Socioecological Model

LYNNE A. ISBELL
University of California, Davis, United States

The field of primate socioecology is the study of ecological determinants of primate social organizations, and one of its main approaches has been to develop conceptual comparative models to explain the wide diversity apparent in primate social organizations. The first conceptual socioecological model was developed by Crook and Gartlan (1966). They presented five "grades" of primates, generally separated by group size but also showing differences in mating structure, male dispersal (of which very little was known at the time), sexual dimorphism, and presence or absence of territoriality. They argued that differences among the grades are based on differences in habitat, diet, and diel activity. For instance, the main ecological conditions favoring Grade I solitary primates were proposed to be forested habitats along with nocturnality and insectivory, the assumption being that insects are best obtained by individuals hunting alone. At the other extreme, the main ecological condition proposed to favor Grades IV and V large-group-living primates was proposed to be open environments, such as forest fringes, "tree savannahs," grasslands, and arid savannahs, the assumption being that these are associated with high numbers of predators which discourage solitary living, and with locally abundant food supplies permitting congregation into large groups without risk of food resource depletion. Their assumptions set the stage for future models emphasizing the importance of predation and food characteristics, particularly food abundance and distribution, in determining social organizations. Underlying social conditions affecting the various grades were largely restricted to aspects of sexual selection involving male reproductive activity and increasing male–male competition for females as groups increased in size. This early socioecological model was strongly influenced by natural history and descriptive field studies.

Another influential paper that built upon natural history and observations from field studies was that of Eisenberg, Muckenhirn, and Rudran (1972). They developed the "age-graded" social concept in which certain demographic conditions—that is, maturation and philopatry of natal males—account for fluidity from single males to multiple males in social groups.

At the same time that natural history-based conceptual models were being developed, so were quantitative theoretical models about social behavior, predation, and food. Three would have particularly strong effects on later conceptual socioecological models. The first was the concept of inclusive fitness, that natural selection can still favor individuals that act in ways that are obviously harmful to themselves if their behavior ultimately benefits themselves through benefits to their relatives. The second was the "selfish herd" concept, that aggregations of animals could occur simply as a result of animals' attempts to avoid predation by moving to put conspecifics between themselves and the predator. Finally, the third was the concept of parental investment as an explanation for sex differences in behavior and morphology, that the sex investing less in offspring evolves to compete for access to the other sex. In mammals, since females invest much more than males in their offspring via gamete production, gestation, and lactation, males invariably compete for females, whereas females compete for energy (i.e., food) to support their high parental investment. This insight led to female primates being viewed as the "ecological sex" and to male primates as mapping onto the distribution of females, now a cornerstone of socioecology.

As the number of field studies increased in the 1960s and 1970s, and with theory providing the backbone to understanding primate social behavior and social organizations, quantitative approaches to examine ecological contributions to social organizations then became possible. Their development and application continued to support and refine the hypothesis that ecology

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underlies differences in social organization. Clutton-Brock and Harvey (1977) conducted one of the most comprehensive early statistical examinations. Following Crook and Gartlan's (1966) broad approach, they classified primates into seven categories by diel activity (nocturnal vs diurnal), habitat (arboreal vs terrestrial), and diet (insectivorous, folivorous, frugivorous). They found that these ecological conditions were correlated with numerous aspects of social organization. For example, nocturnal, arboreal insectivores are small-bodied and often live alone, whereas diurnal, terrestrial folivores are large-bodied and live in groups. They hypothesized that small-bodied primates are typically solitary and nocturnal because they are more dependent on crypsis than active defense to avoid predators. Similarly, they hypothesized that since larger-bodied primates cannot rely on crypsis, they live in groups as a defense against predators.

Shortly afterward, Wrangham (1980) proposed that it was unnecessary to consider predation because characteristics of food could by themselves explain certain types of primate groups. Incorporating the idea that females, being the "ecological sex," map onto food abundance and distribution for greater reproductive success, Wrangham focused on explaining the evolution of multi-female groups based entirely on characteristics of food in a model he called an "ecological model." He proposed that not only the formation of multi-female groups but also the nature of female social relationships within and between multi-female groups could be explained by the spatial distribution of foods. Foods that were spatially clumped would favor competition among females, and groups of females would form to improve their competitive success against other groups. Such groups would be composed of related females because such females would gain inclusive fitness benefits by working together to compete against non-relatives in other groups. By definition, females in these groups would be philopatric, with a suite of other characteristics, including differentiated dominance and grooming relationships. He called such groups "female-bonded." Wrangham hypothesized that female-bonded groups had control over the number of adult males residing in their groups. They would allow in only one resident male if they were territorial, or recruit multiple males if nonterritorial because additional males could help in intergroup competition. In contrast, uniformly distributed foods would not favor competition among females and so there would be no incentive for females to remain in their natal groups with female relatives. Females would readily disperse, would not form bonds with other females, and would not have differentiated dominance and grooming relationships, but would instead gather around males who could protect them from other males. Although Wrangham's model did not consider other types of social organizations such as nocturnal solitary foragers or pair-living primates, it began the modern phase of socioecological models with its more focused attention on the behavior of females.

