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Group size in folivorous primates: ecological constraints and the possible influence of social factors

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Abstract The ecological-constraints model assumes that food items occur in depletable patches and proposes that an increase in group size leads to increased day range due to more rapid patch depletion. Smaller groups become advantageous when an increase in travel costs is not repaid by an increase in energy gained or some other fitness advantage. On the other hand, we also know that group size can be influenced by social factors. Here we contrast the diet and group size of red colobus (*Procolobus badius*) and black-and-white colobus (*Colobus guereza*) in Kibale National Park, Uganda to consider how ecological and social factors are affecting their group sizes. Subsequently, we examine whether the insights gained from this detailed comparison can provide an understanding of why the social organization and group size of mantled howlers (*Alouatta palliata*) and black howlers (*A. pigra*) differ. Two groups of red colobus and two groups of black-and-white colobus were studied over 10 months. Red colobus groups were larger (48 and 24) than black-and-white colobus groups (9 and 6). The two groups of red colobus overlap home ranges with the two groups of black-and-white colobus; 75% and 95% of their home ranges were within red colobus's home range. There was a great deal of similarity in the plant parts eaten by the two species and both species fed primarily on young leaves (red colobus 70%, black-and-

white colobus 76%). In terms of the actual species consumed, again there was a great deal of similarity between species. The average dietary overlap among months for the two neighboring groups of red colobus was 37.3%, while the dietary overlap between the red colobus and the black-and-white colobus group that had its home range almost entirely within the home range of the red colobus groups averaged 43.2% among months. If ecological conditions were responsible for the difference in group size between the two colobine species, one would expect the density of food trees to be lower in the home ranges of the black-and-white colobus monkeys, since they have the smaller group size. We found the opposite to be true. Both black-and-white colobus groups had more food trees and the cumulative size of those trees was greater than those in the red colobus's home ranges. We quantify how these differences parallel differences in mantled and black howlers. The average group size for mantled howlers was 12.9 individuals, and for black howlers it was 5.3 individuals. We explore possible social constraints, such as infanticide, that prevent black-and-white colobus and black howlers from living in large groups.

Keywords Group size · Colobus monkeys · Folivore · *Alouatta* · Infanticide

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Introduction

While there are a variety of potential benefits of grouping, including predator avoidance (Hamilton 1971; Chapman and Chapman 1996; Noë and Bshary 1997; Boinski et al. 2000), foraging advantages (Cody 1971; Wrangham 1980; Struhsaker 1981), and avoidance of conspecific threat (van Schaik and Kappeler 1993; Treves and Chapman 1996; Janson and van Schaik 2000; Steenbeek and van Schaik 2001), the upper size limit of groups is often suggested to be set by increased within-group feeding competition (Terborgh and Janson 1986;

Wrangham et al. 1993; Janson and Goldsmith 1995). This idea has been formalized in the ecological-constraints model (Milton 1984; Janson 1988; Wrangham et al. 1993; Chapman et al. 1995; Chapman and Chapman 2000a). The model assumes that food items occur in discrete depletable patches and proposes that an increase in group size will lead to increased day range due to more rapid patch depletion, necessitating increased travel between patches. Thus, individuals must travel farther and expend more energy if they are in a large group than if they are in a smaller group (Milton 1984; Chapman 1990). Smaller groups become advantageous when an increase in travel costs is not repaid by an increase in nutrients gained or some other fitness advantage (Chapman and Chapman 2000a, b).

Some researchers caution against the widespread acceptance of the model across the primate order, especially with regard to folivores. This suggestion is based on a number of observations. First, previous studies have found no relationship between group size and day range for some folivorous species (Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998). However, if groups are always attempting to maximize group size (e.g., to reduce predation), then they may already be traveling the maximum distance possible in that group's specific habitat. Thus, the lack of a relationship between group size and day range may simply be the result of varying food availability among home ranges. Second, some researchers have suggested that food resources are not limiting for folivores (Isbell 1991; Yeager and Kirkpatrick 1998). If so, there would be no reason to expect their group size to be constrained by food availability and distribution. However, this suggestion runs counter to Milton's protein-to-fiber model, which suggests that the availability of digestible high-protein leaves limits the size of colobine populations (see Milton et al. 1980; Milton 1979, 1982, 1998, for a full description of this model). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several studies have found positive correlations between colobine biomass and this index of leaf quality (Waterman et al. 1988; Oates et al. 1990; Ganzhorn 1992; Davies 1994; Chapman et al. 2002; Chapman and Chapman 2002). Given these considerations, it seems reasonable to evaluate the application of the ecological-constraints model to folivores.

