

# Contest and scramble competition: patterns of female aggression and ranging behavior among primates

The fact that most female primates (and many other mammals) live in groups is paradoxical, given that the presence of others presumably increases competition for foods and may, for some, reduce reproductive success. Competition for food resources is generally inferred from any of the following observations: (1) female dominance hierarchies within groups; (2) female aggression between groups; (3) increasing home-range size with increasing group size; (4) longer day-range length with increasing group size; and (5) lower reproductive rates in larger groups. Both female aggression (interference competition) and adjustments of ranging behavior to group size (exploitative competition) have been linked in the past to patterns of food distribution and abundance. Using data largely from the literature, this paper examines the covariance of female aggression and ranging behavior among 20 species of primates in an attempt to better explain the variation in female relationships within and between groups of primates. Results show that groups of females are aggressive toward other groups and that home-range size increases with increasing group size in most species. In addition, in those species with strong dominance hierarchies within groups, day-range length increases as a function of group size. However, in those species that do not have strong dominance hierarchies within groups, day-range length does not increase as a function of group size. The implications of these results are presented in a model that suggests that intergroup competition is determined by food abundance, whereas intragroup competition is determined by food distribution. This model differs from earlier models in its explanation of the ecological conditions that influence female relationships within and between groups of primates. [*Behav Ecol* 1991;2:143–155]

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Food intake influences a number of parameters that determine reproductive success of female mammals, including age at first birth, interbirth interval, total number of births, and offspring survival (reviewed in Lee, 1987). The presence of other individuals is thought to increase competition for food and, for subordinates, to reduce food intake (Alexander, 1974; van Schaik, 1983; Wrangham, 1980). Therefore, it seems paradoxical that in many mammalian species females live in cohesive and stable groups. Primates are particularly well-suited mammals for addressing issues concerned with sociality. Most live in cohesive groups, and many of these are composed of multiple females.

Wrangham (1980) hypothesized that in many primate species, females live in groups because the benefits of cooperative defense of resources against other females outweigh the cost of intragroup competition. Wrangham distinguished between "female-bonded" species, in which the greater benefit of intergroup competition contributes to differenti-

ated relationships between females within groups, and "nonfemale-bonded" species, in which the inability or lack of necessity of groups to defend food resources does not favor cooperation and differentiation of female relationships within groups.

Closer examination reveals more than a simple dichotomy in female relationships and competition within and between groups (van Schaik, 1989). Competition for food resources is generally inferred from any of the following five observations:

1. Female dominance hierarchies within groups. Aggression between females within groups often results in clearly defined dominance hierarchies. Evidence suggests that the ability of certain females to increase their own food intake at the expense of others within groups is related to the distribution of food resources: clumped resources are more easily monopolized and defended by individuals within groups than are dispersed resources (Harcourt, 1987; Whitten, 1983). High-ranking females may reproduce more successfully

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than low-ranking females when foods are clumped (Harcourt, 1987; Whitten, 1983).

Because fruits tend to be distributed in clumps more often than are leaves or invertebrates, patterns of female aggressive behavior may be predicted by broad dietary type, at least when there is specialization on foods that are distributed in the same way. McKenna (1979) suggests that frugivorous primates tend to have clearly defined female dominance hierarchies within groups, whereas folivorous primates tend to have poorly defined hierarchies. Squirrel monkeys (*Saimiri sciurius*) and patas monkeys (*Erythrocebus patas*) also have poorly defined dominance hierarchies and feed extensively on invertebrates (Boinski, 1988; Chism and Rowell, 1988).

2. Female aggression between groups. Aggression between groups often results in larger groups gaining access to resources at the expense of smaller groups [e.g., vervets (*Cercopithecus aethiops*): Cheney and Seyfarth, 1987; Isbell et al., 1990; toque macaques (*Macaca sinica*): Dittus, 1987; capuchins (*Cebus olivaceus*): Robinson, 1988]. If groups have home ranges that are sufficiently small relative to their daily travel distances, they may defend the boundaries of their home ranges (Mitani and Rodman, 1979). Groups with relatively large home ranges may overlap the home ranges of other groups, but larger groups may deter smaller groups from feeding in areas of overlap by being aggressive.

3. Increasing home-range size with increasing group weight or size. When resources are limiting, the ability of females to obtain foods may also be affected by group size (or group weight). As its numbers increase, each group may be required to expand its home range to compensate for the foods lost to additional group members (Clutton-Brock and Harvey, 1977; Dunbar, 1988). Larger (or heavier) groups tend to have larger home ranges across species, regardless of the distribution of their foods (Clutton-Brock and Harvey, 1977; McNab, 1963; Milton and May, 1976).

