Socioecological model

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Primate socioecology is the study of ecological determinants of primate social organizations, and its main approach to explaining the wide diversity in primate social organizations has been the conceptual comparative model. 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 (see DISPERSAL) (of which very little was known at the time), sexual dimorphism (see SEXUAL DIMORPHISM (NONHUMAN PRIMATES)), and presence or absence of territoriality (see TERRITORY). They proposed that variation in grades is attributable to differences in habitat, diel activity, and diet. For instance, the main ecological conditions favoring Grade I solitary primates were 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 favoring Grades IV and V large-group-living primates was open environments, such as forest fringes, "tree savannahs," grasslands, and arid savannahs, the assumption being that these are associated with high numbers of predators that 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 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 building upon natural history and observations from field studies developed the "age-graded" concept in which certain demographic conditions—that is, maturation and philopatry of natal males—were responsible for observed transitions from single males to multiple males in social groups (Eisenberg, Muckenhirn, and Rudran 1972).

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 models would have particularly strong effects on later conceptual socioecological models. The first was the concept of inclusive fitness (see KINSHIP), that natural selection can still favor individuals acting in ways that are immediately harmful to themselves if they ultimately gain fitness benefits through 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 putting conspecifics between themselves and the predator. 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 females being viewed as the "ecological sex" and to males 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

The International Encyclopedia of Biological Anthropology. Edited by Wenda Trevathan.
© 2018 John Wiley & Sons, Inc. Published 2018 by John Wiley & Sons, Inc.
DOI: 10.1002/9781118584538.ieba0458
Based in part on Isbell, L. A. (2017). Socioecological Model. In Fuentes, A. (ed.) *The International Encyclopedia of Primatology*, John Wiley & Sons, Inc., with permission.

to social organizations became possible. Their development and application continued to support and refine the hypothesis that ecology underlies differences in social organization. Clutton-Brock and Harvey (1977) conducted one of the most comprehensive early statistical examinations. Reminiscent of Crook and Gartlan (1966), they classified primates into seven categories by diel activity, substrate use, and diet (see FORAGING STRATEGIES). 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, and, since larger-bodied primates cannot rely on crypsis, they live in groups as a defense against predators.

Shortly thereafter, Wrangham (1980) proposed that it was unnecessary to consider predation because food alone could explain certain types of primate groups. Incorporating the idea that females as the "ecological sex" map onto food abundance and distribution for greater reproductive success, Wrangham focused on explaining the evolution of multi-female groups based on characteristics of food in what he called an "ecological model." He proposed that the spatial distribution of foods determines not only the formation of multi-female groups but also the nature of female social relationships within and between multi-female groups. Foods that are spatially clumped would favor competition among females, and larger groups of females would form to gain a competitive advantage over smaller groups. Such groups would be composed of related females because of the inclusive fitness benefits of competing together against non-relatives. By definition, females in these groups would be philopatric, with a suite of other characteristics, including differentiated dominance and grooming relationships (see DOMINANCE (SOCIAL)). He called such groups "female-bonded." Wrangham also hypothesized that female-bonded groups would have control over the number of adult males residing in their groups. They would allow in only one 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 them 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. He called such females "non-female-bonded." Wrangham's model began the next phase of socioecological models with its more focused attention on the behavior of females.

van Schaik (1989) challenged Wrangham's model with an alternative that began with the assertion that multi-female groups were initially favored by predation pressure. Otherwise it was in agreement with Wrangham's model that food competition could explain female social relationships within and between groups. According to van Schaik's socioecological model, under high predation pressure, competition would occur mainly within groups. His was the first to incorporate two distinct types of competition, contest and scramble competition. Contest competition is direct and visible, and would be generated by spatially clumped, monopolizable foods (fruits). In contrast, scramble competition is indirect, and reduces energy intake equally for all group members. It would be generated by foods occurring in patches that, relative to group size, are either very small and cannot be monopolized (insects) or very large (leaves). In this model, female social relationships differ as a result of varying degrees of contest and scramble competition within and between groups. van Schaik hypothesized that when scramble competition predominates within groups, females in multi-female groups would develop individualistic, egalitarian dominance hierarchies (Type A). When contest competition predominates within groups, groups of female relatives would develop nepotistic, 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 later amended by Sterck, van Schaik, and Watts (1997). They assigned 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. Importantly, 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 it also incorporated the social component of infanticide avoidance (see INFANTICIDE). 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).

Its label as "the Socioecological Model" has been 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), earlier socioecological models almost always included social behavior in their formulations, especially with regard to male–male competition and male residence in female groups. Second, recent 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. As an alternative, he argued that phylogeny better explains different grouping patterns (Thierry 2013).

A more recent socioecological model still in need of testing is the "dispersal/foraging efficiency" model (Isbell 2004). This model limits itself to dispersal/philopatry for providing the underlying kinship structure, does not make predictions about female social relationships, and offers testable predictions. True to the intent of the earliest socioecological models, it focuses on identifying the ecological conditions responsible for diversity in primate social organizations from nocturnal, solitary foragers to large, diurnal, multi-female groups, while also incorporating the modern issue of phylogenetic conservatism in the form of evolved energetic constraints.

SEE ALSO: Grouping patterns in nonhuman primates; Mating systems (primates)

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FURTHER READING

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