On the other hand, we also know that group size and structure can be influenced by social factors. For example, Boesch (1996) has demonstrated that chimpanzee parties (*Pan troglodytes*) tend to be larger when there are more estrous females in the community. Similarly, Treves and Chapman (1996) demonstrated that when the risk of infanticidal attack from all-male bands was high, groups of langurs (*Presbytis* spp.) were larger and contained proportionately more adult females. Crockett and Janson (2000) documented that infanticide rate in red howlers (*Alouatta seniculus*) increased with increasing adult female group size and suggested that this pressure could limit group size. Building on this

empirical data, Crockett and Janson (2000) proposed a general model that described the relationship between female group size, food competition, and the risk of infanticide (Fig. 1). They suggested that as female group size increases, initially the risk of infanticide is greater than the costs of within-group food competition. However, as groups get larger feeding competition soon becomes a more significant cost because sufficiently large groups can resist group takeovers and ensure a large degree of paternity confusion, thus decreasing the risk of infanticide. However, for those species for which feeding competition limits groups to a size smaller than the point where infanticide risk decreases, females will compete strongly to keep groups small to decrease infanticide risk. In this situation infanticide risk will be paramount and will set the maximum group size.

The objective of this article is to contrast the diet and group size of red colobus (*P. badius*) and black-and-white colobus (*Colobus guereza*) in Kibale National Park, Uganda to consider how ecological and social factors are affecting their group sizes. These two species were selected because preliminary data suggested that group size in red colobus is limited by ecological conditions (Gillespie and Chapman 2001), whereas black-and-white colobus group sizes are influenced by social factors (Crockett and Janson 2000). For black-and-white colobus, takeovers and infanticides have been observed or inferred (Oates 1977a; Dunbar 1987; Onderdonk 2000), and Dunbar (1987) documented that the number of infants per female declined as female group size increased. Subsequently, we evaluate the generality of our findings by examining whether the insights gained from this detailed comparison can provide an understanding of why the social organization and group size of mantled (*Alouatta palliata*) and black howlers (*A. pigra*) differ.

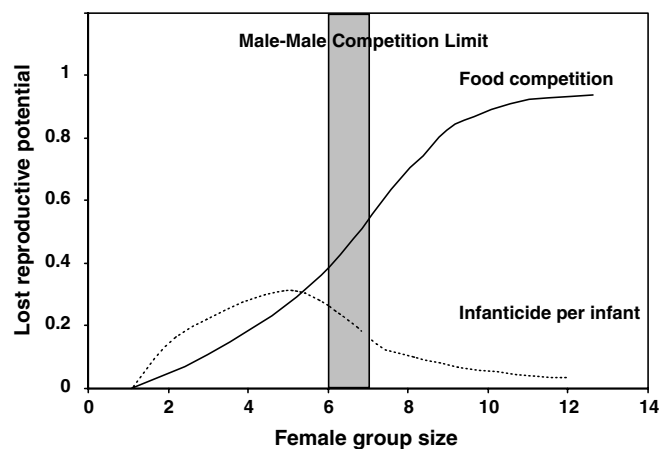


Fig. 1 Hypothetical relationships among food competition, infanticide risk, female group size, male-male competition, and loss of reproductive potential for black-and-white colobus (modified from Crockett and Janson 2000). We suggest that male-male competition may set a limit on upper group size prohibiting stable multi-male groups

Methods

Study species and site

Red colobus are found in social groups that typically vary from 25 to 40 individuals (Struhsaker 1975; Oates 1994). Groups usually contain at least three adult males and many adult females, and females are the dispersing sex. In all populations studied to date, young leaves are the most commonly eaten food item. When animals eat mature leaves, they often select specific sections of the leaf, such as leaf petioles (Struhsaker 1975; Baranga 1982; Oates 1994; Chapman and Chapman 2002). Fruits and flowers are also eaten on a seasonal basis. Black-and-white colobus tends to have smaller groups, and group size ranges from 2 to 19 individuals (Oates 1994). Groups are usually uni-male, but multi-male groups also exist, although they are less stable and tend to break down to uni-male organization (Oates 1977a; Dunbar 1987). Males are the dispersing sex (Oates 1994). Young leaves are the most commonly eaten food item, while mature leaves and fruits are more frequently consumed when young leaves are less available (Oates 1994).

