

Primate Socioecology at the Crossroads: Past, Present, and Future

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Attempts to explain differences in the size and structure of primate groups have argued that they are a consequence of variation in the intensity of feeding competition caused by contrasts in food distribution. However, although feeding competition can limit the size of female groups, many other factors affect the costs and the benefits of sociality to females and contribute to differences in group size. Moreover, interspecific differences in social relationships between females, in female philopatry, and in kinship between group members appear to be more closely associated with variation in life-history parameters, reproductive strategies, and phylogeny than with contrasts in food distribution or feeding competition. The mismatch between predictions of socioecological theory and observed variation in primate social behavior has led to protracted arguments about the future of primate socioecology. We argue that future attempts to understand the diversity of primate societies need to be based on an approach that explores separate explanations for different components of social organization, combines ecological and phylogenetic information, and integrates research on primates with similar studies of other groups of mammals.

Over the last forty years, primate biologists have devoted much time and effort to attempts to establish relationships between variation in

primate social behavior and ecological parameters.^{1–8} Attempts to demonstrate systematic relationships between social organization and ecological parameters were initiated by J. H. Crook, who had previously shown that interspecific differences in the size of weaver bird (*Ploceidae*) colonies and the structure of their nests was consistently related to the habitats they occupied, which ranged from tropical rainforests to semi-arid savannahs.⁹ In 1966, Crook and Gartlan published a short paper in *Nature*¹ arguing that primate societies could be allocated to different categories associated with major differences in habitat and associated selection pressures, suggesting that the smallest groups were found in forest-dwelling arboreal species where the risk of predation was low and resources were abundant, while the largest groups occurred in terrestrial, savannah-dwelling species where predation risks were relatively high and resources were widely distributed.

A BRIEF HISTORY OF PRIMATE SOCIOECOLOGY

As the range of primate field studies increased, it became apparent that some arboreal forest-dwelling primates lived in groups as large as those of terrestrial savannah-dwelling species and that species living in the same habitat might be subject to contrasting selection pressures associated with more detailed contrasts in their diet or anti-predator strategies.¹⁰ Suggested relationships between specific aspects of social behavior, such as group size and range size, and particular ecological parameters, such as habitat or diet type, were subsequently tested using quantitative interspecific comparisons.^{2,11} For example, quantitative analyses showed that diurnal primates live in consistently larger groups than do nocturnal species; that home range size and day range length increase with group size and body size and are larger in frugivores than folivores¹²; that sexual dimorphism in body size and relative canine size are larger in polygynous species than (socially) monogamous ones^{13,14}; and that males of species that live in multi-male, multi-female groups, where the likelihood of sperm competition is likely to be relatively high, have relatively large testes compared to males of species that live in heterosexual pairs or in uni-male groups.¹⁵ While the exploration of interspecific correlations between social and ecological variables suggested answers to some questions about the evolution and ecology of primate societies, they provided little insight into the distribution of other traits, including the distribution of

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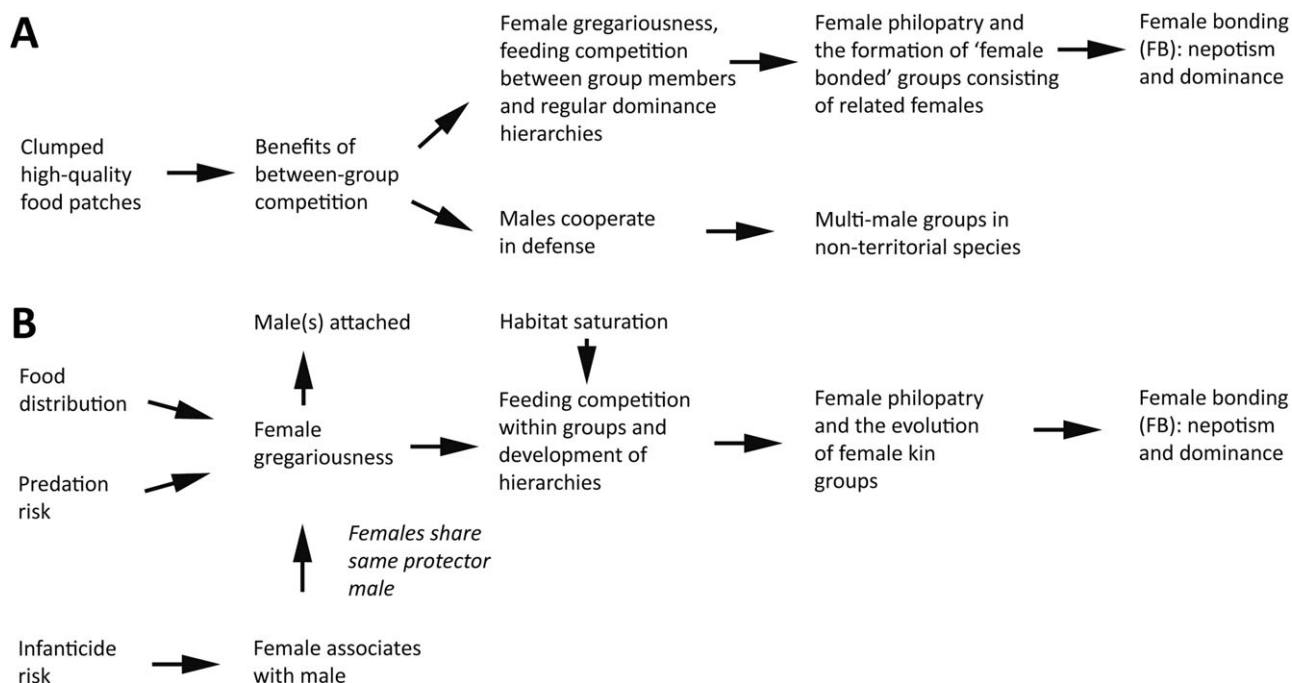


Figure 1. A. Flow diagram of Wrangham's³ explanation of the evolution of female groups. B. Flow diagram of Sterck, Watts, and van Schaik's⁶ explanation of primate societies incorporating effects of male infanticide and habitat saturation.

dominance hierarchies, coalitionary behavior, and kinship structure.

