

CHAPTER TWO

Determinants of Group Size in Primates: The Importance of Travel Costs

COLIN A. CHAPMAN AND
LAUREN J. CHAPMAN



Identifying the ecological factors underlying group size and social organization has been a central theme of primate behavioral ecology (Gartlan and Brain 1968; van Schaik 1983; van Schaik and van Hooff 1983; Terborgh 1983; Butynski 1990). This interest has stemmed from the fact that group size in primates is highly varied across the order (1–320 members) and even within species (e.g., patas monkey, *Erythrocebus patas*: 21–36 members; table 2.1). Determinants of group size have been extensively evaluated in terms of costs and benefits. While disagreement exists as to the relative importance of the different potential advantages of grouping, various authors have suggested that it confers such predictable benefits that differences in group size can be explained by its disadvantages

Table 2.1 Group size, day range, body size, and social system for primates

Species	Group size ^a	Day range (km)	Body size (kg) ^b	Social system ^c	Reference ^d
Lemniridae					
<i>Lemur catta</i>	18.0	0.95	2.5	MF	1
<i>Lemur fulvus</i>	9.5	0.14	1.9	MF	1
<i>Lemur mongoz</i>	2.6	0.61	1.8	SF	1
Indriidae					
<i>Indri indri</i>	3.0	0.25	10.5	SF	1
<i>Propithecus verreauxi</i>	6.5	0.85	3.5	MF	1
Callitrichinae					
<i>Saguinus oedipus</i>	7.4	2.06	0.5	SF	2
<i>Saguinus fuscicollis</i>	4.7	1.37	0.4	SF	2
<i>Saguinus fuscicollis</i>	6.5	1.22	0.4	SF	2
<i>Saguinus imperator</i>	4.0	1.42	0.5	SF	2, 3
Pitheciinae					
<i>Callicebus moloch</i>	3.2	0.57	1.1	SF	4
<i>Callicebus moloch</i>	4.2	0.67	1.1	SF	4
<i>Callicebus torquatus</i>	3.9	0.82	1.1	SF	4
<i>Chiropotes albinasus</i>	25.0	3.75	2.5	MF	4
<i>Chiropotes satanas</i>	19.0	2.50	2.7	MF	4
Atelinae					
<i>Alouatta palliata</i>	9.1	0.12	5.7	MF	5
<i>Alouatta palliata</i>	12.2	0.60	5.7	MF	5
<i>Alouatta palliata</i>	15.5	0.44	5.7	MF	5
<i>Alouatta seniculus</i>	9.5	0.39	6.4	MF	5
<i>Alouatta seniculus</i>	7.1	0.54	6.4	MF	5
<i>Alouatta seniculus</i>	9.0	0.71	6.4	MF	5
<i>Ateles paniscus</i>	18.0 (3.0)	2.70	5.8	F-F	6
<i>Ateles belzebuth</i>	18.0 (3.0)	2.30	5.8	F-F	6
<i>Brachyteles arachnoides</i>	24.5	1.28	9.8	MF	8
<i>Brachyteles arachnoides</i>	45.0 (5.0)	0.63	9.8	F-F	9
<i>Lagothrix lagotricha</i>	33.0	1.00	5.8	MF	6
Cebinae					
<i>Saimiri oerstedii</i>	23.0	3.35	0.6	MF	6
<i>Saimiri sciureus</i>	42.0	1.50	0.6	MF	6
<i>Cebus albifrons</i>	15.0	1.85	2.6	MF	3, 6
<i>Cebus capucinus</i>	17.5	2.00	2.7	MF	6
<i>Cebus olivaceus</i>	20.0	2.30	2.3	MF	6, 7
<i>Cebus apella</i>	10.0	2.00	2.1	MF	6
Colobinae					
<i>Procolobus badius</i>	34.0	0.56	5.8	MF	10
<i>Procolobus badius</i>	20.0	0.60	5.8	MF	10
<i>Colobus guereza</i>	12.0	0.54	9.3	MF	10
<i>Colobus satanas</i>	15.5	0.46	9.5	MF	10
<i>Semnopithecus entellus</i>	19.0	0.36	11.4	MF	10
<i>Presbytis obscura</i>	10.3	0.95	6.5	MF	10
<i>Presbytis melalophus</i>	9.3	1.15	6.6	MF	10
<i>Presbytis melalophus</i>	14.0	0.61	6.6	MF	10
Cercopithecinae					
<i>Cercopithecus ascanius</i>	26.3	1.54	2.9	MF	11

Table 2.1 (continued)