4. Longer day-range length with increasing group size. Larger groups may also compensate for additional members by increasing the distance traveled per day (Clutton-Brock and Harvey, 1977; Dunbar, 1988; Waser, 1977). However, larger groups have been found to travel longer daily distances only among frugivorous species (Clutton-Brock and Harvey, 1977). Among folivorous species, larger groups do not travel farther per day (Clutton-Brock and Harvey, 1977). This suggests that daily travel distance is more sensitive than home-range size to the ways in which foods are distributed.

5. Lower reproductive rates in larger groups. Van Schaik (1983) hypothesized that

as groups become larger, the availability of food resources per female decreases, and food competition therefore increases, resulting in relatively lower reproductive rates for females in larger groups. However, there are other costs of living in larger groups in addition to resource competition that might also explain this pattern, such as disease, parasites, and social conflict (see Discussion). Reproductive rates relative to group size will therefore not be considered in the analyses of scramble and contest competition that follow.

Aggression is considered a form of interference, or contest, competition (Miller, 1967), whereas adjustments of ranging behavior to group size, including home-range size and daily travel distance, are thought to reflect exploitative, or scramble, competition (e.g., van Schaik and van Noordwijk, 1988). Both may reflect competition for limiting resources. Female-female aggression within groups of the same species has been shown to be influenced by resource distribution (Harcourt, 1987; Whitten, 1983), and ranging behavior among species has been shown to be influenced by resource abundance and distribution (Clutton-Brock and Harvey, 1977). Despite this apparent connection between both forms of competition and resource distribution and abundance, there has not yet been an attempt to examine the relationships between female-female aggression and ranging behavior either within or among species.

Here I present results of an examination of variation in patterns of female aggression and ranging behavior among primates living in multifemale groups. Based on the evidence above, I suggest that intergroup aggression and home-range size both determine access of neighboring groups to resources and that intragroup dominance hierarchies and daily travel distance both determine access of individuals within a group to resources. Variation in intergroup aggression and home-range size should thus reflect variation in the expression of intergroup competition, whereas variation in intragroup dominance hierarchies and daily travel distance should reflect variation in the expression of intragroup competition.

I examine whether contest and scramble competition covary within and among groups by testing the following predictions: (1) Species in which females are aggressive between groups also increase home-range size as a function of group size, whereas species in which females are not aggressive between groups do not increase home-range size as a function of group size. (2) Species with strong dominance hierarchies within groups also increase day-range length as a function of group size, whereas species with weak or no domi-

nance hierarchies within groups do not increase day-range length as a function of group size. After examining these predictions, I propose a model that is based on possible species differences in patterns of food abundance and distribution to account for the observed variation in contest and scramble competition.

## METHODS

Although the theoretical basis for this examination may also apply to nonprimate species, I restrict the analyses to primates because they commonly live in cohesive, multifemale groups, and data on daily travel distance for more than one group in the same population are most often available for primates. I surveyed patterns of female aggression and ranging behavior in 20 primate species in which females live in cohesive, multifemale groups. Using data from published studies and personal research, I recorded the following characteristics: (1) strong, weak, or no dominance hierarchies among females within groups; (2) presence or absence of female aggression between groups; (3) day-range lengths for groups of different sizes; and (4) home-range sizes for groups of different sizes.

The species was chosen as the level of analysis because variation existed in these traits on the genus level, and no intraspecific variation existed at the population level. There were four genera for which data on female relationships for more than one species were available. Of these, three exhibited interspecific variation, making it inappropriate to combine congeners in the same cells during statistical analyses.

## Definitions

The "home range" is the area used by a group over a period of time specified by the researcher. For this paper, the minimum time considered adequate for the determination of home ranges was 3 months. Although shorter studies are more likely than longer studies to have underestimated home-range sizes, this bias should not affect the results because each group in the shorter studies was compared only with another group from the same study. "Day-range length," or daily travel distance, is the average or median distance covered by a group daily. Groups were typically followed for full days (range: 5–108 days), and their movements were plotted at regular intervals on range maps or measured directly in the field.

Rigidity of dominance hierarchies is used as the measure of aggressive competition within groups because it is operationally easier to use in interspecific comparisons than fre-

quency of aggression. In this analysis, the presence or absence of dominance hierarchies is not designed to describe the relative intensity of competition of different species. Rather, it is used to describe whether the opportunity exists for individuals within groups to gain priority of access to resources through either overt aggression or the threat of aggression. I classified species as having a strong dominance hierarchy when aggressive interactions between females within a group were observable and predictable (i.e., with few or no reversals). I classified species as having a weak dominance hierarchy when patterns of agonistic interactions between females were difficult to observe because they occurred so rarely or were unpredictable because reversals were common. I classified species as having no discernable dominance hierarchy when aggressive interactions between females were absent. In the analyses below, weak and no discernable dominance hierarchies were placed in one category and strong dominance hierarchies in another. Aggression between females included approach–retreat or approach–avoid interactions, as well as supplanting, chasing, biting, and hitting. Aggression between females of different groups included loud calls in addition to the aggressive behaviors described above. Loud calls were included because there is evidence that they influence spacing between groups (Cheney, 1987).

