

Females, Food, Family, and Friendship

For much of the last twenty years, females have occupied center stage in theoretical and empirical analyses of primate social organization. Richard Wrangham¹ was one of the first to give females top billing, when he suggested that sociality has evolved in primates because it enhances females' access to resources. Female nutritional needs drive the plot because female fitness is largely determined by their access to resources, while male fitness is mainly affected by their access to receptive females. This means that females distribute themselves in space according to how their food is distributed, and males go where females are. Many have criticized Wrangham's plot line, arguing that predation provides the primary selective factor favoring sociality in primates² and that sociality creates dramatic tension by producing substantial intragroup competition for resources.

Although we probably will never be certain why sociality first evolved among primates, there is wide agreement about the rest of the story: Resource competition among females drives the evolution of primate social organization. Resource competition can take different forms—there can be scramble or contest competition, and both can occur within or between groups. Many researchers have explored the dimensions of this space, generating models that bear reassuring similarities to one another.^{2–4} For example, when within-group contest competition is strong and between-group contest competition is weak, we expect to see strong female dominance hierarchies, matrilineal alli-

ances, female philopatry, well-differentiated female relationships, and male dispersal. On the other hand, when within-group contest competition is weak and between-group contest competition is strong, we expect to see egalitarian dominance relationships among females, group-level coalitions against other groups, female philopatry, and poorly differentiated female relationships.⁴

Socioecological models shine the spotlight on females, and primatologists have spent much of the last twenty years collecting data on female life histories, feeding behavior, and social relationships. Some of this work was designed explicitly to test predictions derived from socioecological models, and featured pairwise comparisons of carefully selected species. For example, Mitchell, Boinski, and van Schaik⁵ compared the behavior of closely related species of squirrel monkeys that live in different habitats but rely on different kinds or resources; Isbell and her colleagues^{6,7} are studying two sympatric guenons that focus on different types of resources; and Koenig and his colleagues⁸ compared Hanuman langurs occupying different types of habitats in India. These comparisons mainly fit predictions derived from socioecological models⁹ and have confirmed females' place as lead characters in the story of how sociality evolved among primates.

One of the primary messages of socioecological models is that social relationships among females have adaptive value. This idea seems completely obvious to most of us now, but we should remember that it was not part of the received wisdom when Wrangham published his paper on primate social organization in 1980. At that time it was widely assumed that there was little systematic variation in female reproductive success. As a Ph.D.

student in the late 1970s, I was advised by a well-respected primatologist not to study the sources of variation in reproductive success among female bonnet macaques because I wouldn't find any. But I did, and so have many primatologists since then.^{10–13}

If female reproductive success varies, then we can ask how the form and features of females' social relationships contribute to variability in their fitness.¹⁴ Widespread (but not universal) evidence that female dominance rank influences reproductive performance provides the first clue that social relationships do have adaptive value for females. The strong bonds among maternal kin, nepotistic coalitions, and matrilineal dynasties that we see among baboons, macaques, and vervets provide further evidence that social relationships have fitness consequences for females.

Socioecological analyses sketch the rough outlines of female behavior, documenting the fraction of reversals in dominance matrices, the existence of coalitions during within- and between-group conflicts, the extent of differentiation in female grooming networks, and dispersal patterns. Information about the detailed structure and quality of female social relationships comes from a different branch of primatology. This body of work focuses explicitly on relationships, taking as given that animals live in social groups. This research tradition blends Robert Hinde's emphasis on the dialectic between social interactions, social relationships, and social interaction and Hans Kummer's insight that natural selection guides investment in social relationships that have adaptive value for individuals.

Research on the dynamics of social relationships spans proximate and ultimate levels of analysis. For example, de Waal and his colleagues¹⁵ have ar-

gued that peaceful interactions after conflict (reconciliation) mend social relationships that have been frayed by conflict, while I have suggested that reconciliation provides a timely signal that conflict has ended.¹⁶ Dunbar¹⁷ has emphasized the role of social grooming in creating and maintaining social bonds. There is also a growing interest in how social relationships are calibrated: What do animals know about their own relationships and the relationships of others? How do they regulate the exchange of cooperative interactions that sustain social bonds? And how do they navigate the uncertainties and conflicts of interest that arise in social life?

Other work on social relationships addresses the evolutionary forces that structure social interactions and shape social relationships. Many primates behave as if they had been tutored in the principles underlying kin selection, showing nepotistic biases in most forms of cooperative behavior, including grooming, alliance formation, and food sharing.¹⁸ Others provide good evidence for reciprocity, trading favors in the same currency or swapping one form of altruism for another.^{19–22}

Much of the work on the dynamics of social relationships focuses on females for the same reason that Willy Sutton robbed banks—that's where the money is. For reasons that socioecological models make clear, social relationships, particularly social bonds that extend beyond dominance relationships, are generally a more profitable long-term investment for females than for males.