Kibale National Park (766 km²) is located in western Uganda (0°13′–0°41′N and 30°19′–30°32′E) near the foothills of the Ruwenzori Mountains (Struhsaker 1975, 1997; Skorupa 1988; Chapman et al. 1997). The park consists of mature, mid-altitude, moist semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; Chapman and Lambert 2000). Mean annual rainfall in the region is 1,749 mm (1990–2001, or 1,547 mm from 1903 to 2001); the mean daily minimum temperature is 14.9°C; and the mean daily maximum temperature is 20.2°C (1990–2001). Rainfall tends to be bimodal, with May–August and December–February tending to be drier than other months (Chapman et al. 1999).

Behavioral observations

Observations were made on two groups of red colobus and two groups of black-and-white colobus during dawn-to-dusk observation for 5 days each month from August 1998 until June 1999 (red colobus group 1: 343 h, group 2: 369 h, 3,264 feeding scores; black-and-white colobus group 1: 355 h, group 2: 298 h, 2,281 feeding scores). To obtain an assessment of diet, during each half-hour period the observer was with the group, five point samples were made of different individuals. If the animal was feeding, the species and plant part (e.g., fruit, young leaf, leaf petiole) were recorded. We made an effort to avoid repeatedly sampling conspicuous animals by moving throughout the group when selecting subjects and by sampling both animals that were in clear view and those that were more hidden. On average 68.4 h of observational data were collected each month

for each species (black-and-white average 63.2 h, SD=8.4, minimum 45 h; red colobus average 73.6 h, SD=6.2, minimum 64 h), and typically over twice that many contact hours were obtained each month.

Interspecific dietary overlap between species or between neighboring groups of the same species was calculated using the following formula:

$$D = \sum S_i$$

where D is dietary overlap and S_i is the percentage of diet shared between two species, evaluated on a plant species and part basis. This formula was first used by Holmes and Pitelka (1968) and has become a standard means of expressing dietary overlap for primates (Struhsaker 1975; Struhsaker and Oates 1975; Chapman 1987; Maisels et al. 1994).

To evaluate home range overlap between neighboring red colobus groups and between red and black-and-white colobus groups, the perceived center of mass of the group was plotted on detailed trail maps every 30 min (trails were spaced between 50 and 100 m apart; Waser 1977; Olupot et al. 1994). From these descriptions of day path, detailed maps were made of all grids used by the groups, and the home range of the group was considered as the sum of the areas of all grids entered during the study.

If ecological conditions were responsible for the difference in group size between the two colobine species, then one would expect the density of food trees to be lower in the home ranges of the species with smaller groups. To assess food tree density, we mapped and measured all trees (diameter breast height, DBH, > 10 cm) of those species that any of the four groups fed on for > 1% of their total feeding time throughout each group's home range. A 10-cm cutoff was used for tree DBH, since red colobus rarely feed in smaller trees. Red colobus fed primarily on trees with a DBH of 63.7 ± 54.4 cm. Smaller trees were used much less frequently: 7.3% of the time on trees less than 20 cm DBH and 1.8% of the time on trees less than 10 cm DBH ($n=109$ trees). The small home range used by colobus monkeys facilitates the mapping of all potential food trees instead of relying on sample plot estimates of overall food species abundance. This provides a near complete catalogue, not just an estimate, of available food resources. During the study, 5,960 trees were mapped and measured.

A number of studies support the use of DBH as an indicator of plant productivity. Chapman et al. (1992) demonstrated DBH to be the most consistently accurate method for obtaining good estimates of fruit abundance (both biomass and number) for a variety of tree species. In addition, a number of studies from the forestry literature demonstrate that DBH predicts overall estimates of leaf biomass with a standard deviation of less than 15% (Brown 1978; Harrington 1979; Catchpole and Wheeler 1992). Food availability was assessed using two indices: density of food trees and cumulative DBH per

hectare of food trees, both of which allowed for direct comparison of the groups despite differences in home range size.