During the 1970s, comparative studies of several groups of mammals, including ungulates, bats, and primates, argued that the distribution of resources could affect the intensity of feeding competition and the costs of sociality, and suggested that these factors might play an important role in constraining the size of social groups.^{2,10,16,17} In 1980, an influential paper by Wrangham³ suggested that variation in food distribution and associated differences in the intensity of feeding competition among primates could account for interspecific differences in group size, as well as differences in female social relationships and dispersal patterns. Wrangham suggested that where the distribution of resources generates regular or intense competition for patchily distributed food, selection is likely to favor the formation of dominance hierarchies and the defense of resources by stable groups of related, natal, females (Fig. 1). He argued that, in contrast, where food items are of low individual value or are evenly distributed and feeding competition is less

intense, the benefits of resource defense and the formation of stable kin groups should be reduced, dominance relations between females should be less consistent, and females should be more likely to disperse. One novel feature of his argument was the suggestion that improvements in the ability of larger groups to displace smaller ones in competition for food resources was the principal factor favoring the evolution of sociality rather than improvements in the ability of individuals to detect predators to defend themselves against attacks. Wrangham referred to his explanation of variation in the size and structure of primate groups as a model; the logical framework that he outlined in his paper came to be referred to as the "Socioecological Model" of primate social organization, although it incorporated no formal modeling.

It quickly became apparent that while the Sociological Model generated widespread interest among primatologists, it had important limitations. It focused on the role of contest competition in promoting female sociality and ignored the consequences of scramble competition for

resources and their effects on the evolution of female groups.¹⁸ It assumed that predation played little part in maintaining sociality in primates, despite evidence of the importance of predation in other social vertebrates.¹⁹ It also did not consider the role of male reproductive strategies and life histories on the evolution of social organization and social structure in females. There were also more specific problems. In particular, the model did not provide a satisfactory explanation of the evolution of social groups in species that do not defend resources. Moreover, it did not explain why, in species where individual food items are of low quality and evenly distributed, females should disperse rather than remain in their natal group, thereby avoiding the risks of dispersal.^{5,20,21} Several differences in female philopatry between pairs of related species, including hamadryas and gelada baboons and red and black-and-white colobus monkeys, did not appear to support the prediction that female philopatry should be associated with clumped food supplies and intense feeding competition or that habitual female dispersal should be

associated with a more even distribution of resources and reduced competition for food. In addition, several pairs of species that differed in diet and food distribution (like chimpanzees and gorillas) failed to show the predicted contrasts in dispersal.

In other areas of behavioral ecology, scientists responded to the increasing evidence of the complexity and diversity of interspecific differences in social behavior by abandoning unitary explanations of social organization and focusing their attention on the evolution of specific aspects of social and reproductive behavior.^{22,23} While some primatologists followed the same course, others responded to the limitations of the Socioecological Model by adding refinements and additional categories. Subsequent versions incorporated the effects of the risk of predation on group size, and distinguished between the consequences of scramble and contest competition within and between groups,^{5,6,18,24–26} generating a quantitative, four-part “taxonomy” of competitive regimes: within-group scramble (WGS), within-group contest (WGC), between-group scramble (BGS), and between-group contest (BGC). Van Schaik⁵ merged these new distinctions with Wrangham’s 1980 model, postulating that predation risk is sufficient to explain why females form groups in many primates, but food dispersion determines whether females form alliances with kin. He argued that, when food is clumped, WGC would be the dominant regime, and related females would benefit by joining forces to gain or defend access to food patches against other females in the same group. In contrast, he suggested that when food is not clumped, WGS is more important. In this setting, females gain little from food defense and should not be constrained to be nepotistic or philopatric so that female dispersal is more likely. Subsequently, Isbell²⁴ recognized a third possibility: groups of females with strong BGC over territories rather than food patches and limited WGC, producing philopatry without strong dominance or obvious nepotism.

TABLE 1. The Synthetic Socioecological Model (from Thierry³¹)^a

Social Syndrome	Ecological Conditions		Competitive Regime				Behavioral Expression			
	Predation Risk	Food Distribution and Population Density	Within-Group		Between-Group		Dominance Asymmetry	Coalition Formation	Nepotism	Dispersal
			Scramble	Contest	Scramble	Contest				
Dispersal-egalitarian	High	Food dispersed Low density	High	Low	Low	Occurrence	Weak	Rare	No	Common
Resident-egalitarian	High	Food dispersed High density	High	Low	Low	High	Weak	Rare	No	Rare
Resident-nepotistic	High	Food clumped Low density		High	High	Low	Strong	Common	Yes	Rare
Resident-nepotistic-tolerant Missing information means no assumption.	Low	High density		Potentially high		High	Variable	Common	Yes	Rare

^a The model assumes that variation in predation risk and the abundance and distribution of food resources shape the relationships of females by determining the competitive regimes to which they are submitted. When predation risk is high, animals form cohesive groups to reduce it. According to variation in food distribution and population density, group living may generate three different social syndromes: dispersal-egalitarian, resident-egalitarian, and resident-nepotistic. These syndromes correspond to different levels of contest and scramble competition within or between groups that influence female reproductive success. Within-group competition increases with group size. If some individuals can exclude others from food patches, within-group contest competition prevails. If food is dispersed, scramble competition predominates within groups, but contest competition between groups may be more or less elevated, depending on population density; when habitat is saturated, between-group competition is elevated. A low predation risk produces a fourth social syndrome: resident-nepotistic-tolerant. This results from relatively high within- and between-group contest. Competitive regimes induce different patterns of social relationships. Contests for clumped food lead females to make coalitions with kin. High within-group contest is conducive to strong dominance asymmetry, which translates into stable hierarchies and the use of formal signals of submission. Dispersal does not occur when females need to cluster with relatives to win aggressive contests. In some dispersal-egalitarian species, where scramble competition does not entail significant costs, females gather in groups to reduce rates of infanticide by males aiming to improve their access to reproductive females by shortening the time to fertility.³¹

