

Primate social organization

Primate social organization refers to the size and composition of primate groups, the social behavior and relationships of individuals living in those groups, and the ways in which those features are influenced by demographic and ecological conditions. Primates show an enormous diversity in social organization, more than most other groups of vertebrates: in some species individuals are largely solitary, while in other species animals live in groups that can contain several hundred individuals. The basic types of primate social organization are differentiated primarily by the temporal and spatial aspects of associations between adult males and females (**Fig. 1**).

In the noyau system, males and females range solitarily but come together occasionally to mate. The ranges of males generally encompass the ranges of more than one female, making the mating pattern effectively polygynous. This form of social organization is thought to be characteristic of ancestral primates and is common in nocturnal strepsirrhines and in orangutans.

Roughly 15% of primate species are characterized as monogamous, including gibbons, titi monkeys, sakis, owl monkeys, several strepsirrhines, and many callitrichids. Monogamy involves a more or less permanent spatial association between a single adult male and female, which commonly defend a territory against neighboring pairs. Typically, monogamous primates exhibit some sort of affiliative pair-bonding behavior, such as coordinated vocal duets or visual displays. Some callitrichids can live also in cooperative breeding groups. These groups generally contain a single breeding female and one or more breeding adult males, plus, on occasion, other reproductive-age females which do not reproduce but help care

for the young of the breeders. Nonreproductive females are typically offspring of the breeding female, and the latter may suppress their reproduction behaviorally and/or physiologically.

Many species of primates live in one-male groups, in which a single breeding adult male is spatially associated with several adult females. These females may either be related to one another (as in guenons, patas monkeys, capuchins, and some colobines) or unrelated (as in gorillas, red howler monkeys, and some red colobus monkeys). In some species, bachelor males kept out of reproductive units may associate with one another in all-male groups. A similar form of social organization is known as an age-graded harem, in which several males (which are generally related to one another) reside in a group with several adult females but mating and reproduction are monopolized by the dominant, oldest male.

Some of the most familiar primates, including squirrel monkeys, ring-tailed lemurs, vervets, and macaques, live in bisexual multimale-multifemale groups, which are permanent associations of several breeding individuals of each sex. A few primates, notably chimpanzees, spider monkeys, and some muriquis, show a different type of multimale-multifemale social organization known as a fission-fusion society, in which a community of associating individuals splits into smaller parties of variable composition for daily foraging and travel. In this system, party size and composition are continually reorganized based on the availability of food and on the social and kin relationships among community members. Related males form the core of the community and together defend access to an area containing the ranges of several females, which are largely solitary.

Finally, some papionin primates, particularly geladas and hamadryas baboons, live in multilevel societies. In these species, bands consist of several one-male units, each of which includes a single adult male and several breeding females. Within bands, females are largely unrelated in hamadryas baboons but are matrilineal kin in geladas. In contrast, males within a band are related to one another in hamadryas baboons but unrelated in geladas. In these societies, bands may form temporary associations with varying degrees of regularity, sometimes leading to formation of troops containing hundreds of individuals. Temporary associations of multiple social groups are also seen in other primates.

Determinants. Part of the variety in primate social organization can be explained as the result of ecological factors, particularly the risk of predation and the need to maintain access to food resources for survival. The fact that most nocturnal primates are largely solitary has been interpreted as a strategy to avoid being detected by predators. For diurnal primates, sociality may reduce predation risk because predators are detected more effectively when additional animals are on the lookout (the vigilance effect), because an animal's chance of being the target of a predator's attack decreases as group size increases (the dilution effect), or because group