Species	Group size ^a	Day range (km)	Body size (kg) ^b	Social system ^c	Reference ^d
<i>Cercopithecus ascanius</i>	32.5	1.45	2.9	MF	11
<i>Cercopithecus cephus</i>	10.0	0.90	2.9	MF	1
<i>Cercopithecus mitis</i>	32.6	1.14	4.4	MF	11
<i>Cercopithecus mitis</i>	18.7	1.30	4.4	MF	11
<i>Cercopithecus nictitans</i>	20.0	1.50	4.2	MF	1
<i>Cercopithecus pogonias</i>	15.0	1.75	3.0	MF	1
<i>Cercopithecus neglectus</i>	4.0	0.53	4.0	SF	11
<i>Chlorocebus aethiops</i>	24.0	0.95	3.6	MF	11
<i>Miopithecus talapoin</i>	112.0	2.32	1.1	MF	11
<i>Erythrocebus patas</i>	35.5	4.33	5.6	MF	11
<i>Erythrocebus patas</i>	20.6	2.25	5.6	MF	11
<i>Lophocebus albigena</i>	14.4	1.27	6.4	MF	12
<i>Cercocebus galeritus</i>	19.0	1.29	5.5	MF	1
<i>Papio c. cynocephalus</i>	80.0	6.40	15.0	MF	12
<i>Papio c. ursinus</i>	47.2	10.46	16.8	MF	12
<i>Papio c. ursinus</i>	45.0	4.67	16.8	MF	12
<i>Papio c. hamadryas</i>	68.0 (7.3)	8.60	9.4	F-F	13, 14
<i>Macaca fascicularis</i>	27.0	1.90	4.1	MF	12
<i>Macaca nemestrina</i>	35.0	2.00	7.8	MF	12
<i>Theropithecus gelada</i>	320.0 (113)	2.50	13.6	F-F	1
Hylobatidae					
<i>Hylobates agilis</i>	4.4	1.22	5.7	SF	15
<i>Hylobates klossii</i>	3.7	1.51	5.9	SF	15
<i>Hylobates lar</i>	3.5	1.49	5.3	SF	15
<i>Hylobates syndactylus</i>	4.0	0.79	10.6	SF	15
<i>Hylobates syndactylus</i>	5.0	0.97	10.6	SF	15
<i>Hylobates syndactylus</i>	3.0	0.74	10.6	SF	15
<i>Hylobates syndactylus</i>	3.8	0.93	10.6	SF	15
Pongidae					
<i>Pongo pygmaeus</i>	1.8	0.50	37.0	F-F	16
<i>Pan troglodytes</i>	28.0 (4.0)	3.90	31.1	F-F	1
<i>Gorilla gorilla</i>	9.0	0.70	93.0	MF	17

^aThe number in parentheses is the average subgroup size for species with a fission-fusion social organization.

^bPrimate body weights are for adult females from Clutton-Brock and Harvey 1977b.

^cMF, multifemale groups; SF, single-female groups; F-F, fission-fusion societies.

^d1, Clutton-Brock and Harvey 1977b; 2, Goldizen 1986; 3, Terborgh 1983; 4, Robinson, Wright, and Kinzey 1986; 5, Crockett and Eisenberg 1986; 6, Robinson and Janson 1986; 7, Robinson 1988; 8, Strier 1987; 9, Milton 1984; 10, Struhsaker and Leland 1986; 11, Cords 1986b; 12, Melnick and Pearl 1986; 13, Sigg and Stolba 1989; 14, Stambach 1986; 15, Leighton 1986; 16, Rodman and Mitani 1986; 17, Stewart and Harcourt 1986.

(Terborgh and Janson 1986; Wrangham, Gittleman, and Chapman 1993; Janson 1992).

Benefits of grouping can be considered to fall within three broad categories: predator avoidance, foraging advantages, and avoidance of conspecific threat. Predator avoidance hypotheses suggest that group living facilitates (1) increased probability of predator detection (Rodman 1973b; Struhsaker 1981; Gautier-Hion, Quris, and Gautier 1983; Boinski 1987a, 1989; van Schaik and van Noordwijk 1985, 1989; Cords 1990b; Norconk 1990; Terborgh 1990; Chapman and Chapman 1996), (2) greater confusion of a predator trying to focus on an individual prey (Morse 1977), (3) a decreased probability of each individual being captured by predators (Hamilton 1971; Wolf 1985), and (4) increased defense against predators (Struhsaker 1981; van Schaik and van Noordwijk 1985; Boinski 1987a; Gautier-Hion and Tutin 1988; van Schaik and van Noordwijk 1989; van Schaik and Hörstermann 1994). Foraging benefits may include (1) access to foods otherwise not available (e.g., adult males opening large fruits that immatures cannot open: Struhsaker 1981; Gautier-Hion, Quris, and Gautier 1983; Waser 1984a), (2) efficient use of shared resources (e.g., not returning to areas just depleted by conspecifics: Cody 1971; Terborgh 1983; Cords 1986a, 1987; Whitesides 1989; Oates and Whitesides 1990; Podolsky 1990), (3) increased feeding rates when in a group, possibly associated with a decreased need for vigilance (Klein and Klein 1973; Munn and Terborgh 1979; Podolsky 1990), (4) increased resource detection (Gartlan and Struhsaker 1972; Struhsaker 1981), and (5) cooperative resource defense (Wrangham 1980; Garber 1988a). Recently, several authors have cautiously suggested that the risk of conspecific attack (e.g., infanticide) from nongroup members may also favor group living (Watts 1989; van Schaik and Dunbar 1990; Smuts and Smuts 1993; van Schaik and Kappeler 1993; Janson and Goldsmith 1995; Treves and Chapman 1996). If conspecifics outside of a group create situations in which group members have to bear some costs, such the risk of infanticide, group members should adopt strategies to minimize this cost, such as cooperative defense. The number and age/sex composition of the animals cooperating against outsiders would influence the success of deterring nongroup members.