A series of papers by van Schaik and colleagues (e.g., van Schaik 1989; Sterck, van Schaik, and Watts 1997) challenged Wrangham's model with an alternative that proposed different categories of multi-female groups and delved deeper into female social relationships. van Schaik (1989) proposed four types of multi-female groups that were all initially created by predation pressure. In this he differed from Wrangham, but otherwise he agreed that food competition explains female social relationships within and between groups. According to van Schaik's socioecological model, under high predation pressure, competition would be mainly within groups. He was the first to incorporate two distinctive types of competition, contest and scramble competition. Contest competition is direct and visible, and was argued to be generated by spatially clumped foods (fruits), whereas scramble competition is indirect, reduces energy intake equally for all group members, and was argued to be generated by foods that occur in patches that, relative to group size, are either very small and cannot be monopolized (insects) or very large (leaves). In van Schaik's model, female social relationships in multi-female groups differed as a result of varying degrees of contest and scramble competition within and between groups. He hypothesized that when scramble competition prevails within groups, females in multi-female groups would develop individualistic and egalitarian dominance hierarchies (Type A). When contest competition within groups prevails, groups of female relatives would develop nepotistic and despotic dominance hierarchies (Type B). Under

intermediate or high predation pressure, when foods occur as in Type A, scramble competition would be expressed within groups while contest competition would be expressed between groups, leading to philopatric females and egalitarian dominance hierarchies (Type C). Finally, under low predation pressure, when population density is high relative to the food supply, contest competition between groups would be favored and female relationships within groups would be nepotistic but with egalitarian dominance hierarchies (Type D). He did not consider scramble competition between groups sufficiently important to affect female social relationships.

This socioecological model was amended by Sterck, van Schaik, and Watts (1997), who argued that van Schaik's initial model could not explain all types of female relationships in multi-female social groups. It ascribed new labels to Types A–D: A was now Dispersal–Egalitarian, B was Resident–Nepotistic, C was Resident–Egalitarian, and D was Resident–Nepotistic–Tolerant, based on the intensity of contest competition. For the first time in the field of socioecology, a distinction was made between "ecological models" and "socioecological models." According to Sterck et al., all others were "ecological models," whereas theirs was a "socioecological model" because, along with the ecological factors already described, their model incorporated the social component of infanticide avoidance. They proposed that the risk of infanticide was sufficiently strong that under the condition of low predation and low competition females would readily disperse from their natal groups to form strong associations with protective males, leading to the Dispersal–Egalitarian group (similar to Wrangham's non-female-bonded type of female).

Its label as "The Socioecological Model" has been confusing and unfortunate for two reasons. First, while the introduction of infanticide as an influence on female social behavior was perhaps novel (because Wrangham did not specify the form of male harassment toward females in his non-female-bonded groups when he argued that such females would form groups around protective males), earlier socioecological models almost always included social behavior in their formulations, especially with regard to male–male competition for females and male residence in female groups. Second, criticisms of that model have led to a questioning of the entire conceptual model approach that has been the mainstay of socioecology. Thierry (2008), for example, argued that "The Socioecological Model" is so fraught with problems and inconsistencies that it only reveals that there can be no unified model to explain the diversity of primate social organizations. While the case can be made that the conceptual model proposed by Sterck et al. is flawed, it does not mean that other socioecological models should be abandoned before being tested.