An extended version of the Socioecological Model by Sterck et al.⁶ incorporated many of these issues (see Table 1). Like Wrangham's original model, it was based on the proposition that where the distribution of resources generates strong foraging competition for patchy resources between group members, dominance hierarchies and supportive coalitions are likely to develop, females should associate with relatives, the social costs of dispersing should be high, and females should be philopatric, generating "resident-nepotistic" societies. It suggested that, in contrast, dominance hierarchies and coalitions are less likely to develop where direct competition between group members is weak and constraints on female immigration into established groups may be relaxed, so that the costs of dispersal are low and females may commonly leave their natal group to minimize scramble competition for resources, generating "dispersal-egalitarian" societies. This version of the model also recognized that strong intergroup competition for resource patches can favor female philopatry even if direct competition for resources within groups is weak, generating "resident-egalitarian" societies. It suggested that competition within groups is likely to be a stronger evolutionary force than is competition between groups,⁵ so that "resident-egalitarian" societies should be less common than "resident-nepotistic" ones.⁶ A final addition was a recognition that interdependence between group members resulting from intergroup competition can favor tolerant relationships and low reproductive skew, even if intragroup competition is intense, producing "resident-nepotistic-tolerant" societies.⁶

The considerable complexity of later versions of the Socioecological Model made adequate tests of its assumptions and predictions no easier; and many of the assumptions and predictions of the Socioecological Model were (and still are) difficult or impossible to test. Attempts to generate quantitative measures of resource distribution that can be used to compare species are complicated by contrasts in the spatial scale at which resources are clumped, as

well as by differences in the predictability of resources over time. Measures of the "patchiness" of resources have mostly used botanical indices, such as Morista's Index, which were not developed to gauge feeding competition.¹⁸ A further problem is that the effects of contrasts in food distribution on feeding competition are likely to differ between species of different size, digestive capacity and passage rate, locomotor costs, inter-individual spacing, and life histories. As studies of primate feeding ecology developed, it became increasingly clear that gross dietetic categories did not necessarily reflect either the distribution of food resources or the intensity of foraging competition.^{27,28} Quantitative comparisons

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of the effects of intergroup competition, the consistency of female dominance relationships, and the effect of dominance on female breeding success were still unavailable. It also became clear that some level of female dispersal occurs in almost all primate societies and that contrasts in the frequency of female dispersal are quantitative rather than qualitative.

A further factor complicating attempts to relate variation in social behavior to contrasts in ecology was the increasing evidence that related species often have similar patterns of social organization, despite contrasts in feeding ecology^{29–31} and the fact that relationships between ecological

parameters and social behavior differ between phylogenetic groups.^{32,33} Studies of feeding behavior showed that foraging patterns and food selection vary widely between populations of the same species.³⁴ To minimize the complicating effects of phylogeny, various studies explored correlations between social behavior and feeding ecology across different populations of the same species, across different social groups or, in some cases, across different individuals.^{28,35} However, while this approach minimized the influence of phylogenetic factors, it faced the problem that few studies were able to compare sufficient numbers of populations or groups to demonstrate significant correlations between feeding ecology and social behavior, so that firm generalizations were scarce. In addition, intraspecific comparisons commonly had difficulty in distinguishing between the effects of variation in food distribution and contrasts in food abundance. Differences in population density and group size between populations complicated attempts to identify the effects of variation in food distribution on interactive rates and social structure.

PRIMATE SOCIOECOLOGY TODAY

The Socioecological Model is still commonly invoked by primatologists to explain the diversity of primate societies and continues to play an important role in setting the agenda for comparative research on social behavior. However, there is widespread disagreement about the validity of its assumptions and the accuracy of its predictions. While some primatologists believe that the existing model still provides a useful framework for explaining the diversity of primate societies,^{26,36–38} others are skeptical of its assumptions or emphasize that the distribution of contrasting patterns of social organization is inconsistent with its predictions and may be more closely related to phylogenetic differences than to ecological ones.^{31,39,40} This has led to suggestions for further improvements or refinements of the

model, including arguments that the relevant characteristics of resource distribution and density require more specific definition and more accurate measurement^{36,37,41,42}; additional explanatory factors need to be incorporated^{26,39,43}; the verbal logic of the model should be tested using formal modeling^{44,45}; tests of the model should use phylogenetically controlled analyses³⁸; and comparisons should be restricted to groups of closely related species.⁴⁵ In contrast, others argue that the Socioecological Model has now outlived its usefulness, or even that attempts to relate variation in social behavior to ecological parameters should be abandoned altogether.³¹ Studies of primate socioecology have consequently reached a crossroads. Which way should they go?

A necessary first step is a realistic assessment of the successes and limitations of the existing Socioecological Model. In accounting for the diversity of primate societies, the ideal solution would be a quantitative analysis of interspecific differences in the different behavioral and ecological parameters incorporated in the model in order to measure the degree of association between them; to determine whether it is useful to allocate primate societies to discrete categories and, if so, how many; and to establish whether contrasts in resource distribution and feeding competition are consistently associated with each other in the way that the Socioecological Model predicts. As yet, quantitative estimates of most of the parameters considered by the model are still unavailable and no analysis has attempted a formal test of the degree of association between parameters. We consequently have to rely on qualitative assessments of the evidence supporting its assumptions and predictions. Since there is little reason to suppose that the ecological processes affecting the evolution of social behavior in primates are fundamentally different from those affecting the evolution of social behavior in other groups of mammals, we also consider the extent to which the Socioecological Model explains variation in social behavior in other groups of mammals.

One difficulty in assessing the model is that its structure and predictions are often interpreted in different ways by different researchers. Consequently, we concentrate on three of its most fundamental propositions: that intergroup competition and predation risk favor the evolution of female sociality while, in species that rely on clumped resources, increased feeding competition in larger groups constrains female group size; that variation in the consistency of female dominance relations and the effects of rank on

original usage of “social organization” to refer to contrasts in group size, group stability, and intergroup relations and “social structure” to refer to dominance hierarchies and other aspects of social relationships between individuals,⁸ others have redefined the two terms and reversed their meanings.²⁸ Throughout this review, we use “social organization” and “social structure” in the same way as Crook and use “social behavior” to refer to all aspects of social behavior.