While the relative importance of these different advantages of group living remains controversial, there has been little disagreement when it comes to considering the disadvantages. The most widely acknowledged cost of group living is within-group feeding

competition. Such competition has clear fitness effects, including increased mortality (Dittus 1979) and lower female reproductive rates (Whitten 1983). Within-group competition can reduce foraging efficiency in two ways: direct contests over food resources (interference competition: Nicholson 1954; Janson 1985, 1988a,b; van Schaik 1989) or reduction of resources merely by competitors using the resource, independent of any direct interaction (exploitation competition: Terborgh 1983; Janson 1988b; van Schaik and van Noordwijk 1988). The relative frequency of occurrence of these two types of competition has rarely been quantified. This probably stems from the fact that while contest competition is obvious (e.g., two animals engaged in a fight over a food source), exploitation competition is difficult to verify. If one animal simply beats a second animal to a food source, when the second animal approaches the place where that food source was, it is difficult to say whether there is no food left, or whether the animal does not wish to eat in the area.

This agreement on the costs of group living has led to the development of a model suggesting that exploitation competition can limit group size whenever an individual moves more while in a group than alone. This ecological constraints model, which is detailed in the next section, highlights the importance of understanding determinants of group movement in order to comprehend what constrains the size of primate groups. The foundations of this model have been well established through studies on a variety of vertebrates (Bradbury and Vehrencamp 1976; Pulliam and Caraco 1984; Clark and Mangel 1986; Elgar 1986). However, primates are a particularly well-suited group for testing the generality of the model, since a great deal of descriptive data is available on the order and there is great variation in foraging strategies and group size (see table 2.1).

Currently, we understand little about the mechanisms underlying the ecological constraints model. In this chapter, we propose that an increase in group size leads to increased travel costs through two mechanisms: (1) patch depletion and (2) avoidance of overlap of search field. We review and evaluate support for these two mechanisms, identify gaps in our knowledge, and outline directions for future research.

Evidence suggests that perceived predation risk alters animals' selection of habitats, length of time spent in a patch, and thus probably the size of the group of which an animal chooses to be a

member. For example, desert baboons (*Papio cynocephalus ursinus*) spend less time than expected feeding in high-risk, food-rich habitats, but more time than expected feeding in low-risk, relatively food-poor habitats (Cowlshaw 1997). Unfortunately, there is little quantification of how animals respond to perceived predation risk. As a result, we concentrate on how ecological conditions can constrain group size, but recognize the effect that predation risk could have on how animals weigh the costs and benefits of groups of different sizes (see Boinski, Treves, and Chapman, chap. 3, this volume).

Conceptual Framework of Ecological Constraints on Group Size

Animals must forage over an area that can meet their energetic and nutritional requirements. Therefore, an increase in group size may be expected to increase the area that must be searched to find adequate food supplies (Eisenberg, Muckenhirn, and Rudran 1972; S. A. Altmann 1974; Bradbury and Vehrencamp 1976). Thus, individuals must travel farther and expend more energy if they are in a large group than if they forage in a smaller group or alone (Wrangham, Gittleman, and Chapman 1993; Steudel, chap. 1, this volume). With an increase in the time and energy spent traveling, a point will be approached at which energy spent in travel exceeds the energy obtained from the environment, and a smaller group size should become advantageous. In this way ecological factors can influence movement patterns and foraging efficiency and thereby constrain the size of groups that can efficiently exploit available food resources.

This model assumes that an increase in group size will lead to an increase in within-group feeding competition, which may be expressed as increased day range. The nature of this relationship will vary depending on the nature of the resources used by particular species. With frugivorous and possibly folivorous primates, large groups may deplete patches faster than smaller groups, resulting in longer day ranges. For insectivorous species, resources may not occur in patches, or the patches may not be divisible, so additional group members may lead to an increase in the overlap of individual search fields, reducing per capita encounter rates with food and increasing the area that must be searched. (A search field is the area over which a foraging animal is visually exploring for food items.) As a result, the ecological constraints model has one or two key assumptions: (1) food items are assumed to occur in discrete deplet-

ing patches, and an increase in group size leads to more rapid patch depletion, necessitating increased travel between patches and/or (2) it is assumed that as group size increases, individual search fields overlap, reducing per capita encounter rates with food, and consequently the size of the search area increases.

The Patch Depletion Process

For species that use resources that occur in discrete depleting patches, an increase in group size increases the rate of patch depletion, simply because there are more mouths to feed. Once a patch is depleted, animals will have to travel on in search of other feeding sites. Thus, an increase in group size increases the time and energy invested in travel. For this process to operate, resources must occur in patches and patches must be depleting.

Examining the assumption that food items occur in discrete depleting patches has proved difficult. The first challenging step has simply been to define a patch. A number of theoretical or conceptual definitions have been proposed (S. A. Altmann 1974; Hassell and Southwood 1978; Addicott et al. 1987). However, most field studies have simply considered a patch to be an aggregation of food items structured so that animals can use the area without interrupting their feeding. For forest-dwelling primates this definition is often operationalized as an isolated tree (e.g., a fruiting fig tree; Chapman 1988a, 1989a, 1990a,b; Symington 1988b; White and Wrangham 1988; Strier 1989; Chapman, White, and Wrangham 1994).