One such socioecological model is the "dispersal/foraging efficiency" model (Isbell 2004). It begins with the position that because dispersal can be costly, even to the point of death, mothers can increase their reproductive success by allowing their daughters to stay in the natal home range whenever possible. What makes it possible, according to this socioecological model, is whether the mother has the ability to expand her home range to accommodate her daughter's potential offspring, and this in turn depends on the extent to which the mother is constrained energetically in her foraging movements. Females that are so energetically constrained that missing a meal would be a hardship require foods that occur in highly predictable, dependable locations. Such females will not be able to expand their home ranges easily or share their home ranges with other reproductively active females, partly because expansion of home ranges involves going into new areas, which, by definition, have uncertain food locations, and partly because other females would make food locations more uncertain if they eat there first. These females are predicted to travel directly from food site to food site. At the other extreme, females far less energetically constrained such that frequent failure to find food is not a hardship will be able to expand their home ranges and share them with other reproductively active females, because they are not as adversely affected by uncertainty as to where their foods are located. Such females are predicted to meander and forage more while moving toward major food sites.

According to this socioecological model, the degree to which mothers are able to allow their reproductive daughters to stay determines female grouping patterns, and then males build upon what the females do. This creates the mating

system (monogamy, polygyny, or polyandry). Females that are highly energetically constrained will have male counterparts that are similarly constrained and require certainty in food locations. Such males will limit themselves to one reproductively active female's home range and will travel as females do, by moving directly from food site to food site. Male counterparts to females that are less energetically constrained will not limit themselves to one reproductively active female's home range and will similarly travel more circuitously, searching for foods while moving toward major food sites. Accordingly, there are five types of social organizations defined by the movements and ranging behavior of reproductively active females, with mating systems mapped onto them:

- *Stingy mothers* have minimal home range overlap at most with other reproductively active females, including their adult daughters. In all cases, female offspring either disperse at sexual maturity or remain but do not reproduce (through hormonal or behavioral suppression). Individuals are predicted to move directly between major food sites without foraging along the way. With some exceptions, males map onto these home ranges such that they have access to only one reproductively active female. Exceptions are species in which males remain philopatric and can gain inclusive fitness benefits from sharing mating access to a given female. The mating system will be social monogamy or, when males are philopatric, polyandry. Examples: *Perodicticus*, *Callithrix*, *Hylobates*, some individuals of *Pan*.
- *Generous mothers* share large portions of their home ranges with their adult daughters, but they do not typically travel together. Individuals are predicted to meander more in their movements between major food sites compared with "stingy mothers." Males map onto female home ranges such that they have access to multiple reproductively active females. The resulting mating system will be polygyny. Examples: *Galago*, *Microcebus*, *Pongo*, some individuals of *Pan*.
- *Incomplete suppressors* share their entire home range and travel together with their reproductively active daughters and other related, reproductively active females. Individuals are predicted to exhibit both meandering and goal-directed travel between major food sites but more goal-directed travel. Home range boundaries are stable over generations, and once the number of females reaches the maximum for that home range, reproduction by low-ranking females is discouraged, for instance, by targeted aggression, sometimes leading to expulsion from the group. The number of males associating with such groups depends on the ability of individual males to monopolize access to the females within a group. The mating system will be polygyny. Examples: *Alouatta seniculus*, *Lemur catta*.
- *Facilitator mothers* share their entire home range and travel together with their reproductively active daughters and other related and reproductively active females. Individuals meander more than they move directly between major food sites. The number of females in a group is unconstrained by home range area because home ranges are expandable. The number of males associating with such groups depends on how well males can monopolize access to the females. The mating system will be polygyny. Examples: all cercopithecines, *Cebus*.
- *Indifferent mothers* live in groups with other adult females, but they neither suppress nor facilitate their adult daughters' reproduction. Females have little fidelity to a particular home range or group, and the movements of individuals are predicted to be influenced less by the meandering/goal-directed dichotomy than by male social behavior. The mating system will be polygyny. Examples: *Procolobus*, *Gorilla*.

This latest socioecological model allows for variation in grouping patterns within populations and species depending on the interplay between ecology and evolved internal constraints (which could contribute to phylogenetic patterns in social behavior that are now being more carefully considered). It limits itself to dispersal/philopatry for providing the underlying kinship structure, and it offers testable predictions but does not make predictions about finer details of female social relationships. True to the original intent of traditional socioecological models, it focuses on

identifying the ecological conditions responsible for diversity in social organization, while also recognizing the modern issue of phylogenetic conservatism in the form of evolved energetic constraints.

SEE ALSO: Dispersal; Foraging Strategies; Grouping Patterns; Inclusive Fitness; Infanticide; Kinship; Mating Systems; Predation; Social System (Social Structure)

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