Sociality and Group Size

The explanation of differences in group size proposed by current versions of the Socioecological Model incorporates three main propositions: that group-living reduces the *per capita* risk of predation and improves success in agonistic encounters between groups; that it affects the intensity of competition for resources between group members and that this effect is strengthened by uneven distribution of resources in space and time; and that where resources are unevenly distributed, the increasing intensity of foraging competition in larger groups offsets the benefits of sociality and constrains group size.

All three of these propositions are common to explanations of sociality in many other social animals and are supported by research on primates as well as on a wide variety of other social animals^{8,12,26,32,33,48–53}.

1. In both primates and other diurnal mammals, there is considerable evidence that sociality reduces predation risk,^{6,32,54–57} although much of that evidence is circumstantial and quantitative studies of predation rates are scarce and do not necessarily reflect predation risk.^{58,59} There are several lines of evidence: larger groups⁶⁰ or associations⁶¹ are usually more likely to detect predators while individuals spend less time alert and more time foraging; when there is a threat of attack, individuals bunch together or move toward larger or stronger group members⁵⁷; and studies of carnivores provide direct evidence that sociality can reduce the risk of predation by show-

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female fitness are consequences of variation in the intensity of foraging competition and the distribution of food resources; and that where food is unevenly distributed and foraging competition is intense, females are likely to remain in their natal group and form long-lasting bonds with relatives, whereas where food is more evenly distributed and feeding competition is less frequent, they are more likely to disperse to breed. Like previous authors, we focus on the behavior of females on the grounds that the distribution and behavior of males is governed principally by the distribution of available mating partners.^{46,47} An idiosyncrasy of research on primate social behavior is that, while some authors follow Crook's

ing that the hunting success of predators is higher when their prey are solitary than when they are in groups.^{62,63} In addition, comparative studies suggest that the risk of predation is important in maintaining sociality. Diurnal primate species living under high risk of predation typically aggregate in large, stable groups.^{32,48} Intraspecific comparisons suggest that groups tend to be larger and more cohesive where individuals are exposed to high rates of predation than where predation is scarce.^{35,55,64} There is also extensive evidence that competition between neighboring groups is common in social mammals. Larger groups usually displace smaller ones from resources and can often obtain priority of access to resources,^{3,65} although the energetic consequences of displacements on food intake have rarely been measured⁶⁶ and female reproductive success in primates seldom increases with group size.⁶⁷ In several social animals, including chimpanzees, lions, meerkats, and some social insects, larger groups regularly attack members of smaller neighboring groups, sometimes killing juveniles or adults.⁶⁸ Repeated interactions between large and small groups can lead to range loss, reductions in breeding success or survival and, in some cases, to the extinction of smaller groups.^{3,21,69} Finally, where several individuals disperse from their natal group together, the chance that individuals will successfully establish a new breeding group is often related to the number of individuals that leave together, which in turn depends on female group size, so that larger groups are more likely to produce successful emigrants.^{70,71}

2. Studies of a wide range of social mammals have shown that the intensity of scramble and contest competition for resources typically increases with group size.^{32,72} For example, within and among frugivorous primate species, home range size and day range length increase with group size.^{32,53,73} Similarly, studies of several social mammals have shown that the frequency of within-group agonistic interactions over resource access rises with group

size^{6,74,75} and that individuals living in groups of above-average size show reduced body condition, breeding success, and survival, as well as heightened levels of cortisol.^{67,75,76} There is also empirical and theoretical evidence that the intensity of both forms of feeding competition is affected by the value of individual food items, the amount of food in typical food patches, the mobility of prey, and the risk of feeding interference.^{52,70,74}

3. There is extensive circumstantial evidence that feeding interference and feeding competition can play an important role in constraining group size and that contrasts in

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group size are often associated with variation in the value, distribution, or mobility of resources.^{16,32,77–79} For example, large groups are found in mammals that depend on food resources that are dense, relatively immobile, and distributed in large patches, so that the frequency of intensity of competition between group members for individual food items is low.^{16,51,80,81} Within species that form stable groups, individuals in

groups of above-average size commonly show increased rates of emigration.^{67,75,76} Similarly, in species that live in fission/fusion societies, increased levels of foraging competition in larger parties frequently raise the frequency with which individuals leave to forage on their own or in smaller parties.^{72,82} A limited number of experimental studies that manipulated food distribution show that variation in food density and clumping affects the intensity of foraging competition and the size of feeding groups.⁸³ Although there is general support for the suggestion that variation in feeding competition associated with contrasts in food distribution often plays an important role in restricting group size and can generate contrasts in sociality between and within species, our understanding of the reasons for variation in group size is still far from complete. It is unclear how the distance between food patches interacts with the value of individual food items and the size and predictability of food patches to determine their relative impact on feeding competition and group size.⁸⁴ A variety of ecological mechanisms other than foraging competition can contribute to limiting group size and group stability (including the effects of group size on detectability by predators, exploitation by parasites, reproductive interference between females and rates of infanticide by males^{21,75,85,86}), and we know little about their relative importance. Moreover, it is becoming progressively obvious that the costs and benefits of sociality vary widely between species, so that no single explanation is likely to account for interspecific differences in group size either in all mammals or all primates.

Dominance Asymmetries and Female Coalitions

The second proposition of the Socioecological Model is that where food items are distributed in patches of high value, direct competition between group members should be common and females should develop consistent, linear dominance rela-

tionships and supportive coalitions that affect their access to resources as well as their condition and breeding success.^{3,5,26} Several field studies of primates confirm that intraspecific variation in food distribution can affect the frequency of competitive interactions.⁷ For example, rates of aggression in vervet monkeys increase when food is patchily distributed and usurpable⁷⁴ while, in Japanese macaques, aggressive interactions over food are most frequent and the benefits of dominance most marked when the animals feed on abundant food sources in small, widely separated patches.⁸⁷ Research on brown capuchin monkeys provides additional evidence that rates of aggression over food and effects of dominance on food access are reduced when animals feed in large patches⁶⁶ and that differences in food intake between dominants and subordinates increase when food distribution allows single individuals to control individual patches.^{66,83} Some comparisons between populations also suggest that feeding competition and high rates of interaction can increase the consistency of female dominance hierarchies and the frequency of coalitions.²⁶ For example, in one population of savannah baboons where resources were concentrated, competitive interactions and coalitions between females were common, while dominance relationships were obvious and correlated with rates of food intake. In contrast, in a second population where resources were widely dispersed, competitive interactions were less frequent, dominance relations were inconsistent, and coalitions did not occur.^{35,88}