While this definition may apply to large-bodied primates that specialize on high-quality fruit resources, it is difficult to see how the resources of other species could be considered to occur in patches. For insectivorous primates, resources may be more or less uniformly dispersed (or they may occur in indivisible patches). For example, redbtail monkeys (*Cercopithecus ascanius*), for which insects constitute 22–28% of the diet (Cords 1987), typically feed in groups that are dispersed over a 50 m swath. Individuals catch isolated insects, and rarely does an animal stay at an insect capture site for more than a few seconds. These animals tend to congregate at fruiting trees, yet it is rare to find all group members feeding in one tree. For such species, insects may represent a dispersed food resource, and even when they are feeding on patchy food resources (e.g., a fruiting tree), they may have the option of reducing competi-

tion by shifting from feeding in the fruit patch to searching nearby for insects. The decision to shift between fruit patch feeding and searching for insects probably depends on an interaction between competition, which is a function of the size and richness of a fruit patch, and the density of dispersed insects. With species such as the redbellied monkey, the question then becomes, does the mechanism involving avoidance of overlap of search fields operate, or, since they rely on both fruit and insect resources, to what degree are they constrained by one process over the other, or does the model apply at all?

If we follow the simplifying assumption that for many primates a patch is equal to a tree, the question becomes whether or not primates typically deplete the patches they use. Theoretically, a patch may be considered depleted when the feeding activity of the consumer has led to the disappearance of all food items. However, as food items become rare within a tree, they become progressively harder to obtain. Thus, a patch will be functionally depleted before all of the food items are eaten. From this perspective, patches can be considered depleted when the rate of food intake drops to a level equal to the average intake in the environment (Charnov 1976; Stephens and Krebs 1986).

Although the concept is fundamental to several models of primate social organization (van Schaik 1989; Isbell 1991; Cheney 1992), there are few data on primate patch depletion (Janson 1988b). We have examined the assumption that primates deplete patches using four different species (cebus monkeys, *Cebus capucinus*; spider monkeys, *Ateles geoffroyi*; howler monkeys *Alouatta palliata*; and chimpanzees, *Pan troglodytes*: Chapman 1988a; Chapman, Wrangham, and Chapman 1995). Four lines of evidence suggest that patch depletion occurs. First, all species were commonly observed feeding in a number of individual trees of the same species in direct succession, rarely revisiting the same tree on the same day (see also Garber 1988a). Second, for most trees, the rate of food intake was higher at the start of the feeding bout than later. (For some tree species, feeding rate did not change over the feeding bout, suggesting that this relationship is not caused simply by satiation.) Third, for species with variable group sizes (e.g., spider monkeys and chimpanzees), members spent more time traveling as subgroup size increased, suggesting that large subgroups deplete patches of equal size faster than smaller subgroups. Finally, for species with

variable group sizes, the amount of time spent feeding in a patch was generally a function of the size of the patch and the number of animals using the patch. Preliminary data on the folivorous colobus (*Procolobus badius*) provides similar evidence of patch depletion for some trees (C. A. Chapman and L. J. Chapman unpub.).

These data, and studies reviewed by Janson (1988b, 1992), suggest that some primate species frequently deplete their feeding patches. However, for specific food types or during some seasons food resources may be so abundant that within-group competition is relaxed. For spider monkeys, for example, the rate of intake of food items during a feeding bout in a single patch is typically higher at the start of the feeding bout than later in the same feeding session (Chapman 1988a). However, when spider monkeys feed in large fruiting fig trees (*Ficus* sp.), fruit intake rate does not change during the feeding bout, suggesting that fruit is so abundant in these trees that spider monkeys are unable to deplete them. Similarly, in brown capuchins (*Cebus apella*), Janson (1988a) found that per capita feeding time decreased with group size in small patches but was independent of group size in large patches. In primate populations that may have been reduced below carrying capacity by disturbance (Collins and Southwick 1952; Work et al. 1957) or hunting (Eaton 1990; Chapman and Onderdonk 1998), patch depletion may be more common than in high-density populations.

Three aspects of depleting resources can affect movement patterns and in turn affect group size: patch size, density, and distribution (fig. 2.1). Patch size may influence day range directly by determining the amount of food available in a given patch. A large group will spend less time in a depleting patch (e.g., a fruit tree with a finite supply of ripe fruit) of a given size than a smaller group because it depletes the patch more quickly. Once a patch is depleted, animals will have to travel in search of other feeding sites. At this point, the density of patches directly influences travel costs and group size. When resource patches occur at a high density, the distance to the next patch is short, travel costs are low, and animals can afford to be in large groups. In this situation, additional costs associated with being a member of a large group, such as the time to visit many patches, can be easily recovered. For example, the chimpanzees of Kibale National Park, Uganda, are feeding on the fruits of *Pseudospondias microcarpa*, the distance to the next

ing tree is short because *P. microcarpa* is found in groves. In 1993 one small grove contained twenty-eight large fruiting trees with an average interpatch distance of only 35 m (C. A. Chapman and L. J. Chapman, unpub.). At this time chimpanzees were found in large subgroups (Chapman, Wrangham, and Chapman 1995), and although these large subgroups had to travel to many *P. microcarpa* trees in a single day, the distance between feeding trees was small. While the density of trees is often a good index of presumed travel costs, travel costs are more appropriately evaluated relative to intake. Thus, if the patches are small or unproductive, travel costs could be high relative to intake, even if the patches are close together. Resources such as corms and insects may occur in small or unproductive patches, but for frugivorous primates feeding in large canopy trees, or even smaller understory trees, when trees are at high densities, travel costs are low, permitting large groups.

