Grouping Patterns

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Primates exhibit a wide range of grouping patterns, also called social organizations. Traditional grouping patterns are classified based on field observations of the number of adult animals traveling together, along with their sexes. Numbers of immature individuals of each sex are counted when group size and composition are included in grouping patterns. Grouping patterns are often viewed as being organized from simple to more complex, with an implicit and sometimes explicit view that there was an evolutionary transition from one to the next, starting with the basic ancestral mammalian social organization of the solitarily foraging mother and her dependent offspring sharing the same home range. Although alternative descriptive terms exist, grouping patterns or social organizations are traditionally classified into the following seven types:

Solitary: adults that travel and forage by themselves. More recently, "solitary forager" is preferred to highlight the fact that animals that live alone nonetheless have social interactions with their neighbors. Most solitary foragers are smaller-bodied, nocturnal, strepsirhine primates, such as *Cheirogaleus*, *Loris*, and *Galago*, the one exception being the very large-bodied, diurnal, haplorrhine *Pongo*.

Pairs: adults that share the same home range with one other adult of the opposite sex. In the past, this term was used interchangeably with monogamy, a term describing a particular mating system, but it is now evident that individuals within pairs may engage in extra-pair copulations. Individuals within pairs can travel and forage separately (e.g., *Phaner*) or together (e.g., *Indri*, *Callicebus*, and *Hylobates*) and are typically territorial, actively defending the boundaries of their home ranges.

Extended families: adults that travel together in the same home range with one or more adults of the same or opposite sex but with only one breeding female. Extended families can develop from pairs if maturing offspring do not disperse from the natal home range. In such cases, adult offspring of both sexes may assist in caring for the young of the breeding female. Examples: *Callithrix*, *Cebuella*, *Leontopithecus*.

Single-male/multi-female groups: adult females that travel together in the same home range with other adult females and one adult male. This grouping pattern is sometimes referred to as a "harem," a term that has fallen out of favor because it erroneously implies that males control females in the group. Numbers of adult females in such groups can vary from two to more than 20. Examples: *Alouatta*, *Cercopithecus*, *Erythrocebus*, *Semnopithecus*, *Procolobus*, *Gorilla*.

Multi-male/multi-female groups: adult females that travel together in the same home range with other adult females and more than one adult male. With some exceptions (e.g., *Eulemur, Propithecus,* and *Chlorocebus*), primates exhibiting this grouping pattern typically have more adult females than single-male/multi-female groups. Examples: *Lemur*, *Alouatta*, *Cebus*, *Macaca*, *Papio*, *Semnopithecus*, *Procolobus*, *Gorilla*.

Multilevel groups: adult females that travel together in the same home range with other adult females and at least one adult male, and who regularly assemble with similar units at common sleeping sites. Depending on the species, the smallest units are called "reproductive units" (or "one-male units", OMUs); when they interact with each other they are called "bands" (or "clans"), and several bands (or clans) that interact are called "herds" (or "bands"). Examples: *Theropithecus*, *Papio*, *Nasalis*, *Rhinopithecus*.

Fission–fusion groups: adult females that at different times travel alone or with other adults of either sex within the same home range. Examples: *Ateles*, *Pan*.

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A recent evolutionary framework uses the same classifications to argue that, rather than the stepwise fashion of increasing size and complexity of social organizations described above, the initial solitary forager social organization led to loose aggregations of multiple females and males, and then to cohesive multi-male/multi-female groups approximately 52 million years ago (m.y.a.). This social organization then spawned both pairs and single-male/multi-female groups approximately 16 m.y.a. (Shultz, Opie, and Atkinson 2011).

Frameworks that view grouping patterns as stepwise evolutionary transitions do not readily account for the fact that different grouping patterns can be expressed in the same species, and even seasonally in the same group. A demographic framework provides an alternative approach, suggesting, for example, that the transition from one male to multiple males in a group can occur when maturing males do not disperse but remain in the group; that is, the "age-graded" group (Eisenberg, Muckenhirn, and Rudran 1972). Although this framework does not consider transitions between other types of social organizations, it importantly advances the idea that dispersal patterns can contribute to our understanding of grouping patterns. Dispersal patterns are directly responsible for the kinship structure underlying observed grouping patterns, and reveal another weakness of the evolutionary framework. For example, both *Chlorocebus* and *Procolobus* live in multi-male/multi-female groups and, according to the evolutionary stepwise framework, would be expected to have evolved from the same precursor. However, female *Chlorocebus* are philopatric and remain in their natal groups throughout their lives, whereas female *Procolobus* disperse to other groups at sexual maturity, suggesting that their social organizations evolved independently from a different precursor. A parallel from taxonomy illustrates this point. Based on physical and behavioral similarities, *Tarsius* had long been considered more closely related to other prosimians than to anthropoids. When underlying phylogenetic relationships could be discerned, however, *Tarsius* was found to be more closely related to anthropoids. The classification scheme was then changed to reflect that underlying phylogenetic structure.

While unrelated genera such as *Chlorocebus* and *Procolobus* can have similar grouping patterns, at least superficially, species within the same genus more often have similar grouping patterns. This suggests that there are evolutionary forces at work on social organizations to some degree, if not in the transitions between grouping patterns, at least in phylogenetic constraints. For example, the genus *Macaca* has the most widespread distribution of all nonhuman primates, but all species within this genus live in multi-male/multi-female groups. Similarly, in the genus *Cercopithecus*, all 20 species live in single-male/multi-female groups. It is important to recognize, however, that consistency within a particular genus may at times be a human construct. For example, until recently vervets, which typically live in multi-male/multi-female groups, were included in the genus *Cercopithecus*. Now *Cercopithecus* consists only of species with single-male/multi-female groups.

That unrelated species can have similar social organizations has been interpreted as convergent evolution driven by similar ecological conditions. Habitat preference, diet, and diel activity have long been thought to influence grouping patterns (Clutton-Brock and Harvey 1977). For example, almost all nocturnal insectivores are solitary foragers regardless of phylogenetic relatedness, and nearly all terrestrial primates live in large multilevel or multi-male/multi-female groups. Predation and food abundance and distribution have also been viewed as important ecological factors influencing grouping patterns. For instance, group living has long been thought to be a function of predation pressure, as it is commonly assumed that there is greater safety in numbers. A corollary is that having more group members further reduces predation risk, the evidence coming from primates that live in open habitats where predation pressure is assumed to be greater than in forested habitats. This assumption has yet to be tested. In contrast, evidence does exist that in many species, maximum group size is a function of energetic constraints on daily travel as group size increases. Animals in larger groups typically move farther per day than animals in smaller groups within the same habitat and species, and maximum group size may be reached when food intake

cannot provide enough energy for farther travel. Understanding the underlying causes of the diversity of grouping patterns is a major focus of the field of socioecology.

SEE ALSO: Dispersal; Foraging Strategies; Group Movements (and Collective Decision Making); Mating Systems; Social System (Social Structure); Socioecological Model

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