## Dietary classification

Data on daily feeding patterns such as the amount of time spent feeding or foraging on clumped or dispersed foods are generally not available. In the absence of these data, I used major proportions of food types in the diet as a first approximation of the ways in which the foods of different primate species are distributed (the drawbacks of this approach are discussed below).

## Selection of data sets

Data from the literature were used only when they came from groups living under naturally occurring, relatively undisturbed, and unprovisioned conditions. I eliminated groups within a population that were reported to have home ranges with obviously different resource bases because these differences in home-range quality can obscure differences in home-range size and daily travel distance caused by group size (Butynski, 1990; Harcourt, 1987; Mitani and Rodman, 1979). I included data from groups that were not reported to have differences in home-range quality; groups that fissioned but continued to use the former group's general home range in the same habitat; and

groups that were either reduced or expanded in size but continued to use areas within the same home range. These categories reflect a progressively decreasing potential for differences in home-range size and daily travel distance to be influenced by differences in habitat quality. Correlational tests were not possible to do in most cases (but see below) because the numbers of groups sampled within populations were generally very small ( $n = 2-3$ ). Although sample sizes could be increased by combining data from different populations, this would increase the probability of the results being confounded by habitat differences. Instead, I compared the smallest and largest groups within the same population for each species.

#### **Criteria for classifying differences in ranging patterns between groups**

When differences in ranging behavior between groups were statistically compared by the reporting researchers, I used their results independent of the methods they used to measure differences between groups. For example, several investigators were able to run correlational tests when their sample sizes permitted (e.g., Dunbar and Dunbar, 1974; Struhsaker and Leland, 1987). Others used  $t$  tests or Wilcoxon tests to compare the ranging behavior of two groups (e.g., Chism and Rowell, 1988; Whitesides, 1989). When statistical tests were not reported, I classified home-range size or day-range length as increasing with group size when home-range size or day-range length for the largest group was more than 10% greater than the smallest group. This cutoff point was used because it approximated the value for the smallest difference in group size, and it created no ambiguous cases (there was a break in the data set in increases in home-range size and day-range length between 2% and 14%). The data used in the analyses are provided in Table 1.

### **RESULTS**

Data were available for 20 species from 11 genera. Data sets on female relationships between groups, group size, and home-range size were available for 16 species from 9 genera. Data sets on female relationships within groups, group size, and day-range length were available for 14 species from 10 genera (Table 1).

#### **Intergroup aggression and changes in home-range size**

There is a tendency for species in which females are aggressive between groups to in-

crease home-range size as a function of group size, and for species in which females are not aggressive between groups not to increase home-range size as a function of group size ( $p = .07$ ) (Table 2). Fourteen of 16 species (88%) fit this pattern. The strength of this association is limited because there are so few species in which groups are not aggressive or show no increase in home-range size as group size increases. This is consistent with the hypothesis that food resources limit the population growth of most species (through individual reproductive success).

#### **Dominance hierarchies within groups and changes in day-range length**

There is a significant statistical association between day-range length as a function of group size and patterns of female aggression within groups ( $p = .01$ ) (Table 3). Among species that have strong female dominance hierarchies, larger groups have longer day-range lengths, whereas among species that do not have strong hierarchies, larger groups do not have longer day-range lengths. Twelve of 14 species (86%) fit this pattern.

These relationships apparently do not exist as a result of any association between intragroup and intergroup expressions of scramble or contest competition. All species that have strong dominance hierarchies within groups also show female aggression between groups. However, many species without strong dominance hierarchies also show female aggression between groups. For this reason, interspecific variation in female aggression between groups is only weakly related to variation in aggression within groups (Fisher's Exact test:  $p = .12$ ,  $n = 17$ ). Similarly, increased home-range area with increasing group size is not evidently related to longer day-range length with increasing group size (Fisher's Exact test:  $p = .67$ ,  $n = 10$ ). This result suggests that species do not necessarily adjust the distance traveled per day to the size of their home range (see also Mitani and Rodman, 1979).

