses and zebras. Females form social groups of closely related individuals that persist for many generations as matriline. Harems form when a single male attaches himself to one or more matriline. Armitage's

analysis shows that males always benefit reproductively by having a large harem, but that females do not. He shows that inter- and intramatriline competition leads to social suppression of reproduction by the younger females. Apparently parents are attempting to maximize their own reproduction without damaging too severely the long-term reproductive interests of their young. According to Armitage, suitable habitat is rare and since the risks of predation during dispersal are large, young females are induced to stay home and make the best of a bad job. Given that the nature of marmot harems and the ecological forces maintaining them are markedly different from those of horses and zebras, the usefulness of calling these social systems by the same name is questionable. Moreover, determining exactly why these offspring stay at home, compete with their mother, and breed with limited success, whereas those of jackals, hornbills, and scrub jays stay at home and help their parents, remains a fascinating problem.

In Chapter 15, Dunbar shows that gelada baboon society has two major levels: harems, which are stable one-male reproductive matriline, and herds, which are unstable collections of harems. According to Dunbar, the need to reduce the risks of predation and the physiological side-effects of crowding lead to conflicting social pressures. On the one hand, predation favors the formation of large groups, which gelada are capable of doing because, like zebras, they are grazers. On the other hand, crowding leads to strife and physiological suppression of reproduction, much like the marmots. The social system that results is a compromise. Dunbar argues that related females form matrilineal harems to keep other unrelated females away and thus reduce the physiological effects of crowding. To support this conclusion Dunbar shows that harems only merge to form herds as a last resort when gelada find themselves in habitats where the ease of detecting and escaping from predators is extremely low. What is fascinating is that the compromise is only partially successful. Even within harems, low-ranking females suffer from reproductive suppression. As Dunbar shows, this tension among female kin leads to a diverse array of social strategies. Aging females form coalitions to hold on to their rank, low-ranking females attach themselves to "follower" males to form new groups, and females assess and alter their loyalty to their male depending on his effectiveness in inter-harem confrontations. Of particular importance is Dunbar's finding that rudimentary forms of these social relationships exist even in the phylogenetically distant forest-dwelling baboons that live in multi-male groups.

In Chapter 16, the limits of the ecological control of social organization are explored in Wrangham's study of chimpanzees and pygmy chimpanzees (bonobos). Although very closely related, field studies show that bonobo social organization is substantially different from that of chimps. Whereas female chimpanzees forage largely alone because of intense feeding competition, bonobo females form fairly stable subassociations. As for the

males, they are often found in all-male coalitions in chimpanzees, but in bonobos they usually associate with the female subgroups. Wrangham suggests that the availability of a *secondary* or less preferred resource holds the key to understanding the differences. Although both species prefer fruit, bonobos regularly eat the ubiquitous terrestrial herbaceous vegetation (THV), just like their relatives, the gorilla. The drier habitats of chimps seemingly deny them access to this type of vegetation and thus prevent them from reducing their high levels of feeding competition. Wrangham concludes that bonobos have become so much like the gorilla that the formation of stable groupings has subsequently permitted the formation of protective relationships between males and females. But the transformation to the gorilla lifestyle is not complete. Wrangham cites a case where high-ranking males pursue a chimplike strategy of banding together and continuously patrolling the entire community of females. Clearly, further studies on this "missing link" will help clarify our understanding of the evolution of sociality in the great apes.

Of the polygynous mating systems, leks have been the most difficult to interpret. In Chapter 17, Gibson and Bradbury's analysis of sage grouse social relationships provides some important new insights. First, preliminary data show that female home ranges are extremely large and overlapping, and that females tend to use major traffic routes when moving from roosting to feeding area. All these features support the hot-spot model, which predicts that males will not follow females about in their large home ranges, but will sit and wait for them to pass by, especially if they predictably travel along certain routes. Then they examine male-female relationships on the lek, and produce a number of startling results. First, leks are not as stable as previous workers have thought since some males move display sites often. Second, male dominance is often relative, not absolute, as males generally win encounters only within their core area. Third, females do not necessarily choose central males, rather, chosen males become the center of attention. And fourth, females appear to choose males on the basis of strut rate. Interestingly, female-female competition, but not copying, seems to occur. How this competition affects the mating success of both sexes should prove to be fascinating.