A group of primatologists gathered at the recent meetings of the International Primatological Society in Adelaide, Australia, to consider what we have learned over the last twenty years about the form and function of primate social relationships. The symposium, entitled "What are Friends For? The Adaptive Value of Social Bonds," was intended to provide a forum for presenting new data on the nature of social relationships among primates, mainly females, and to explore the evolutionary forces that shape these relationships and generate adaptive consequences. (Most of the papers presented at the symposium

will be published in a forthcoming issue of *Behaviour*).

Several of the papers presented in the symposium were explicitly rooted in socioecological models. Lynn Isbell and Truman Young (Davis) compared and contrasted socioecological models, delineating commonalities between the models and pointing out their differences. Sue Boinski (Florida) presented new data on a third species of squirrel monkeys from Surinam. At first glance, Surinamese squirrel monkeys seem to challenge socioecological models because resource competition among them is intense, but female bonds are quite weak. However, these monkeys rely on foods that occur in small, dense clumps that feed only one, making cooperation in resource defense unprofitable. Ronald Noë (Strassburg) described the ecology and social

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behavior of three sympatric colobine species in the Tai Forest, and suggested that they may represent different peaks in the adaptive landscape.

But not all data fit neatly into socioecological models. Anne Pusey (Minnesota) presented data from long-term studies of chimpanzees at Gombe that contravene the notion that female dispersal is typically associated with an absence of feeding competition among females. Her analyses reveal that immigrant females face stiff competition from resident females, and that such competition is directly reflected in females' reproductive performance. Marina Cords' (Columbia) analysis of blue monkeys suggests that they do not fit neatly into socioecological categories either. Females cooperate in inter-

group encounters, but rarely form coalitions in within-group contests. However, females have quite well-differentiated social relationships and stable linear dominance hierarchies.

Karen Strier (Wisconsin) discussed social relationships among male muriquis, a species that contradicts nearly all of our generalizations about primate social relationships: Males form closer ties than females do; bonds are strong, but grooming is rare; males rarely fight and freely share access to resources, even receptive females. Louise Barrett and Peter Henzi (Capetown) raised questions about the essential nature of social relationships among female baboons, suggesting that females often use grooming for strategic purposes such as gaining access to newborn infants, not for building long-term social bonds. They speculate that monkeys are simply not smart enough to manage the accounting problems that long-term reciprocity in multiple currencies would present.

Several of the papers considered proximate factors that influence the development of social relationships. Thus, Filippo Aureli and Colleen Schaffer (Liverpool) addressed the role of emotion, particularly anxiety, in regulating social interactions that shape social bonds. Jeanne Altmann (Princeton) considered the role of demography in defining individuals' social options and shaping their adaptive outcomes.

Finally, Anja Widdig and her colleagues presented a remarkable set of data indicating that monkeys can recognize paternal kin. Using genetic data to identify paternal kin and behavioral data to assess social relationships, Widdig and her colleagues showed that female rhesus macaques on Cayo Santiago display strong affinities for paternal kin. The monkeys seem to rely on two kinds of cues to recognize paternal kin. First, they show marked preferences for age-mates. Similarity in age is likely to be a good proxy for kinship when one male monopolizes mating activity,²³ and this holds true on Cayo Santiago. But females also prefer paternal kin over unrelated females when they interact with nonpeers. This suggests that monkeys may be able to recog-

nize paternal kin from phenotypic cues alone. These results are consistent with an independent dataset from Amboseli;²⁴ if widely replicated, they will radically change our interpretations of the evolutionary basis of social behavior in primate groups.

The diversity of the papers presented at this symposium reflects the diversity of ongoing work on primate social relationships. This is an extremely healthy development in the field. However, the diversity of the papers also illuminates the gaps in our knowledge of primate social relationships. We still know relatively little about many primate species, making it difficult to test socioecological models broadly or to be confident that we have sampled the full range of social solutions to ecological problems. Methods for studying primate social relationships are poorly developed and inadequately validated, limiting our ability to assess relevant elements of social relationships and to draw comparisons among dyads, groups, or species. We have largely assumed that social relationships exist, and that they are roughly analogous to human friendships, although we have little evidence that close bonds extend beyond kin boundaries or that these relationships have any or all of the properties that we associate with our own friendships. Finally, although theory tells us that social relationships have adaptive value for females, empirical support for this proposition is quite limited. We do not know whether or how variation in the quality of social

relationships across individuals contributes to variation in fitness among individuals in primate groups. A lot of work still needs to be done to understand the connections among females, food, family, and friendship in nonhuman primates.

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