### **DISCUSSION**

#### **The relationship between ranging behavior and female aggression**

##### *Home-range size and intergroup aggression*

Home-range size measures the area over which groups move in search of their foods. Home ranges may expand with lower densities of food resources or groups and with larger group size. Similarly, home ranges may contract with higher densities of food resources or groups and smaller group size. This is particularly evident among territorial species. For

example, as densities of food resources and groups decreased in Amboseli National Park, Kenya, five groups of vervets expanded their territories. However, the largest group expanded into the territories of smaller groups, thereby reducing the area available to the smaller groups (Cheney and Seyfarth, 1987; Isbell et al., 1990). When groups have overlapping home ranges, the presence of other groups should not only reduce the absolute amount of food available, but should also make food less predictable in areas that overlap. Therefore, whether territorial or not, groups of females are expected to act aggressively toward other groups to minimize their food losses whenever abundance of food limits reproductive success.

If food abundance does not limit reproductive success, groups of females will not be required to increase their home ranges as groups increase in size and should not act aggressively toward females of other groups. Under these conditions, some other factor must limit female reproductive success. Possible limiting factors other than food might include disease (May, 1986; Young TP, unpublished data), parasites (Freeland, 1976; May, 1983), predation (Hairston et al., 1960), and social conflicts (Dunbar, 1987); some of these may be density dependent.

Among the folivorous red colobus (*Colobus badius*) and mantled howlers (*Alouatta palliata*), the absence of both strong dominance hierarchies within groups and female aggression between groups, coupled with the lack of changes in ranging behavior with increasing group size, suggests that foods may not be limiting in the study populations. It is perhaps notable that the population of red colobus in Kibale Forest has one of the highest densities of any primate studied to date (Struhsaker and Leland, 1987). Alternatively, foods may be limiting, but it is possible either that foods were temporarily abundant during the study periods or that female–female aggression and ranging behavior are not useful indicators of competition in these populations (see Figure 1).

For most primate species, foods probably do limit reproductive success. This is supported by the fact that in most species (75%) examined here, larger groups have larger home ranges and also exhibit intergroup aggression. Home range expansion may have costs such as increased risk of predation (Isbell et al., 1990) and unfamiliarity with the locations of foods. These costs are apparently overcome by the benefits of range expansion, such as access to more foods. For instance, as the vervets in Amboseli expanded their home ranges into unfamiliar areas, females and immatures suffered greater mortality, most likely

due to predation. However, the largest group was able to supplant smaller groups and increase the number of trees in its home range at the expense of the supplanted groups (Isbell et al., 1990). In most species, groups of females should benefit by being aggressive toward other groups, not necessarily just at territorial boundaries over which they can search for foods, whether or not foods can be monopolized within their groups. Resources need not be clumped within the home range for the group to be able to act aggressively (see below).

### **Day-range length and intragroup dominance hierarchies**

Day-range length largely measures the distance a group moves each day as the individuals in the group obtain their food. The distance that is traveled is likely to be the result of a balance between the energetic benefits of obtaining food and the energetic costs of moving from one food site to another. Among species whose food occurs in discrete clumps, individual food patches should be depleted more quickly by larger groups, and larger groups may be required to travel farther than smaller groups to obtain the same amount of food per capita (Clutton-Brock and Harvey, 1977; Dunbar, 1988; Waser, 1977).

Because clumped foods are also monopolizable, however, certain females will be able to obtain more foods per patch than other females, regardless of group size. This priority of access to foods will be expressed as a dominance hierarchy. As group size and day-range length increase, the first to suffer energetic costs of increased group size will be the lowest-ranking, lactating females.

When foods are dispersed, individuals are likely to avoid the paths of other group members as they travel, and groups will forage in wide swaths (the Cody/Altmann foraging model in Rodman, 1988). Daily travel distance and, hence, energetic costs of travel need not increase in larger groups of swath foragers provided that they are able to fan out over a wider area. This may explain why path width, but not path length, is proportional to group size in patas monkeys (Chism and Rowell, 1988). Because foods are dispersed, females within groups will be unable to monopolize them, and strong dominance hierarchies may not be favored. Thus, daily ranging behavior and female dominance hierarchies within groups may covary because both are influenced by the distribution of resources.