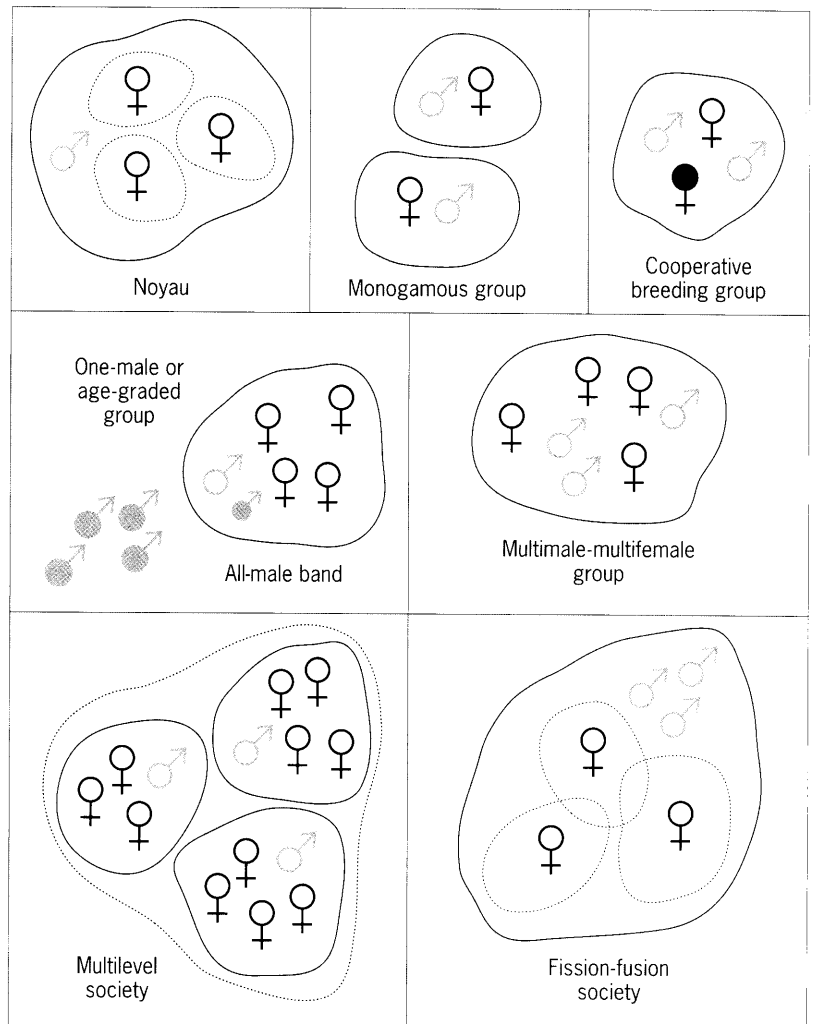


Fig. 1. Basic types of primate social organization. Only adult individuals are shown. Solid symbols represent nonreproductive animals. (After J. G. Fleagle, *Primate Adaptation and Evolution*, 2d ed., Academic Press, San Diego, 1999)

members might participate in cooperative defense against a predator. In terms of access to food, group living is generally considered to be costly to individuals because of intragroup feeding competition. If food resources are limited and must be divided among group members, an individual's share of a given resource decreases as group size increases. Consequently, animals living in larger groups may need to travel farther or spend more time feeding to meet their resource needs. On the other hand, living in a group can enhance an individual's access to food if groups can locate novel resources more readily than individuals, if group members share information about the locations of food sources, or if larger groups can displace smaller groups from desired food patches.

Socioecological theory maintains that other features of primate social organization, such as sex biases in dispersal patterns, the sexual composition of social groups, and the patterning of social relationships within groups, are also ultimately shaped by ecological factors—particularly by the way in which

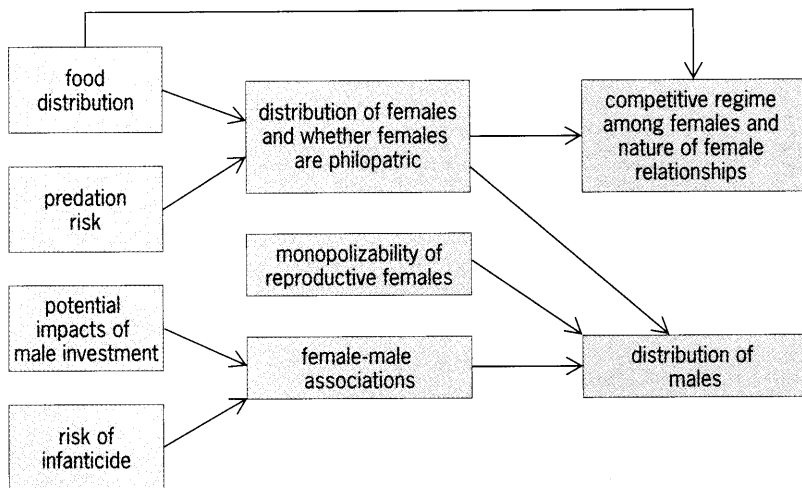


Fig. 2. Ecological and social influences on aspects of primate social organization. (After N. B. Davies, *Mating systems*, in J. R. Krebs and N. B. Davies, eds., *Behavioral Ecology: An Evolutionary Approach*, 3rd ed., Blackwell Scientific Publications, Oxford, 1991; and E. H. M. Sterck et al., *The evolution of female social relationships in nonhuman primates*, *Behav. Ecol. Sociobiol.*, 41:291–309, 1997)

the risk of predation and the distribution of food resources jointly determine the dispersion of females in the landscape and the nature of social relationships among females, and by how female dispersion subsequently influences the dispersion of males (Fig. 2). The primacy of females in this model stems from the fact that, for most mammals, females invest far more in offspring (through pregnancy, lactation, and other postpartum care) than do males. A female's fitness—the number of offspring she can raise in a lifetime—is closely tied to and limited by her access to food resources, and thus the distribution of resources determines the distribution of females. Females are expected to aggregate where resources are clumped and to be more evenly spaced where resource distribution is more uniform. Predation risk also influences female distribution in that, when high, it is an additional pressure favoring female groupings. Ecological factors also determine sex biases in dispersal. Where females benefit more than males in terms of foraging efficiency or protection from predators by remaining in a familiar natal range, females should be philopatric (remain in their natal groups for life) and males should disperse.