When females exercise choice, they need not be limited to doing so on leks. While it is true that leks afford females the opportunity to shop around and make an informed choice, there are other ways by which the same amount of information can be extracted. In Chapter 18, Jarman and Southwell describe the novel information-gathering technique employed by the eastern grey kangaroo. When females become sexually receptive, which lasts about a week, they begin roaming widely, picking up male escorts. As time goes by, the train of males-in-waiting lengthens, but the largest male is always right behind the female. As Jarman and Southwell argue, the

longer and more widely she moves the more likely she is to detect, and mate with, the largest and oldest male in the population. This seems to be important in kangaroos and may even be based on a unique marsupialian feature. Marsupials are indeterminate growers, so as they age they keep getting larger. Thus, if a male lives long enough, he will become the largest male and exert total dominance over all other males in the area. If estrus females have time enough to travel over the entire area, then the largest male could theoretically mate with all receptive females in the neighborhood. As Jarman and Southwell note, many of the ungulate (the kangaroo's eutherian counterparts) social relationships do not appear in kangaroo societies. The possibility that early phylogenetic divergence has led to such major differences in social responses to similar ecological features is fascinating, and should encourage even more comparative field studies.

If diet plays only a permissive role in shaping ape, equid, and gelada baboon societies, it plays the controlling role in shaping felid societies, especially that of the lion. As Packer notes in Chapter 19, the stealthy hunting habit of felids virtually requires a solitary lifestyle. So why are lions social? One explanation, that group hunting facilitates the capture of large prey, is not substantiated when Packer analyzes the average size of the prey in relation to female size. Leopards and cougars often prefer relatively larger prey than do lions. Another explanation is that group living occurs because hunting success is higher for pairs of lions than for solitary lions. By reanalyzing Schaller's data, Packer concludes that solitary hunters do best. He then shows that peculiarities of contemporary lion habitat make group living a "best of a bad job" situation. Lion society is based on a pride of genetically related females that share a common range, but travel in small open membership groups that regularly fuse and fission. Such a pattern of sociality is adaptive because in open habitats that are crowded, conspecifics can readily locate large carcasses. Thus, if lions are going to lose food to other lions, they might as well lose it to close kin who can at least augment inclusive fitness and might actually assist in driving strange lions away. Thus, kinship and mutualism seem to organize female relationships by reducing costs. Group hunting seems minor. Interestingly, for males the situation is somewhat different. Mutualism helps males take over prides and augment per capita reproductive success, regardless of the kinship relations among the helpers. Such major sexual differences in the social cements are intriguing and should encourage others to examine social relationships in this light.

As the examples described above show, many of the same behavioral pieces appear in many of the social puzzles. But they fall into place in different ways. For example, habitat limitation repeatedly induces juveniles to remain with their parents. Some juveniles, however, forgo breeding and help their parents raise young, whereas others attempt to breed and limit

their own reproduction as well as that of their parents. Moreover, differences in which sex (male or female young) stays, and for how long, vary from study to study. Making sense of differences like these requires a detailed understanding of differences in ecology, demography, physiology, and phylogenetic histories of each species. Usually such an understanding is incomplete. In this volume, the authors have been encouraged to approach the problem of unravelling the links between ecology and behavior from a broad interdisciplinary perspective. Judging from the ideas, and the level to which they are developed, in the subsequent chapters, this approach has borne fruit. In a final chapter, we search for commonalities and specificities in the operation of each environmental pressure and extract a set of general rules that help shape the evolution of bird and mammal societies.