However, as yet, no study has demonstrated a significant correlation between social structure and feeding competition across a sufficient number of populations or groups to allow the association to be formally tested. In addition, there is little indication that interspecific differences in the frequency of agonistic interactions, the regularity of dominance hierarchies, or the frequency of female coalitions are consistently associated with interspecific differences in diet, food distribution, or feeding competition. Consistent female

hierarchies have been reported in primates allocated to each of the main dietetic categories and some species that show low frequencies of agonistic interaction still have significantly linear hierarchies.⁸⁹ Comparisons of some pairs of primate species have suggested that contrasts in food distribution are associated with the presence or absence of female hierarchies^{90,91} but, in other groups, there are marked contrasts in the consistency of hierarchies, which appear to be more closely related to phylogeny than to variation in diet.^{92–94} Conversely, similar patterns of social structure are often found among related species with contrasting feeding ecologies.^{29,40}

There also is no strong evidence that interspecific differences in the effects of female rank on female breeding success are consistently related to variation in diet, food distribution, or foraging competition, either among primates or among other social mammals. Although correlations between female rank and components of fitness (including growth, age at first reproduction, reproductive rates, offspring survival, and longevity) have been demonstrated in various primates as well as in other social mammals, no broad-scale attempt has been made to compare the extent of reproductive skew among females between species with contrasting diets or resource distributions. In many mammals, females compete intensely for breeding opportunities as well as for food,⁹⁵ with the result that there may be no direct correlation between the intensity of competition for resources and social structure or the strength or regularity of dominance hierarchies. The limited comparisons available suggest that the magnitude of reproductive skew in females may depend primarily on the extent to which dominant females can control reproduction among subordinates.^{21,96}

One suggested explanation for the lack of close association between the strength or consistency of dominance relations and contrasts in diet or food distribution is that neither gross dietetic categories nor existing measures of food distribution provide an accurate basis for assessing

the intensity of feeding competition.^{41,45} For example, some of the cases where female social behavior differs most conspicuously from the predictions of the Socioecological Model involve folivores,⁸⁹ where feeding competition may depend on local differences in leaf quality, an aspect of food distribution that is difficult to quantify or compare.^{97,98} However, the available evidence suggests that interspecific contrasts in social structure may be more closely related to contrasts in life-history parameters and reproductive strategies than to differences in resource distribution or feeding competition. For example, female hierarchies appear to be highly developed in species where females live in large, stable groups and groups contain females belonging to several distinct matrilineal, so that level of kinship varies widely between group members,⁹⁹ as in many of the baboons and macaques, as well as spotted hyenas.^{21,65,100}

An additional prediction of the Socioecological Model is that female hierarchies should be more predictable and female rank should have a stronger effect on female fitness where females remain and breed in their natal group than in species where females habitually disperse to breed and groups consist of unrelated immigrants. No systematic attempt has yet been made to compare either the predictability of dominance relations or the frequency of female coalitions between these groups, although it has been suggested that female hierarchies are more predictable and female coalitions are more frequent where females commonly remain and breed in their natal group than in populations where females habitually disperse to breed.⁶ If so, there are obvious exceptions, including species where females are commonly philopatric but female hierarchies have not been reported^{6,25,101} and species where females habitually disperse but there is evidence of female dominance hierarchies.^{89,102–104} Moreover, several different factors may affect the formation of female hierarchies. For example, in lionesses, the possession of potentially lethal weapons

may make escalated contests and the establishment of consistent dominance relations too costly for regular hierarchies to develop.¹⁰¹ Even if it proves to be the case that there is an association between female philopatry and the presence of consistent dominance relations, there are several alternative explanations apart from the one suggested by the Socioecological Model.⁹⁹ For example, the benefits of dominance may be greater in species where females are philopatric because groups are larger and kinship between group members varies widely, providing opportunities for females to influence the rank and breeding success of close relatives at the expense of more distant relatives or unrelated females, reversing the direction of causation shown in Figure 1.

Female philopatry and the kinship structure of groups

The third proposition of the Socioecological Model is that in species where resources are patchily distributed, contest competition is frequent, and dominance hierarchies are well developed, females should form kin-based coalitions and seldom transfer between established groups, so that female group members are usually close relatives (Fig. 1; Table 1). In contrast, where resources are more evenly dispersed and scramble competition predominates, the model predicts that females should gain fitness benefits by dispersing and groups should consist primarily of immigrant females. On the grounds that competition between group members for resources may be a more potent selection factor than intergroup competition, it has been suggested that female philopatry should be relatively common and habitual female dispersal should be relatively rare.⁶

To judge arguments about the evolution of female philopatry and dispersal in primates and other social mammals, it is important to recognize that these predictions apply to plural breeders (species where social groups include multiple breeding females) rather than to singular

breeders, where almost all females have to leave their natal group to breed. In addition, it is important to appreciate that wherever recruitment exceeds mortality and resource competition increases with group size, a substantial proportion of females will leave their natal group, either by dispersing individually or through group fission. As a result, contrasts in kinship between female group members are not necessarily closely related to variation in the proportion of females that disperse to breed.