The distribution of patches is a critical parameter that is often ignored. When large or small food patches are clumped, the distance to the next patch is short, travel costs are low, and animals can form large groups as long as the clump of patches can support the group's foraging activity (fig. 2.1B). At such times, any additional cost associated with being a member of a large group, such as the need to visit many patches, can be easily recovered. If food patches are clumped, scarce, and found in either large or small patches, animals may not be constrained from being in large groups in the short term (e.g., spider monkeys: Chapman, Wrangham, and Chapman 1995), but may be forced to live in small groups if those resource conditions persist on a longer temporal scale. When food patches are uniformly distributed, regardless of their size, we expect food density to be the key determinant of group size for the following reasons: when patches are dense, animals can congregate because the distribution and density of their food resources do not impose high travel costs. When depleting patches are rare, small groups are favored. Individuals minimize travel costs by being in small groups that can feed in a single patch for long periods, since there are only a few mouths to feed, and patches are depleted slowly. Similarly, when depleting patches are uniformly distributed, large, and rare, small groups will be advantageous.

While the size, density, and distribution of patches may be key variables determining travel costs and group size, the situation can be assessed in a simpler fashion. When animals generally deplete

Patches Depleting and Clumped

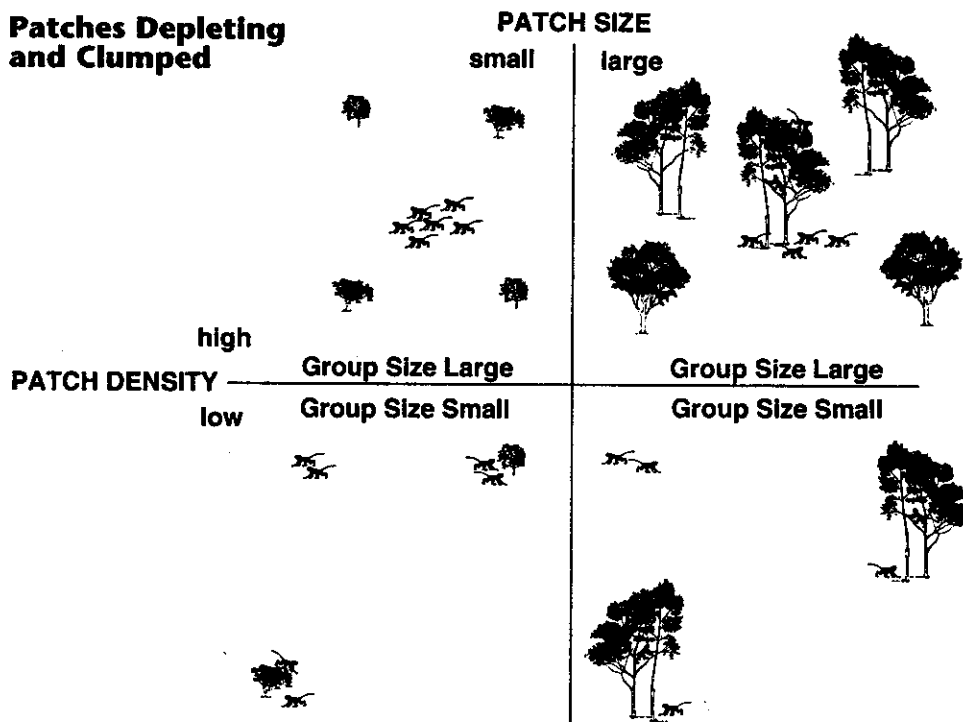
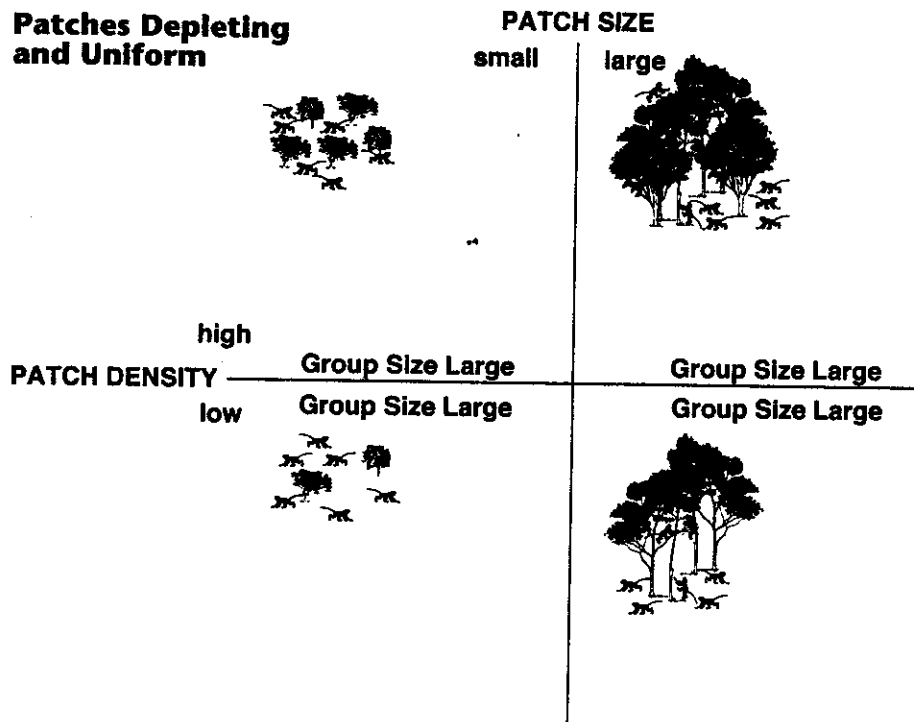