When there are appreciable differences in the mean values of the use of different food items, variation can be evaluated using the coefficient of variation (CV; Sokal and Rohlf 1981). The CV was calculated as the standard deviation divided by the mean.

Results

Group size and composition

Although our study groups were all using the same section of forest, they differed in group size. The two red colobus groups had 48 (group 1) and 24 individuals (group 2), whereas the black-and-white colobus groups contained 9 (group 1) and 6 individuals (group 2). The larger red colobus group contained on average 7 adult males, 20 adult females, 5 subadults, 7 juveniles, and 9 infants, and the smaller group had 6 adult males, 8 adult females, 3 subadults, 2 juveniles, and 5 infants. The larger black-and-white colobus group had on average 1 adult male, 3 adult females, 2 subadults, 2 juveniles, and 1 infant, and the smaller group had 1 adult male, 3 adult females, and 2 juveniles (an infant was born to this group during the period of observation but it only survived for 16 days; the cause of death is not known).

Home range size and overlap

Red colobus group 1 used an area of 26.4 ha, while group 2 used an area of 21.9 ha. The area of home-range overlap was 10.7 ha, which represents 41% of group 1's home range and 49% of group 2's home range. During the days we observed group 2 it spent 70% of the observation time in this area of overlap, while group 1 spent 49% of its time in the area of overlap.

For the black-and-white colobus, group 1 used an area of 12.5 ha, while group 2 used an area of 8.4 ha. The area of home-range overlap was 3.5 ha, which represents 28% of group 1's home range and 42% of group 2's home range. There were a number of other black-and-white colobus groups (at least six) that were in the vicinity. Group 1 had 75% of its home range within the home range of the two focal red colobus

groups, and group 2 had 95% of its home range within red colobus's home range.

Description of diet

In general, there was a great deal of similarity in the plant parts eaten by the two species (Table 1). Both species fed primarily on young leaves. Although both groups of red colobus ate more leaf petioles than did the black-and-white colobus, there were few other differences where both groups of a species ate more or less of a plant part than the other species.

In terms of the actual species that each of the colobus monkeys relied upon, again there was a great deal of similarity between groups and species (Table 2). All groups of both species fed upon the young leaves of *Celtis durandii* and *C. africana* very frequently. Many of the differences that are seen likely result from differences in the availability of the different species in the areas used by the different groups.

Struhsaker and Oates (1975) evaluated dietary overlap between groups of red and black-and-white colobus with adjacent home ranges in continuous forests of similar composition. They reported the dietary overlap between these two species was only 7.1%. Calculating dietary overlap in a similar fashion for the two neighboring groups of red colobus (home range overlap was up to 49% and up to 70% of the time was spent in the area of overlap) illustrates that their diet overlapped by 37.3% (overlap averaged among months; Table 3). The dietary overlap between the red colobus and the black-and-white colobus group that had its home range almost entirely within the home range of the red colobus group averaged 43.2% among months. It is most appropriate to contrast these two groups since the foods available to be eaten by groups with overlapping home ranges are more similar than those available to groups that do not use the same area; thus this most appropriately illustrates the potential similarity in diet.

Density of food trees

If ecological conditions were responsible for the difference in group size between the two colobine species, one would expect the density of food trees to be lower in the home ranges of the black-and-white colobus monkeys

Table 1 The percentage of total feeding observations that different colobus groups in Kibale National Park, Uganda spent eating different plant parts (leaf buds are included in young leaves). Percentages do not add to 100% in situations where groups ate food items not listed here

	Ripe fruit	Unripe fruit	Flowers	Young leaves	Mature leaves	Petioles	Bark
Red colobus							
Forty-eight members	5.0	1.6	3.5	75.6	5.6	7.9	0.3
Twenty-four members	6.4	2.5	0.8	64.1	13.3	6.4	6.4
Black-and-white colobus							
Nine members	0.0	0.0	2.2	84.4	3.6	0.8	0.0
Six members	2.4	7.2	0	77.7	5.8	0.4	4.8