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The crucial parameter affecting kinship between female group members is the frequency with which females immigrate into established breeding groups or found new groups with unrelated individuals. In many social mammals, females rarely immigrate into established breeding groups and new groups are typically formed by related females, as in many of the cercopithecine primates.¹⁰⁵ However, in a minority of species, adolescent females or young adults habitually disperse to breed, individuals seldom breed in their natal group, and most or all breeding females are immigrants, as in spider monkeys and their relatives,^{106,107} some colobines,^{108,109} hamadryas baboons,¹¹⁰ and all three African apes.¹¹¹ In some of these species, female group members are usually unrelated but, in others, related females may immigrate into the same breeding group simultaneously or sequentially so that some immigrant females can be close relatives.¹¹²

Some intraspecific comparisons suggest that there could be an association between the frequency of female immigration, resource distribution, and feeding competition.^{26,113} For example, in two baboon populations that differed in food distribution and dominance relationships, some females transferred between groups and group fission was common in the population that lived on dispersed resources whereas most females were philopatric in the population that lived on clumped resources.^{114,115} A similar association between food distribution and female dispersal has been described between two populations of hanuman langurs.⁹⁷ However, no study has yet demonstrated a significant correlation between food distribution and immigration rates across an adequate sample of populations of the same species.

In contrast, there is little evidence that interspecific contrasts in the frequency with which females immigrate into established breeding groups, in the proportion of breeding females that are of natal origin, or in the kinship structure of female groups are consistently related to variation in food distribution or feeding competition. While comparisons of some pairs of closely related primate species are consistent with the predictions of the Socioecological Model,⁹¹ others are not. For example, female dispersal and immigration into neighboring groups is the norm in the frugivorous chimpanzees as well as in the folivorous gorilla^{111,116}; among cercopithecine monkeys, female philopatry is usual in the primarily frugivorous savannah baboons, guenons, and mangabeys, as well as the herbivorous gelada, while among the omnivorous hamadryas baboons, females typically leave their natal group and join other breeding units.^{117,118} Among the partially frugivorous, partially folivorous colobine monkeys, females are usually philopatric in black-and-white colobus as well as some langurs, but females typically disperse to breed in red colobus and some langurs.^{108,109} Among the New World monkeys, female philopatry is common in the frugivorous/insectivorous

capuchin monkeys as well as in common squirrel monkeys, whereas females habitually disperse and immigrate into other groups in the frugivorous spider monkeys, woolly spider monkeys, and woolly monkeys.^{90,106,119–122}

There is also little evidence of any close association between patterns of female dispersal and diet, food distribution, or the defensibility of resources among other plural breeding mammals: female philopatry is common in herbivores, frugivores, and carnivores, while female groups consisting primarily of immigrants are found in the social equids, several tropical bats, and some social carnivores.^{105,123} Among both primates and other social mammals, female philopatry and the formation of female groups consisting of natal relatives are common in species that do not defend resources (like many baboons, as well as elephants and several ungulates) as well as in those that do. Unless contrasts in diet are altogether uncorrelated with differences in feeding competition, it is difficult to avoid the conclusion that the Socioecological Model fails to provide a satisfactory explanation of the evolution of interspecific contrasts in female philopatry in plural breeders, either in primates or in other social mammals.

So what other explanations are viable? In this case, there is an alternative explanation: that contrasts in female philopatry and rates of female immigration are consequences of differences in male life histories and the risk of inbreeding to females rather than the intensity of feeding competition.^{20,124} There is substantial evidence of the costs of inbreeding in outbred animals.^{124–126} Also, in a number of species, including primates and rodents, the probability of dispersal by females increases if a close relative of the opposite sex is present in the group or if there is no unrelated member of the opposite sex.^{127,128} One possible explanation of the distribution of habitual female dispersal and subsequent immigration is that this occurs where females that remain in their natal group would otherwise lack access to unrelated males.^{20,129} As this explanation

would predict, a characteristic of plural-breeding mammals where adolescent females habitually disperse and immigrate into other groups is that the average breeding tenure of individual males or male-kin groups exceeds the age of females at first breeding, so that natal females commonly reach breeding age while their father or brothers are reproductively active in their group.^{20,130} Moreover, analysis of evolutionary transitions from female philopatry to habitual female dispersal indicates that the evolution of habitual female dispersal has been confined to lineages where the relative duration of male tenure already exceeds female age at first breeding.¹²³

One objection to this explanation is that there are some social primates where females commonly remain and breed in their natal group but male tenure exceeds the average age of females at first breeding. For example, in capuchin monkeys, male tenure is often longer than the age at which females begin to breed.¹²¹ However, dispersal is not the only strategy by which individuals with close relatives of the opposite sex in their group can avoid inbreeding. In mammals where females typically remain and breed in their natal group and natal females commonly reach maturity during the reproductive tenure of their father or other close relatives, they often avoid close inbreeding by avoiding matings with first-order relatives or by mating with visiting males from other social groups.^{121,124,131} Why females of some species use these tactics to avoid close inbreeding while dispersal is the solution in other species is not known, but one possibility is that females are more likely to disperse in species where resident males are able to exclude unrelated male visitors or immigrants from access to receptive females.

This argument emphasizes the need to understand both the causes of variation in the duration of male breeding tenure and the relative capacity of resident males to monopolize reproductive access to females in their group. As yet, estimates of male tenure are available for too few mammals for quantitative compari-

sons to be reliable, but existing studies suggest that the duration of male tenure is negatively related to the intensity of intrasexual competition between males¹⁰⁵ and is longer in socially monogamous species.¹³² However, it seems likely that the duration of male tenure is affected by multiple factors. Extrinsic rates of male mortality may be important: for example, mortality rates may be relatively low in the large-bodied atelines and gorillas, as well as in the social equids.^{57,130,133} Life-history adaptations could also be involved: for example, in chimpanzees, the tenure of male kin groups may be long because their low rate of reproduction means that rival communities rarely produce enough adolescent males to generate dispersing splinter groups large enough to displace resident groups of males. In contrast, in African lions, the synchronous production of relatively large numbers of cubs by female group members generates dispersing male subgroups capable of displacing resident groups of males, leading to relatively high rates of turnover of resident male groups.¹³⁴ In langurs, the formation of bachelor groups of males that regularly invade breeding groups and displace resident males may also reduce male tenure,^{135,136} while support from females and sons may help dominant males retain their status, as in capuchin monkeys.^{137,138}

WHERE NOW? THE FUTURE OF PRIMATE SOCIOECOLOGY

The Socioecological Model's explanation of variation in female sociality and female group size is shared with more general explanations of variation in animal sociality and group size, and is more strongly supported than its explanations of variation in the structure of female relationships or contrasts in female philopatry and in the kinship structure of groups. Among both primates and other mammals, contrasts in food distribution and associated differences in feeding competition play an important role in determining the frequency of agonistic interactions

between females, the extent to which breeding females tolerate each other within a common range, and the size of female groups, although a substantial number of other ecological mechanisms can mediate their influence. However, there is little evidence of any consistent association between contrasts in diet or food distribution and interspecific differences in rates of agonistic interaction, in the consistency of female dominance hierarchies, in the frequency of female coalitions, or in the prevalence of female philopatry. Instead, these differences may be more closely associated with variation in life-history parameters and reproductive strategies and often show a strong phylogenetic signal.