### **Female–female aggression within and between groups**

The simplest explanation for the observed differences in female–female aggression within

Table 1

Differences in group size, home-range size, day-range length, female aggression among and within groups, and diet for 32 populations of 22 primate species

Species	Female aggression		Diet <sup>a</sup>	Reference(s)	Group size
	Among groups?	Within groups?			
<i>Lemur catta</i>	Yes	Yes	F/FO	Jolly, 1966	17 21
<i>Alouatta palliata</i>	No	No	FO/F	Whitehead, 1989; Crockett and Eisenberg, 1987	12 18
<i>A. seniculus</i>	Yes	?	FO/F	Sekulic, 1982a,b; Crockett and Eisenberg, 1987	9 13
<i>A. seniculus</i>					6 9
<i>Cebus olivaceus</i>	Yes	Yes	F/I	Robinson and Janson, 1987	8 25
<i>Cercopithecus aethiops</i>	Yes	Yes	F	Cheney, 1987; Isbell LA, unpublished	7.3 11.8
<i>C. aethiops</i>					17.2 49.9
<i>C. ascanius</i>	Yes	No	F/I	Cords, 1987a,b	15 45-50
<i>C. cephus</i>	?	?	F/I	Gautier-Hion and Gautier, 1988	3-5 8
<i>C. diana</i>	Yes	No	F/I	Whitesides, 1989, personal communication	20 27
<i>C. mitis</i>	Yes	No	F/I	Cords, 1987a,b; Butynski, 1990	11 19
<i>C. mitis</i>					13 33
<i>Erythrocebus patas</i>	Yes	No	I	Chism and Rowell, 1988; Cords, 1987a	16 47
<i>Cercocebus albigena</i>	Yes	Yes	F	Waser, 1977; Cheney, 1987; Melnick and Pearl, 1987	6 28
<i>Macaca fascicularis</i>	Yes	Yes	F/I	van Schaik et al., 1983; Cheney, 1987	? ?
<i>Macaca fuscata</i>	Yes	Yes	F	Cheney, 1987; Melnick and Pearl, 1987	40 100
<i>M. fuscata</i>					11 57
<i>M. fuscata</i>					15 37
<i>M. fuscata</i>					16 71
<i>M. fuscata</i>					11 57
<i>M. mulatta</i>	Yes	Yes	F	Cheney, 1987; Melnick and Pearl, 1987	6 ~90
<i>M. mulatta</i>					31 ~90
<i>M. silenus</i>	Yes	?	F/I	Johnson, 1985; Kumar and Kurup, 1985	6 27
<i>Papio anubis</i>	Yes	Yes	F/FO	De Vore and Hall, 1965	17 28
<i>P. anubis</i>					45 50.5
<i>Colobus badius</i>	No	No	FO	Struhsaker, 1975; Struhsaker and Leland, 1987	20 68
<i>C. badius</i>					9 68
<i>C. guereza</i>	Yes	No	FO	Oates, 1977a,b; Struhsaker and Leland, 1987	3 11
<i>Presbytis entellus</i>	Yes	No	FO	Cheney, 1987; Struhsaker and Leland, 1987	17 23
<i>P. entellus</i>					10 24

Table 1, extended

$\Delta$ (%)	Home range (ha)	$\Delta$ (%)	Day-range length (m)	$\Delta$ (%)	Reference(s)
	7.9				Mertl-Millhollen, 1988
+24	9.1	+15			
	11.6		324		Chivers, 1969
+50	10.9	-4	328	+1	
	5.1		375		Sekulic, 1982a
+44	7.4	+45	355	-5	
	0.7				Neville, 1972
+50	1.6	+129			
			?		de Ruiter, 1986
+212			?	SI <sup>b</sup>	
	7.0				Isbell LA, unpublished
+62	8.5	+21			
	19.4				Struhsaker, 1967
+190	33.7	+74			
	28.0		1595		Struhsaker and Leland, 1988
$\geq +200$	67.5	+141	1198	-25	
	18				Gautier-Hion and Gautier, 1974
$\sim +100$	45	+150			
	41		1019		Whitesides, 1989
+35	29	-29	1513	SI	
	26.8		1291		Butynski, 1990
+73	44.5	+66	1176	-9	
	15.2				Cords and Rowell, 1986
+154	23.0	+51			
	2340		3830		Chism and Rowell, 1988
+194	3200	+37	4220	NS	
			$\sim 900$		Waser, 1977
+367			$\sim 1950$	$\sim +117$	
			?		van Schaik et al., 1983
			?	SI	
	267		800		Ikeda, 1982
+150	470	+76	1500	SI	
	24				Maruhashi, 1982
+418	110	SI			
	250				Takasaki, 1981
+147	366	+46			
	380				
+344	1030	+171			Takasaki, 1981
	24				
+418	1100	+448			Takasaki, 1981
	130				Makwana, 1978
+1400	1340	SI			
			431		Makwana, 1978
+190			1248	+190	
	50				Johnson, 1985
+350	600	+1100			
	2383				De Vore and Hall, 1965
+65	4014	+68			
			2400		Sharman and Dunbar, 1982
+12			7500	+212	
	70.7				Struhsaker, 1975; Isbell LA, unpublished
+240	62.5	-12			
			578.3		Struhsaker and Leland, 1987
+656			592.5	NS	
	1.6	SI <sup>c</sup>			Dunbar and Dunbar, 1974
+267	2.5				
	18.0				Yoshiba, 1967
+35	26.6	+48			
	10.3				Sugiyama, 1967
+140	31.5	+206			