Table 2 Percentage of foraging time spent eating any species/part combination for only those foods that were fed on for more than 1% of total feeding time for the black-and-white (BW) and red colobus (RC) groups studied in Kibale National Park, Uganda. Species/parts are arranged from the most frequently eaten to the least. *YL* young leaves, *ML* mature leaves, *UF* unripe fruit, *RF* ripe fruit, *FL* flower

Species (part)	Black-and-white colobus		Red colobus	
	Nine members	Six members	Forty-eight members	Twenty-four members
<i>Celtis durandii</i> (YL)	31.58	26.26	18.29	5.34
<i>C. africana</i> (YL)	12.79	11.11	6.80	7.94
<i>Markhamia platycalyx</i> (YL)	9.63	4.80	4.09	1.90
<i>Parinari excelsa</i> (YL)	0.40	2.40	6.43	7.73
<i>Dombeya mukole</i> (YL)	7.00	0.38	7.07	2.25
<i>Strombosia scheffleri</i> (YL)	2.78	2.78	5.32	4.57
<i>Prunus africana</i> (ML)	0.00	3.66	2.07	7.45
<i>P. africana</i> (YL)	0.27	6.69	1.59	4.50
<i>Funtumia latifolia</i> (YL)	1.28	4.17	2.87	4.57
<i>Albizia grandibracteata</i> (YL)	3.50	5.18	1.12	2.95
<i>Bosqueia phoberos</i> (YL)	0.40	0.38	7.44	3.87
<i>Funtumia latifolia</i> (RF)	0.00	0.51	3.93	4.21
<i>Ficus brachylepis</i> (YL)	3.64	1.52	2.07	1.12
<i>Markhamia platycalyx</i> (petiole)	0.67	0.38	4.63	1.12
<i>Olea welwitschii</i> (YL)	4.65	1.14	0.94	0.00
<i>Chrysophyllum</i> spp. (YL)	0.07	2.65	1.28	1.90
<i>Celtis durandii</i> (UF)	0.00	3.28	1.22	1.34
<i>Strombosia scheffleri</i> (petiole)	0.07	2.78	2.92	1.62
<i>Millettia dura</i> (YL)	1.82	0.51	1.12	0.56
<i>Macaranga schweinfurthii</i> (YL)	0.00	1.39	0.50	2.11
<i>Diospyros abyssinica</i> (YL)	2.02	1.52	0.00	0.14
<i>P. africana</i> (RF)	0.00	0.76	0.11	2.67
<i>P. africana</i> (bark)	0.00	0.00	0.00	2.32
<i>Mimusops bagshawei</i> (YL)	0.00	0.00	0.27	1.69
<i>Celtis durandii</i> (FL)	0.94	0.00	1.01	0.00
<i>Balanites wilsoniana</i> (YL)	0.00	0.25	0.00	1.12
<i>Pancovia</i> sp. (YL)	0.00	0.00	0.17	1.05
<i>Funtumia latifolia</i> (FL)	0.20	0.00	1.01	0.00
<i>Pancovia</i> sp. (petiole)	0.00	0.00	0.00	1.05

Table 3 Comparison of the overlap in diet (specific plant species and parts) of red colobus (*Procolobus badius*) and the black-and-white colobus (*Colobus guereza*) group that had the greatest home range overlap with a red colobus group and, for comparative purposes, between neighboring groups of red colobus in Kibale National Park, Uganda

Year and month	Diet overlap	
	<i>P. badius</i> vs <i>C. guereza</i>	<i>P. badius</i> 1 vs <i>P. badius</i> 2
1998		
August	44.76	38.66
September	41.61	36.80
October	25.90	5.81
November	27.79	38.13
December	72.25	46.74
1999		
January	37.08	62.22
February	36.94	25.82
March	44.29	32.61
April	66.59	60.41
May	34.55	25.43
Average	43.18	37.26

when compared to the red colobus since they have the smaller group size. We found the opposite to be true. Both black-and-white colobus groups had more food trees (species fed on for > 1% of foraging time) and the cumulative DBH of those trees was greater than that available to the red colobus (black-and-white colobus group 1: 164 food tree/ha, 4,692 cm DBH/ha; group 2:

153 food tree/ha, 4,262 cm DBH/ha; red colobus group 1: 145 food tree/ha, 3,842 cm DBH/ha; group 2: 138 food tree/ha, 3,823 cm DBH/ha).