Figure 2.1 Hypothesized associations between food states (patch size, density, and distribution) and primate group size. Two classes of depleting patches are considered: (*this page*) clumped and (*opposite page*) uniformly distributed. Within these classes, each "quadrat" represents a different patch size/patch density combination. The predicted group size is indicated in each quadrat. This figure represents extremes of the parameters and should not be considered to represent all situations an animal could experience. Its purpose is to visualize how the size, density, and distribution of patches could influence travel costs and thereby constrain group size. A hypothetical travel route is illustrated for each ecological condition.

the patches they use, measures of habitat-wide food availability will probably adequately reflect the size, density, and distribution of patches. Thus, group size may be a function of food availability. An illustration of this is provided in figure 2.2 for the spider monkeys of Santa Rosa National Park, Costa Rica. This species has a very flexible fission-fusion type of social organization. In Santa Rosa, subgroup size can range from one to thirty-five individuals, but on average about five individuals are found traveling together. For this population, 50% of the variance in mean monthly subgroup size can be predicted from relatively crude measures of the size, density, and distribution of food patches (Chapman, Wrangham, and Chapman 1995).

**Patches Depleting
and Uniform**



Testing the Model: Patch Depletion Process

The relationships between group size, factors thought to influence exploitation competition (patch size, density, and distribution), and day range have been examined in detail for only a few primate species (e.g., spider monkeys: Chapman 1988a, 1990a; Symington 1987; Chapman, Wrangham, and Chapman 1995; woolly spider monkeys (*Brachyteles arachnoides*): Milton 1984; Strier 1989; howler monkeys: Leighton and Leighton 1982; Chapman 1988a, 1990b; chimpanzees: White and Wrangham 1988; Chapman, White, and Wrangham 1994; Chapman, Wrangham, and Chapman 1995; bonobos (*Pan paniscus*): White and Wrangham 1988; Chapman, White, and Wrangham 1994), and rarely have all of the components (size, density, and distribution of patches) been examined in one study. Tests of the ecological constraints model are difficult to conduct because one must relate changes in group size to a set of ecological conditions, and for most species group size tends to be only slowly modifiable through births and deaths. To examine this model with such species would require either a long-term research program or a correlative approach requiring the habituation of many

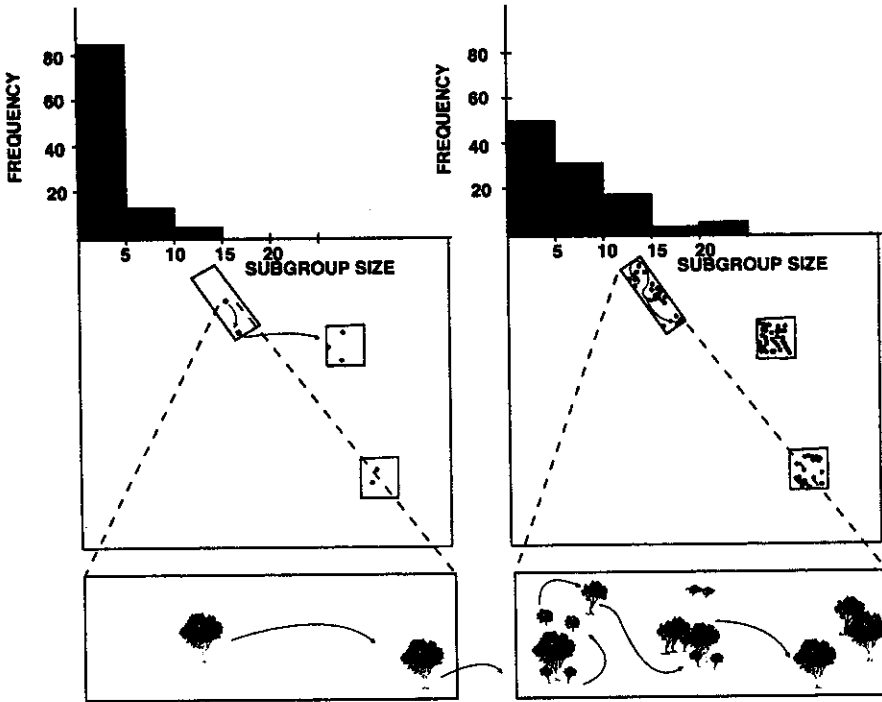


Figure 2.2 The ecological conditions corresponding to the sample periods when the spider monkeys in Santa Rosa National Park, Costa Rica, were observed to occur in (*left*) the smallest and (*right*) the largest subgroups. The frequency histogram of subgroup size is depicted at the top of the figure. The large squares represent the home range of the spider monkeys. Within their home range were three 4 ha ecological sampling grids (represented by the smaller squares or rectangles). Each dot within a sampling grid represents a food patch available to the spider monkeys. One of these sampling grids is expanded to illustrate the actual size, density, and distribution of food trees in the sampling grid. (Adapted from Chapman 1990b.)

groups. Consequently, researchers have often used fission-fusion societies (e.g., chimpanzees, spider monkeys, woolly spider monkeys) to examine the ecological constraints model (Milton 1984; Symington 1987; Chapman 1990a; Chapman, Wrangham, and Chapman 1995). In fission-fusion societies, animals from a single community are found in small subgroups that change size and composition frequently (i.e., two or three times a day). Because subgroup size is flexible, animals can respond to ecological changes that occur over short temporal and spatial scales. It is then possible to relate short-term variation in food resources to changes in subgroup size (Klein and Klein 1977; Milton 1984; Symington 1987; Chapman 1990a,b).