(continued)

**Table 1, continued**

Species	Female aggression		Diet <sup>a</sup>	Reference(s)	Group size
	Among groups?	Within groups?			
<i>P. melalophos</i>	?	No	FO	Bennett, 1983, 1986; Struhsaker and Leland, 1987	12 18
<i>P. rubicunda</i>	?	?	FO	Supriatna et al., 1986	3 8
<i>Gorilla gorilla</i>	No	No	FO	Fossey and Harcourt, 1977; Harcourt, 1979; Stewart and Harcourt, 1987	10 15
<i>G. gorilla</i>					≤5 11–12
<i>G. gorilla</i>					11 24
<i>G. gorilla</i>					3 5

<sup>a</sup> Dietary classifications: FO = folivorous; F = frugivorous; I = insectivorous; FO/F = primarily folivorous but also eats fruits; F/I = primarily frugivorous but also eats invertebrates; F/FO = primarily frugivorous but also eats foliage.

<sup>b</sup> SI = statistically significant increase in day-range length or home-range size with group size; NS = no statistically significant difference in day-range length or home-range size with group size.

groups (expressed as dominance hierarchies) and between groups may be that *when resources are limiting in abundance, females should be aggressive toward other groups regardless of the distribution of resources, but they should be aggressive within groups only when those limiting resources are clumped*. Figure 1 presents a model of the relationships hypothesized to exist between resource abundance and distribution and patterns of female–female aggression and ranging behavior.

A comparison of the model with what is known about primate diets reveals both trends and inadequacies. The species listed in Figure 1 are those for which data are sufficient to place them in the model. Some species for which there is evidence of intragroup competition were included without data on intergroup competition because in the species studied, intergroup competition is never absent when intragroup competition exists.

Diets of primate species are usually classified according to the foods that represent

greater proportions in their diets. Unfortunately, these may not be the same foods that are limiting or that determine whether competition will occur. For instance, although the two more folivorous species are separated from the more frugivorous species in this model, the frugivorous species are further split into two categories. In reality, many frugivorous species are likely to feed on both clumped and dispersed foods (see Table 1). For example, redtails (*Cercopithecus ascanius*) feed heavily on fruits, a clumped resource, but they also spend much of their time foraging for invertebrates, a dispersed resource (Cords, 1987b). Similarly, blue monkeys (*C. mitis*) feed primarily on fruits but also on leaves and invertebrates, both dispersed resources (Butynski, 1990; Cords, 1987b). It may be that fruits influence competition more for macaques (*Macaca* spp.), olive baboons (*Papio anubis*), gray-cheeked mangabeys (*Cercocebus albigena*), and wedge-capped capuchins (*Cebus olivaceus*) and that invertebrates influence competition more for

**Table 2**  
Association between the presence of intergroup aggression and increases in home-range size as a function of group size within species

		Are groups of females aggressive toward one another?	
		Yes	No
Do larger groups have larger home ranges?	Yes	12	1
	No	1	2

Fisher's Exact test,  $p = .07$  (Siegel, 1956).

**Table 3**  
Association between intragroup dominance hierarchies and increasing day-range length as a function of group size within species

		Do groups of females have strong dominance hierarchies?	
		Yes	No
Do larger groups have longer day-range lengths?	Yes	6	2
	No	0	6

Fisher's Exact test,  $p < .01$  (Siegel, 1956).