Comparison of group size for two howler species

The average group size for mantled howlers was 12.9 individuals, while for black howlers it was 5.3 individuals (Table 4). Not only is the group size of black howlers less than half of that of mantled howlers, the CV of mantled howlers is 32%, while that of black howlers is 17%. No data have been offered to suggest that the food supply of black howlers is consistently more limited than that of mantled howlers, and there is no relationship between the average group size for a site and rainfall (a possible surrogate parameter for habitat productivity) for either species (mantled howlers $r = -0.313$, $P = 0.494$; black howlers $r = 0.0771$, $P = 0.127$, averaging neighboring sites with the same rainfall).

Discussion

To date the ecological-constraints model has provided insights into temporal variation in subgroup size for primate species with fission–fusion social organizations (Milton 1984; Chapman et al. 1995), interspecific and

Table 4 Mean group size and rainfall for sites describing population characters of *Alouatta palliata* and *A. pigra*

Species	Group size	Rainfall (mm)	Site	References
<i>A. palliata</i>	13.8	1,531	Santa Rosa, Costa Rica	1
	13.8	1,878	Palo Verde, Costa Rica	2
	5.2		Coiba, Panama	3
	18.9		Chirque, Panama	4
	12.5	1,450	La Pacifica, Costa Rica	5
	9.1	4,953	Los Tuxtlas, Mexico	6
	11.5	1,450	Toboga, Costa Rica	7
	13.8	4,015	La Selva, Costa Rica	8
	17.6	2,730	Barro Colorado Island, Panama	9
	<i>A. pigra</i>	5.6	2,032	Bermudian Landing 1, Belize
4.5			El Jova, Mexico	11
5.0			Chable, Mexico	11
5.4		1,350	Tikal, Guatemala	12
5.5		1,350	Coban, Guatemala	13
6.5		2,200	Palenque, Mexico	14
5.0		2,032	CBS, Belize	15
5.0		2,032	St. Pauls, Belize	16
6.0		2,032	Willow's Bank, Belize	17
6.2		2,032	Bermudian Landing 2, Belize	18
3.2			Muchukox Forest, Mexico	19
6.6	4,570	Monkey River	20	

1 Freese (1976), Fedigan et al. (1985), Fedigan (1987), Fedigan and Jack (2001), 2 Rodriguez (1985), 3 Milton and Mittermeier (1977), 4 Baldwin and Baldwin (1972, 1976), 5 Heltne et al. (1976), Clarke et al. (1986), Zucker and Clark (2003), 6 Estrada (1982), 7 Heltne et al. (1976), 8 Fishkind and Sussman (1987), 9 Carpenter (1934, 1962), Collias and Southwick (1952), Altmann (1959), Bernstein (1964), Chivers (1969), Mittermeier (1973), Smith (1977), Milton (1982), 10 Bolin (1981), 11 Horwich and Johnson (1986), 12 Coelho et al. (1976), Schlichte (1978), Horwich and Johnson (1986), 13 Schlichte (1978), 14 Estrada et al. (2002a, b), 15 Ostro et al. (2001), 16 Ostro et al. (2001), 17 Ostro et al. (2001), 18 Ostro et al. (2001), 19 Gonzalez-Kirchner (1998), 20 Pavelka (2004)

intraspecific variation in primate group size (Wrangham et al. 1993; Janson and Goldsmith 1995; Fimbel et al. 2001; Gillespie and Chapman 2001), and temporal and spatial variation in mixed-species associations (Chapman and Chapman 1996). With respect to colobus, Fimbel et al. (2001) provided strong evidence that the reason the Angolan black-and-white colobus (*Colobus angolensis*) occurs in groups in excess of 300 individuals is the relative abundance of high quality mature leaves in their habitats, supporting this model. Gillespie and Chapman (2001) found differences in day range and activity patterns of groups of red colobus that differed in size, consistent with predictions from this model.