So do we now need to refine the Socioecological Model once again and to incorporate additional categories and complexities, as some primatologists suggest?^{36,45} Or should we abandon it? Or should we even give up the “dream of ecological determinism” altogether?³¹ There is a strong case for retaining some components of the Socioecological Model. For example, it would not be sensible to discard the general argument that contrasts in food distribution and feeding competition play an important role in constraining the extent to which breeding females tolerate each other’s proximity. In addition, an important insight of Wrangham’s original paper was his emphasis on the extent to which large group size generates benefits in competitive encounters between groups. In contrast, the case for retaining the other components of the model as a conceptual framework that can be used to guide future research is much weaker. The evidence that interspecific differences in rates of agonistic behavior, female dominance relations, and female philopatry are consistently related to variation in food distribution and feeding competition is unconvincing. We should be prepared to abandon these components of the Socioecological Model and move on.

But where to? Table 2 lists some of the most obvious challenges to research on primate socioecology, together with potential solutions. One

explanation of the limited ability of the Socioecological Model to predict the distribution of differences in social relationships and philopatry is that the gross dietetic categories often used as proxies for food distribution do not reflect consistent differences in the intensity of scramble or contest competition, even if leaves and fruits are, on average, resources that engender different intensities of competition.^{32,66} There is widespread agreement among primatologists that improved techniques of measuring food distribution to allow reliable comparisons to be made between populations and species are needed, as well as more satisfactory methods of comparing the predict-

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ability of dominance relations and their effects on female fitness.^{26,36}

There are also many questions concerning the effects of feeding competition on female social behavior that have still to be asked or answered. For example, we know little about the extent to which feeding competition among primates affects the intensity of reproductive competition between females, or their readiness to interfere with each other’s breeding attempts or to kill each

other’s offspring, yet studies of other social mammals indicate that interactions of this kind may be common.^{139,140} The relationship between feeding competition and reproductive skew among females also has still to be systematically investigated, and we know little about the demographic consequences of behavioral interactions between females. For example, few studies of social mammals have yet quantified the role of different social and demographic mechanisms in generating variation in age structure or in regulating the size of female groups.^{138,141} The increased availability of long-term datasets,¹⁴² combined with new techniques of demographic analysis,^{143–145} provide opportunities to explore these issues.

The limitations of the Socioecological Model also point to the need to reevaluate our strategy and our approach to explaining the diversity of primate societies. Past research has involved the investigation of relationships between ecology and social behavior at different levels: across species, populations, groups, and individuals. It is important to recognize that each of these approaches has its own strengths as well as its own limitations.^{44,45,146} Interspecific comparisons have the advantage that, where there are consistent contrasts in social behavior, these are likely either themselves to represent adaptations or to be by-products of related adaptations. Other advantages include the opportunity to compare species that differ substantially in their ecology, the feasibility of incorporating large enough samples of species to allow formal testing of relationships, and, where genetic phylogenies are available, the opportunity to explore sequences of evolutionary changes.¹⁴⁷ However, they have the disadvantage that the precision of comparisons and the comparability of data typically decline as the number of species considered increases and that associations between ecological parameters and social behavior may be consequences of phylogenetic differences.

Interpopulation comparisons remove or greatly reduce the problems introduced by phylogenetic diversity

TABLE 2. Some Challenges Faced by Socioecological Studies of Primates and Potential Solutions

Challenge	Potential solution
Lack of consistent relationships between diet and feeding competition.	Improve measures of food distribution and feeding competition to provide a reliable basis for measuring continuous variation between populations and species. Manipulate food distribution and observe effects on conspecifics.
Lack of consistent association between different aspects of social behavior across species.	Test degree of association between traits; where necessary, focus on the distribution of particular traits rather than syndromes.
Lack of consistent association between species differences in feeding competition and social organization.	Focus on particular traits; control for effects of phylogenetic variation; explore the impact of variation in life-history parameters and reproductive strategies in both sexes; reconstruct evolutionary sequences to identify adaptive constraints.
Correlation between ecological parameters and specific differences in social behavior differ from those between ecological parameters and intraspecific differences.	Distinguish between questions concerning the evolution of adaptation and questions concerning the immediate consequences of ecological variation. In general, to investigate evolutionary questions, explore the correlates of interspecific differences or selection operating on individuals within populations; to assess the immediate consequences of contrasts in feeding ecology or population density, compare the same population at different times or different populations. But remember that interpopulation differences can also be a consequence of contrasts in selection, while interspecific differences can be a consequence of evolutionary constraints.
Effects of variation in food distribution on interspecific differences cannot be separated from those of differences in population density or demographic structure.	To identify effects of population density, examine the effects of temporal changes in density on social behavior in the same population; to assess consequences of interpopulation differences, control for density effects or manipulate food distribution.
Lack of consistent relationships between ecological parameters and dominance relations.	Improve indices of the consistency of outcome in interactions to provide indices that can be used to compare species, populations, and individuals; consider effects of reproductive competition on dominance relations; explore the costs as well as the benefits of establishing dominance.
Constraints in the effects of variation in kinship on social relationships.	Improve measurement of kinship; incorporate realistic estimates of benefit and cost; focus on circumstances or periods where competition is likely; recognize that benefits of discrimination are likely to decline as average relatedness increases.
Lack of obvious pattern in the distribution of female dispersal.	Focus on the distribution of philopatric breeding and female immigration; distinguish between singular and plural breeders; separate analyses of the origin of breeders, the probability of dispersal, and dispersal distance; incorporate the role of male tenure length and mating strategies on female dispersal decisions.
Taxonomic variation in behavioral parameters.	Investigate evolutionary transitions and the circumstances in which they occur as well as the distribution of traits among contemporary species; where the number of transitions is low, extend analyses to include related taxonomic groups.