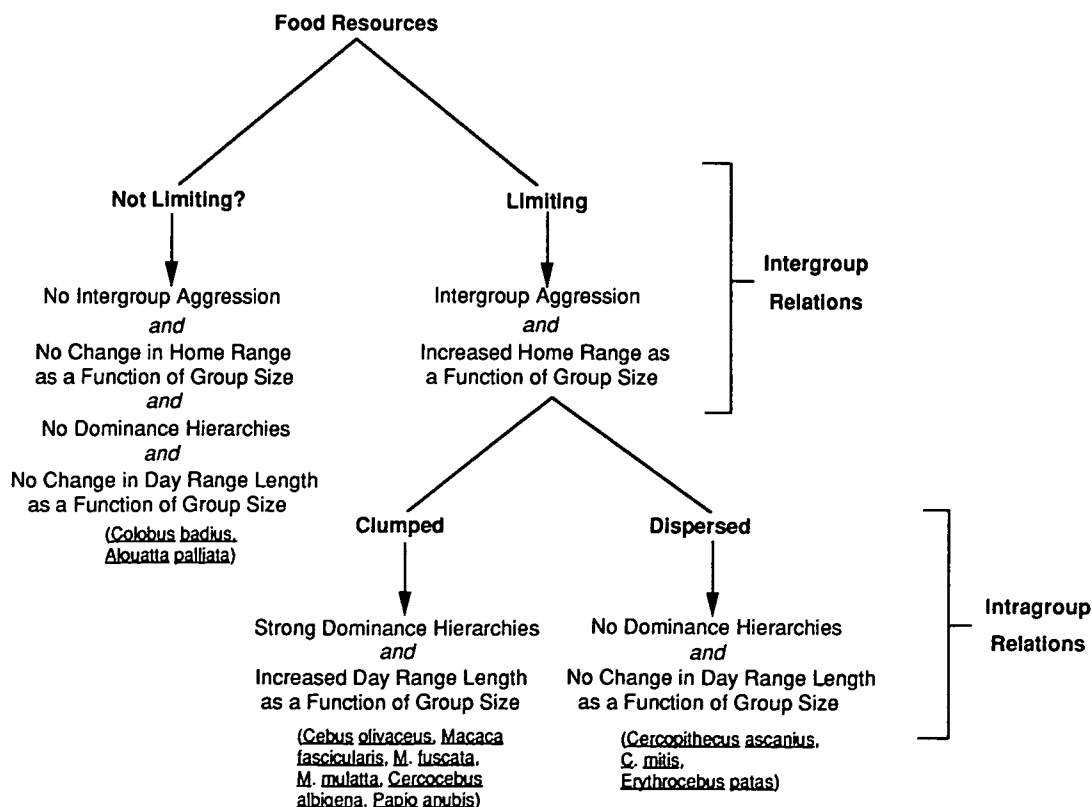
Table 1, extended

$\Delta$ (%)	Home range (ha)	$\Delta$ (%)	Day-range length (m)	$\Delta$ (%)	Reference(s)
			894		Bennett, 1983, 1986
+50			682	-24	
	33				Supriatna et al., 1986
+167	99	+200			
	490		350		Fossey and Harcourt, 1977
+50	810	+65	450	+29	
	200				Jones and Sabater Pi, 1971
$\geq +120$	1200	+500			
	1036		337		Schaller, 1963
+118	1554	+50	473	+40	
			332		Elliott, 1976
+67			592	+78	

<sup>c</sup> Difference considered significant here because although home-range size was not significantly correlated with group size, there was a statistically significant positive correlation between group size and food abundance within home ranges.

blue, redbtail, and patas monkeys. Another possibility is that individuals in species that feed on both clumped and dispersed foods might have the option to reduce competition with others in their groups by shifting from clumped to dispersed foods when patches are occupied by other group members (Chapman C, personal communication). Perhaps the proportion of time that individuals spend feeding or foraging on clumped versus dispersed foods would better address this problem.

Although the model presented here does not consider ultimate causes of living in groups, the fact that groups are aggressive toward each other *and* that home-range size increases as a function of group size in most species is consistent with Wrangham's (1980) hypothesis that females live in groups for cooperative defense of food resources. However, the model presented here differs from Wrangham's in that it focuses on different ecological conditions that influence relationships within and between groups and recog-



**Figure 1**  
Hypothesized associations between food abundance and distribution and patterns of female aggression and ranging behavior. Food abundance may affect whether larger groups will have larger home ranges and whether groups of females will be aggressive toward females of other groups. Food distribution may affect whether larger groups will have longer day-range lengths and whether females will be aggressive toward other females within their groups. Species listed are those for which sufficient data are available to include them in the model.

nizes more than two types of female relationships. Wrangham's model suggests that resources will only be defendable by groups of females if the resources are clumped in distribution and that dominance hierarchies will only exist when resources within those clumps are variable in quality. In his model, therefore, the distribution of resources influences both intra- and intergroup competition.

By contrast, in the model presented here, food distribution influences only intragroup competition, whereas food abundance influences intergroup competition. In this model, whenever foods limit reproductive success, groups of females should benefit by being aggressive toward one another because groups have the potential to reduce food abundance for other groups. Intergroup aggression is therefore expected to occur regardless of the ways in which foods are distributed within home ranges. This interpretation is supported by the finding that intergroup competition commonly occurs whether species are frugivorous, folivorous, or insectivorous.

In addition, in Wrangham's model, females are classified as either female bonded or non-female bonded depending on patterns of intergroup transfer. In female-bonded species, females do not transfer between groups and have frequent interactions and differentiated relationships within groups. In nonfemale-bonded species, females do transfer between groups and do not have differentiated relationships within groups. The model here reveals three types of relationships: species with no female transfer and with differentiated relationships (female bonded), species with female transfer and without differentiated relationships (nonfemale bonded), and species with no female transfer but without differentiated relationships (e.g., most guenons).