In light of this widespread applicability of the ecological-constraints model, the apparent inability of this model to explain group size differences between black-and-white and red colobus requires explanation. Steenbeek and van Schaik (2001) suggested that female reproductive success in Thomas's langurs (*Presbytis thomasi*) was maximized in small and mid-sized groups, because larger groups experience higher rates of take-overs and infanticide (Steenbeek 2001). These authors

suggested that this social factor, infanticide risk, results in small groups having a selective advantage (see also Crockett and Janson 2000). We suggest that a similar pattern may be occurring in black-and-white colobus. In a 15-month study of black-and-white colobus in Kibale, Oates (1974) recorded the disappearance of 9 infants out of 16 known births. Although the actual cause of death was never known, infanticide was suspected in several cases (Oates 1977a). Onderdonk (2000) observed a male that had just joined a black-and-white colobus group in Kibale commit infanticide. Subsequently, we have observed two infant killings and one involved a male that had just joined a group (C.A. Chapman and L.J. Chapman, unpublished data). Struhsaker and Leland (1985) described observed and suspected infanticide in red colobus; however, we have not observed infanticide in red colobus in over 6,000 h of observations. Unfortunately, given how rarely infanticide occurs, we believe that data are not yet sufficient to reliably contrast infanticide rates for these two species.

It is not clear how the risk of infanticide would limit the size of black-and-white colobus groups, when they have apparent access to a high density of food that should permit the formation of multimale groups. Crockett and Janson (2000) suggested infanticide risk would only be important when food competition limited the ability of females to increase group size to the point that it induced a multimale social structure with an associated large degree of paternity confusion and low incidence of infanticide. Infanticide is expected to be less likely if a group contains multiple reproductively active males, because male immigration and subsequent violent take-over and infanticide are less likely to occur when the newcomer is faced with several possible sires of the infants (van Schaik 1996). Empirical studies have shown that infanticide risk is lower in multimale groups than in single-male groups in Hanuman langurs (*Presbytis entellus*; Newton 1986) and mountain gorillas (*Gorilla gorilla*; Robbins 1995). Thus, increased risk of infanticide should presumably favor increased group size and multiple males per group, a situation not seen in black-and-white colobus. Likewise, multimale groups would be expected in black howlers, where infanticide associated with male take-overs has been observed (Brockett et al. 1999; M.S.M. Pavelka, unpublished data). Black-and-white colobus appear to have ample food resources to form larger groups, which would decrease the risk of infanticide, yet they do not form large groups.

It is possible that the nature of male-male interactions in black-and-white colobus makes large groups unstable. Thus, even when ecological conditions would permit large groups to form, social conditions preclude their formation. It could be simply that as the number of males increases in a group the level of aggression increases. This level of within-group conflict would also be costly for the females and would put an upper limit to group size regardless of levels of feeding costs and infanticide risk (Fig. 1). Oates (1994) states that multimale groups revert to smaller, uni-male groups over time through group

fission or emigration. Oates (1977a) suggested that black-and-white colobus were adapted to the exploitation of secondary and riverine forests and in such habitats groups may not experience heavy predation (Oates 1977b) and thus the advantages of large groups would be reduced. This is not the case in Kibale where predation by crowned hawk-eagles (*Stephanoateus coronatus*) has a major impact on the populations of adult male black-and-white colobus, but less so for red colobus (Struhsaker and Leakey 1990). If black-and-white colobus are adapted to secondary and riverine forest, as Oates (1977a) suggests, the interesting question becomes why their social organization cannot be more flexible.

There are a number of striking parallels between the red and black-and-white colobus situation and that of mantled and black howler monkeys. Everywhere black howlers have been observed they have been found in small groups: even in situations where they are found in continuous forest with an apparent abundance of food resources, such as Tikal National Park, Guatemala (Coelho et al. 1976; Schlichte 1978; Bolin 1981). We suggest that like the black-and-white colobus, black howlers are limited to small social groups due to social constraints. They too appear to be adapted to disturbed or secondary riparian habitats, often seasonally flooded forest (Horwich and Johnson 1986; Horwich and Lyon 1990; M.S.M. Pavelka, submitted).

Further research is needed to verify if social constraints are limiting group size in black-and-white colobus and black howlers, and to eliminate the possibility that their group size is being determined by some unknown ecological constraint. However, if social constraints prove to be limiting their group size, then it raises a number of interesting questions for future study. For example: what is the nature of these constraints? Why are these social constraints present in these species and not closely related ones? Why do some species show considerably less flexibility in social organization than do their close relatives?

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