and the increasing evidence of correlations between social behavior and phylogeny has prompted arguments that primate socioecology should focus on exploring contrasts between populations or groups of the same species.^{28,34,45} However, it is seldom possible to compare sufficient numbers of populations or groups to allow correlations to be formally tested and it is usually difficult to identify the ecological factors that are responsible for observed contrasts in social behavior. A possible solution to this dilemma would be to

concentrate on indices that can be measured in unhabituated animals, thereby allowing both easier study design and a broader sampling of study systems. Although not applicable to every species, possible examples of such indices would include group size and approximate diet,¹⁴⁸ mean and variation in habitat productivity via remote sensing, and kinship¹¹² and sex ratio via noninvasive genetic sampling.¹⁴⁹ In addition, it is important to appreciate that contrasts in social organization between populations may often be

nonadaptive by-products of population demography rather than the result of heritable, adaptive differences in behavior: for example, even in species where female sociality is maintained by reductions in predation risk, group size may decline with increasing predation risk because high rates of predation reduce female recruitment and longevity.⁵⁹

A growing number of studies of primates and other mammals have explored correlations between social behavior and ecology across individ-

uals.¹⁵⁰ This approach offers a variety of advantages, including the possibility of sample sizes large enough to permit formal testing, the chance to investigate direct relationships between variation in social behavior and components of fitness, and the possibility of controlled experiments to investigate the causal basis of correlations.¹⁵⁰ In addition, it offers opportunities to explore the genetic basis of individual differences and to assess the heritability of different traits.¹⁵¹ However, here, too, it is often difficult to determine which of several correlated ecological or social parameters is responsible for variation in behavior without experiments, and differences between individuals, like those between populations or groups, can either be nonadaptive by-products of ecological or social mechanisms or adaptations that increase the fitness of individuals.

The contrasting strengths and limitations of exploring correlations between social behavior and ecology at different levels argue for the integration of research on similar questions at different levels, an approach that is now starting to become feasible.^{28,152} In addition, the difficulty of separating the effects of different ecological parameters emphasizes the need for experimental approaches to explore the causal mechanisms responsible for correlations.¹⁴⁶ Because experiments frequently present logistical and ethical problems, it may be sensible to focus experimental research on a limited number of model species that provide unusual opportunities for field manipulation.

The limitations of the Socioecological Model also point to the need to reconsider the nature of associations between ecology and social behavior. Many of the problems of the Socioecological Model stem from the assumptions that different aspects of social organization and structure are closely correlated with each other and that a small number of ecological parameters control the evolution of many different aspects of social behavior. Neither of these assumptions is likely to be correct: many aspects of social behavior do not appear to be closely associated with

each other, and the relative importance of particular ecological parameters probably differs widely between traits and between species. In this situation, we may make better progress by exploring the evolution and distribution of specific social traits or strategies than by attempting to explain contrasts in entire social systems. In addition, as well as considering the potential impact of feeding competition and predation, we need to consider how they are likely to interact with variation in the reproductive strategies and life-history parameters of both sexes.

We also need to confront the evidence that phylogenetic proximity often predicts variation in social organization and social structure more accurately than does variation in ecology. This sometimes is interpreted as indicating that differences in social behavior are a consequence of nonadaptive interspecific differences in genetic architecture.³¹ However, while phylogenetic signals may sometimes be a consequence of coincidental, nonadaptive differences in genetic architecture, they can be caused by several other evolutionary mechanisms.^{147,153} In some cases, related species may share similar environments or ecological niches, so that correlations between behavior and phylogeny reflect the effects of common ecological variation.¹⁵⁴ Alternatively, the evolution of major differences in anatomy, reproductive physiology, or life history parameters may constrain the evolution of subsequent adaptations, either through their effects on selection pressures or through their influence on developmental processes and learning. For example, the evolution of reproductive suppression and cooperative breeding in mammals appears to have been restricted to species where mating is monogamous, so that average levels of kinship between group members are high, and breeding females produce multiple litters per year, so that assistance for helpers can contribute significantly to their reproductive output.¹⁵⁵ The recent development of gene-based phylogenetic supertrees and statistical techniques capable of identifying evolutionary sequences^{156,157} now makes

it possible to explore the effects of previous adaptations on the subsequent evolution of specific aspects of social behavior within particular phyla.^{158–161} This development also offers important opportunities to identify adaptive constraints and to explore how phylogenetic factors and variation in ecology interact to affect the course of evolution¹⁴⁷ while, in future, genomic approaches may make it possible to identify the effects of differences in genetic architecture.

There is also a need to integrate research on primates more closely with studies of other vertebrates and, in particular, with research on other social mammals. Although the questions that preoccupy primatologists differ to some extent from those that interest behavioral ecologists working with other groups of animals, overlap between the aims and interests of primatologists and other behavioral ecologists are more conspicuous than differences.¹⁶² Long-term, individual-based studies of other vertebrates have demonstrated extensive similarities in the ecological and evolutionary processes affecting social behavior and shown how research on distantly related species can provide insights of general importance.^{142,162} Moreover, transitions between many traits are not sufficiently numerous among primates for it to be possible to identify their association with variation in ecology, reproductive biology, or life-history parameters. For example, obligate monogamy appears to have evolved no more than six times in primates while reproductive suppression and the cooperative rearing of young appears to have evolved no more than once.¹⁵⁵ As a result, a broader taxonomic sample is necessary in order to identify the circumstances associated with these transitions. Finally, while primates provide unusual opportunities to investigate many important aspects of social behavior and communication, logistical problems often constrain attempts to measure important ecological parameters or to manipulate them in order to test explanations of the causal mechanisms underlying correlations. Parallel research on

more tractable species may consequently help to shed light on ecological processes affecting primate social behavior. A closer integration of primate studies into mainstream behavioral ecology should enrich our understanding of primate societies, as well as help to extend explanations of the diversity of social behavior in other animals.

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