Although the present model is consistent with Wrangham's hypothesis that resource competition is the ultimate cause of living in groups (see also Isbell et al., in press), it is not necessarily inconsistent with the hypothesis that females ultimately live in groups for the benefit of reduced predation (Alexander, 1974; van Schaik, 1983). It has been suggested that predation also ultimately causes variation in female relationships within and between groups (van Schaik, 1989). In van Schaik's model, high predation risk forces females to live in cohesive groups, thereby increasing competition within groups and creating strong dominance hierarchies, whereas low predation risk allows groups to form that are less cohesive, thereby minimizing intragroup competition and creating egalitarian relationships. In contrast, the model presented here suggests that food resource abundance and distribution are by themselves sufficient to de-

termine the nature of female relationships within and between groups. Isbell et al. (1990) have shown that intergroup competition can indirectly result in increased predation rates, whereas van Schaik suggests that high predation results in increased intragroup competition. These observations illustrate how closely connected predation and competition may be, and it remains a central problem to resolve the causal relationships between them.

### Group size and reproductive rates

It is currently thought that animals living in groups inevitably incur food-related costs either in aggressive competition for resources from other group members or increased energetic expense in traveling to food sites (Alexander, 1974; Terborgh and Janson, 1986; van Schaik, 1983; Wrangham, 1980). The results presented here suggest that in species characterized by weak or absent dominance hierarchies within groups and no increase in daily travel distance as a function of group size, energetic costs associated with competition for resources within groups may not exist. This does not mean that intragroup competition does not occur in these species. It is more likely that these measures do not appropriately reflect competition for dispersed resources. An alternative indicator of competition when resources are dispersed might be that intervals between visits to a given area within the home range decrease as groups become larger. More frequent visits to food sites might reduce the availability of foods within groups, and reproductive rates might then decline as groups become larger. Because females in these species cannot monopolize dispersed foods, declining abundance should affect all females equally. This possibility is consistent with van Schaik's (1983) hypothesis that larger groups have lower reproductive rates because competition for food is greater in larger groups, but it has not yet been examined.

Alternative causes of declining reproductive rates in larger groups that are not based on resource competition have been examined only rarely. A decline in reproductive rate in larger groups is a form of density dependence that can limit population size. As mentioned above, there are several mechanisms other than food limitation that could produce this reproductive decline. First, diseases may spread more rapidly in larger groups, resulting in reduced reproductive rates (Pulliam and Caraco, 1984). Second, parasite loads may increase as group size increases (Freeland, 1976; Rubenstein and Hohmann, 1989) and may have a similar effect on reproductive rates.

A third explanation considers the effect of

behavioral differences between males and females on reproduction. Male and female reproductive strategies often conflict (Trivers, 1972). For example, infanticide is clearly costly to females, yet is beneficial to infanticidal males because it increases their own reproductive success (Hrdy, 1974, 1977). The effect of male-male competition on female reproductive rates may be underestimated, particularly among species that live in single-male, multifemale groups where male intrasexual competition may be more intense than in multimale, multifemale groups (e.g., Leland et al., 1984). Because larger groups are less defensible by single resident males than are smaller groups (Andelman, 1986; Cords, 1987a), females in larger single-male groups may be harassed either directly or indirectly by extra-group males more frequently than females in smaller single-male groups. That this phenomenon occurs in redtail monkeys is suggested by Struhsaker and Leland (1988). They found no evidence that resources influenced differential reproductive rates between two recently formed groups of redtail monkeys because these groups continued to use the same habitat as before when both groups were one. Struhsaker and Leland instead found that after the fission occurred, reproductive rates increased in the smaller group, which experienced less frequent male aggression than the larger group.

### Future directions

The results presented here suggest several directions for future studies of primate social systems. First, data on ranging behavior from more species should be collected. This requires, at the least, observations of groups of different sizes living in similar habitats. Second, comparisons of daily ranging patterns of species that have strong female dominance hierarchies with those that have no hierarchies should examine how resource distribution affects the ability of females to monopolize resources, why daily travel distance increases in some species but not in others, and other indicators of competition when female aggression within groups and positive associations between day-range length and group size do not provide evidence of competition. Third, although variation in food intake may translate into variation in reproductive success among groups of females with strong dominance hierarchies, yet to be explored is whether there are discernable patterns of variation in female lifetime reproductive success within groups with weak or no discernable dominance hierarchies. Finally, the effect of male reproductive strategies on female reproductive rates within groups is worthy of greater

attention because it provides an alternative, nonfood-based explanation for the decline in reproductive rates with increasing group size.

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