Studies of fission-fusion societies have provided support for

many of the components of the ecological constraints model. Relationships between patch size and feeding group size has been documented for woolly spider monkeys (Strier 1989), howler monkeys (Leighton and Leighton 1982; Chapman 1988a), and chimpanzees (White and Wrangham 1988; Ghiglieri 1984). In spider monkeys (*Ateles paniscus*) in Peru, 62% of the variance in monthly subgroup size was accounted for by habitat-wide food availability (Symington 1987). Symington also found that individuals in larger subgroups travel farther each day and spend less time feeding than individuals in smaller subgroups. Based on two 6-year studies, Chapman (1990a,b) and Chapman, Wrangham, and Chapman (1995) were able to explain 50% of the variance in spider monkey subgroup size and 22% of the variance in chimpanzee subgroup size using measures of patch size, density, and distribution. Furthermore, during specific periods when the chimpanzees were feeding almost exclusively on one species of fruiting tree and it was possible to measure food abundance and travel costs directly, 77% of the variance in subgroup size could be explained by the density and distribution of resources (Chapman, Wrangham, and Chapman 1995). Although this chimpanzee study community had a diverse diet, changes in the abundance of only three key fruiting tree species (*Mimusops bagshawei*, *Pseudospondias microcarpa*, *Uvariopsis congestis*) correlated with changes in chimpanzee party size (C. A. Chapman and R. W. Wrangham, unpub.).

Wrangham, Gittleman, and Chapman (1993) conducted an empirical review to determine whether variation in primate and carnivore group size relates to exploitation competition. They suggested that two factors directly affect the intensity of exploitation competition: density of food resources and travel efficiency. These variables are important because they influence the relationship between group size and per capita energy balance. Thus, as food density rises (with travel efficiency constant), more individuals can feed within a given travel distance. If selection favors large groups, increases in food density will therefore result in increased group size. Similarly, these authors argue that as travel efficiency rises, the intensity of competition falls, because by traveling farther, each individual encounters more food. A multiple regression analysis using indices of the density of food resources and travel efficiency explained up to 46% of the variance in primate group size and 57% of the variance in carnivore group size (see Janson and Goldsmith 1995 for an alternative analysis).

Avoidance of Overlap of Search Fields

Several studies have provided evidence to suggest that patch depletion may not occur in some species (e.g., folivores) or may occur only sometimes in others (e.g., when species eating fruits and insects congregate to feed in a fruiting tree). An alternative explanation to account for group size constraints in these situations is the avoidance of search field overlap. Larger groups travel farther than smaller groups in some species (*Lophocebus albigena*: Waser 1974, 1977a; Olupot et al. 1994; *Macaca fascicularis*: van Schaik et al. 1983; van Schaik and van Noordwijk 1988; *Cebus olivaceus*: de Ruiter 1986; *Cebus apella*: Janson 1988a; *Ateles paniscus*: Symington 1988a,b), but not all (*Procolobus badius*: Isbell 1983; *Papio anubis*: Bronikowski and Altmann 1996). Isbell (1983) documented a red colobus group of nine individuals that had a day range of 578 m, while a group of sixty-eight red colobus had a day range of 593 m (Isbell 1983, 1991; Struhsaker and Leland 1979, 1986). One could question the generality of this finding with respect to red colobus: it could simply be that the group of sixty-eight individuals had significantly more resources in its home range than the group of nine individuals. Alternatively, it may be that folivores like the red colobus do not deplete leaf resources (Isbell 1991).

A second situation in which the patch depletion process may not be operating to constrain group size involves species that rely on dispersed food items (or small nondivisible patched ones), such as some insects. For such species, additional group members may not increase the rate of patch depletion and thus may not lead to increased day ranges.

For species that either do not deplete the patches in which they feed or which feed on dispersed foods, an alternative process may be operating. As group size increases, individual search fields may overlap, reducing per capita encounter rates with food, thereby increasing the area that must be searched to find food. Van Schaik et al. (1983) described such a process in their study of long-tailed macaques (*Macaca fascicularis*). In this species time spent traveling increased monotonically with group size ($n = 7$ groups). Long-tailed macaques have a mixed diet that includes not only a significant proportion of fruit, but also more dispersed foods including insects; young leaves, and mushrooms (van Schaik and van Noordwijk 1988). Van Schaik et al. (1983) suggested that foraging animals tend to move away when approached by others, presumably since their conspecifics reduce the availability of dispersed food items. They termed this behavioral mechanism "pushing forward."