The nature of female social relationships within groups is also related to food distribution through its impact on the competitive regime over food. For species where females are philopatric, where resources are distributed such that they can be monopolized by dominant individuals or coalitions, female social relationships tend to be strongly hierarchical and characterized by nepotistic patterns of affiliation and cooperation. In contrast, where resources are less clumped and defensible, female relationships tend to be more egalitarian and cooperation between females less common.

As male fitness depends less on access to food resources than on access to females, male distribution patterns are determined by the distribution of

females. Where multiple females, or the resources needed by those females, are easily monopolized by a single male, polygynous social systems (noyau, one-male units) can arise. Similarly, where lone males cannot defend access to multiple females, either monogamous or multimale-multifemale groups may arise, depending on whether females are solitary or grouped.

This ecological model does not address why, in many primates, the sexes should associate permanently. In particular, why should female primates tolerate the presence of males which in most instances are unrelated and may compete with them for food? Some researchers have argued that the benefits of male investment in offspring provided the impetus for females to group permanently with males which provided such paternal care. This hypothesis may help to explain the evolution of some monogamous and cooperatively breeding social systems, but is less satisfactory for the majority of primates, in which direct male care of offspring is negligible. More recently, researchers have argued that the evolution of permanent male-female associations is due mainly to the risk of infanticide. Female primates may benefit from permanent associations with males, if those males in some way help protect infants from other, potentially infanticidal males. These influences on primate social organization are summarized in Fig. 2.

While ecological factors are obviously important in shaping primate social systems, there is also a clear phylogenetic component to primate social organization. For example, among cercopithecine primates many species show similarities in group structure and intragroup social behavior despite having varied ecologies. These similarities include male-biased dispersal and female philopatry; the existence of stable, linear dominance hierarchies among females; and affiliative female social behavior that is directed along matrilineal kin lines. These social organization traits appear to be part of a suite of behavioral features that evolved in the ancestor of the Old World monkeys and are retained in most descendant taxa.

Genetics. Molecular techniques such as restriction analysis, mitochondrial and nuclear DNA sequencing, DNA fingerprinting, and nuclear marker analysis are increasingly used as tools to examine the genetic underpinnings and consequences of primate social organization. For example, DNA fingerprinting and multilocus genotyping have been employed to examine the breeding systems of several primates, including chimpanzees, marmosets, red howler monkeys, and a number of macaques. Multilocus genotyping has also been used to determine patterns of intragroup relatedness for comparison with behavioral data to investigate the role of kinship in structuring social relationships. For example, a molecular study of chimpanzees in Gombe National Park, Tanzania, revealed that males were more closely related to one another than females, supporting the suggestion that the social core of the community consists of close male kin.

Some of the genetic consequences of primate social structure have been examined by comparing genetic variability in both maternally inherited mitochondrial DNA and nuclear DNA within and between populations. In macaques, mitochondrial DNA shows little variation within local populations but substantial variation between populations. In contrast, most of the overall variation in nuclear DNA is found within rather than between groups. This result is consistent with field observations of male-biased dispersal and female philopatry in these species. Primates in which females disperse, such as chimpanzees and spider monkeys, should show far less of a difference between mitochondrial and nuclear DNA variability within groups.

The development of the polymerase chain reaction, which can be used to amplify minuscule amounts of genetic material obtained from feces, shed hairs, or noninvasively collected tissue samples, along with the growing availability of easily screened neutral genetic markers such as microsatellites, promises to facilitate more widespread application of genetic techniques to the study of primate mating systems, dispersal patterns, and intragroup relatedness.

For background information *see* BEHAVIORAL ECOLOGY; PRIMATES; SOCIAL MAMMALS; SOCIOBIOLOGY in the McGraw-Hill Encyclopedia of Science & Technology.

Anthony Di Fiore

Bibliography. E. Delson et al. (eds.), *Encyclopedia of Human Evolution and Prehistory*, 2d ed., Garland Publishing, New York, 2000; R. I. M. Dunbar, *Primate Social Systems*, Cornell University Press, Ithaca, 1988; J. G. Fleagle, *Primate Adaptation and Evolution*, 2d ed., Academic Press, San Diego, 1999; D. J. Melnick and G. A. Hoelzer, The population genetic consequences of macaque social organization and behaviour, in J. E. Fa and D. G. Lindburg (eds.), *Evolution and Ecology of Macaque Societies*, Cambridge University Press, 1996; P. A. Morin et al., Kin selection, social structure, gene flow, and the evolution of chimpanzees, *Science*, 265:1193-1201, 1994; B. B. Smuts et al. (eds.), *Primate Societies*, University of Chicago Press, 1987; E. H. M. Sterck, D. P. Watts, and C. P. van Schaik, The evolution of female social relationships in nonhuman primates, *Behav. Ecol. Sociobiol.*, 41:291-309, 1997.