Chapman (1990b) conducted a field study on a group of white-faced capuchin monkeys (*Cebus capucinus*) to examine the ecological constraints model. Since this species has cohesive groups, it was hypothesized that group members would spread out to reduce within-group competition. Contrary to what was predicted, inter-individual distance was not related to the density and distribution of tree resources. However, when fruiting trees occurred at low densities and patch depletion was more likely, capuchin monkeys spent more time eating insects. Similarly, when the monkeys were using small trees that could hold only a few individuals at a time, again insect feeding was prevalent. This finding suggests that within-group competition may be reduced by shifting from feeding at a fruiting tree to searching nearby for insects when the fruit patch is occupied by others. Identifying mechanisms whereby species reduce within-group competition will be a profitable avenue for future research. A detailed quantification of intake and movement rates in relation to nearest neighbors among insectivorous primates or species whose diets are composed of corms and bulbs of grasses (Whiten, Byrne, and Henzi 1987) is needed to understand the interactive and independent effects of patch depletion and search field overlap on travel costs.

Pushing Forward Mechanism

For animals that are feeding on dispersed food items, it may be costly to have to share the area that is being searched for food because such sharing will lead to a reduction in per capita encounter rates with food. To avoid overlap of search fields, animals may move on to new areas. If increasing group size increases the tendency for search fields to overlap, then larger groups will tend to travel farther than smaller groups to avoid the overlap of search fields. The "pushing forward" mechanism has not been fully explored and may be applicable to species that forage extensively on insects or species that feed on grasses, corms, or bulbs. This pushing forward process could operate for purely ecological reasons, whereby animals avoid others entering their foraging space and depressing their rate of food intake (van Schaik and van Noordwijk 1988). Alternatively, ecological factors may interact with social factors to produce the observed patterns (e.g., animals avoiding dominants approaching from behind). Observations on chimpanzees suggest that displacements can occur for social reasons. When subadult male chimpanzees are feeding in large fruiting trees, they are often displaced from the tree by adult males, even when there appear to be sufficient

feeding locations in the tree for all members of the subgroup and when adjacent trees may also be fruiting. Such displacements may ensure the maintenance of the dominance hierarchy, but they also directly influence the immediate movement patterns of the animals involved. An intriguing avenue for future research is the relative importance of exploitation competition versus social factors in determining the rate and extent of pushing forward. If some proportion of the pushing forward effect is a function of social avoidance, this may represent a hidden cost of sociality that has not been fully investigated (Smuts and Smuts 1993). When groups are feeding on very small fruit patches (e.g., shrubs) or slowly depleting one-animal insect patches (e.g., bark insects), investigations integrating local food resource availability, the tendency to be pushed forward, and the dominance rank of the patch holder may provide a means to explore social versus ecological influences on the pushing forward mechanism.

It seems likely that the pushing forward process may be affected differently by food types that engender aggressive (contest) food competition (e.g., small patches in which only one animal can feed) than by foods that engender purely exploitation (scramble) competition (e.g., dispersed food items). Resources that engender contests may not result in increased travel distances in all situations. For example, if a subordinate animal is feeding in a small patch in which only one animal can feed, it may be aggressively displaced by a dominant animal, leading to increased travel, but if the dominant has access to the patch, it may not give it up, and no increased travel will occur. When feeding on dispersed items that engender exploitation competition, both dominant and subordinate animals may avoid overlap of search field by increasing travel. Investigations of the degree to which displacements occur with respect to food type may provide insights into primate grouping patterns.

Conclusions: What Next?

The current body of evidence supports the notion that exploitation competition can limit primate group size whenever a group must travel farther per day than a solitary forager to satisfy its food requirements. Animals must forage over an area that can meet their energetic and nutritional requirements. Therefore, an increase in group size may be expected to increase the area that must be searched to find adequate food supplies. Thus, individuals must travel farther and expend more energy if they are in a large group

than if they forage in a smaller group or alone. With an increase in the time and energy spent traveling, a point will be approached at which energy spent in travel exceeds the energy obtained from the environment, and a smaller group size should become advantageous. In this way ecological factors can influence movement patterns and foraging efficiency and thereby constrain the sizes of groups that can efficiently exploit available food resources.

To date, detailed tests of the ecological constraints model are limited to a relatively few studies of species that have similar ecological requirements and similar social systems. In addition, the model rests on a number of assumptions for which there are reasons to question their widespread acceptance. For example, it is unclear whether the ecological constraints model is useful in accounting for variation in group size in insectivorous species that rely on dispersed food items or in folivores that have been suggested to feed in nondepleting patches. Furthermore, tests of the model have been primarily restricted to species with fission-fusion social organizations. Thus, it may be useful to ask how well a model developed through assessment of the short-term costs and benefits of being in a "subgroup" that changes in size and composition a number of times throughout the day will apply to "group" sizes that are relatively stable, modified only by births and deaths. With questions like these remaining to be answered, it is clear that investigations attempting to understand what determines animal group size will be an exciting area for future research.

Areas of future research include:

1. Do strict folivores, such as red colobus or black-and-white colobus (*Colobus guereza*), deplete leaf resources (paying attention to the fact that not all leaves are the same)? Do increases in folivore group size lead to increased day range?
2. How does competition over dispersed foods, such as possibly insects, corms, or bulbs, increase with group size? Is the shape of the relationship between group size and per capita foraging loss the same for species feeding on clumped depleting patches as for species feeding on dispersed food resources?
3. Is there a social component to the pushing forward effect that is independent of an ecological component?
4. Is the pushing forward process affected differently by food types that engender aggressive (contest) food competition than by foods that engender purely exploitation (scramble) competition?
5. How do primate populations reduced by disease or hunting respond to a reduction in within-group competition, and how does this influence group movement?