

RESEARCH ARTICLE

Test of the Ecological-Constraints Model on Ursine Colobus Monkeys (*Colobus vellerosus*) in Ghana

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For group-living mammals, the ecological-constraints model predicts that within-group feeding competition will increase as group size increases, necessitating more daily travel to find food and thereby constraining group size. It provides a useful tool for detecting scramble competition any time it is difficult to determine whether or not food is limiting. We tested the ecological-constraints model on highly folivorous ursine colobus monkeys (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary in Ghana. Three differently sized groups were followed for 13 months and two others were followed for 6 months each in 2004–2005 using focal-animal sampling and ranging scans; ecological plots and phenology surveys were used to determine home-range quality and food availability. There was relatively little difference in home-range quality, monthly food availability, diet, adult female ingestion rates, and rate of travel within food patches between the groups. However, home-range size, day-range length, and percent of time spent feeding all increased with group size. We performed a single large test of the ecological-constraints model by combining several separate Spearman correlations, each testing different predictions under the model, using Fisher's log-likelihood method. It showed that the ecological-constraints model was supported in this study; scramble competition in this population is manifesting in increased ranging and time spent feeding. How costly this increased energy expenditure is for individuals in larger groups remains to be determined. *Am. J. Primatol.* 71:49–59, 2009.

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INTRODUCTION

The benefits and drawbacks of group living have been much discussed [Clutton-Brock & Harvey, 1977; Eisenberg et al., 1972; Hamilton, 1971; Janson, 1988; Janson & van Schaik, 1988; van Schaik, 1983; van Schaik & Kappeler, 1993; Terborgh, 1983; Treves & Chapman, 1996; Wrangham, 1980]. The consensus seems to be that group living is so beneficial that group size should only be restricted by its costs [Dunbar, 1987; Parrish & Edelman-Kashet, 1999]. Two main costs have been proposed: an increase in within-group feeding competition [Janson & Goldsmith, 1995; Terborgh & Janson, 1986] and higher rates of disease transmission [Freeland, 1976]. Competition for food resources can occur when individuals directly contest for food and/or when others exploit food resources before an individual can encounter them (scramble competition) [Janson, 1985, 1988; Nicholson, 1954; van Schaik, 1989]. The behavioral manifestations of contest competition are often thought to be relatively simple to measure [displacements over food; but see Koenig, 2002]. In the absence of contest, it is difficult to determine if and when food is limiting for

group-living animals. This led to the establishment of the ecological-constraints model, which suggests that food availability limits group size any time a group must travel further per day than a solitary forager to meet the energetic requirements of its members [Chapman & Chapman, 2000a; Chapman et al., 1995; Janson, 1988; Milton, 1984; Wrangham et al., 1993]. If food patches can be depleted, larger group size will lead to faster depletion rates and day range will increase as members have to travel between patches. If food is dispersed and patches cannot be depleted, individual search fields may increasingly overlap with an increase in group size so that encounter rates with food drop off and

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individuals are “pushed forward” in search of food, thus increasing day range [Chapman & Chapman, 2000a; Janson, 1988; van Schaik & van Hooft, 1983]. If group size continues to grow, a point will be reached where the energy budget cannot support increased travel (given the amount of food ingested), and smaller groups will become advantageous [Chapman & Chapman, 2000a].

The relationship between daily travel distance and group size is dependent upon food availability [Wrangham et al., 1993]. If travel efficiency is held constant but food density rises, more individuals will be able to feed within a certain area. If food availability is held constant, an increase in group size should lead to an increase in home-range size or day-range length [Chapman & Chapman, 2000a; Chapman et al., 1995; Janson & Goldsmith, 1995; Milton, 1984; Wrangham et al., 1993]. Additionally, group spread per individual should increase in larger groups as members offset the presence of other feeding individuals by spreading out and decreasing the proportion of overlap in their search fields [Chapman & Chapman, 2000a; van Schaik et al., 1983]. Changes in day range, home range, and group spread can covary, making straightforward relationships difficult to tease apart.

Variation in activity budgets for differently sized groups may also indicate scramble competition [Chapman & Chapman, 2000b; Isbell, 1991; de Ruiter, 1986; van Schaik et al., 1983; Steenbeek & van Schaik, 2001]. Individuals in larger groups may have to travel or feed more and rest less than those in smaller groups because they need to search a greater area for food.

Thus far, the relationships among group size, ranging behavior, activity budgets, and food availability have predominantly been tested on mostly frugivorous primate species showing fission–fusion behavior [reviewed in Chapman & Chapman, 2000b]. These studies have shown that travel costs and resource availability limit feeding party size. Questions still remain, however, about the applicability of the model to species that are largely folivorous. Leaves are often assumed to be low quality, abundant, and evenly distributed relative to fruit; therefore, folivores are thought to be less constrained by food than frugivores [Isbell, 1991; Janson & Goldsmith, 1995; Wrangham, 1980]. Indeed, studies have shown that larger groups of folivores often do not have longer day ranges in similar habitats [i.e. *Alouatta pigra*: Arrowood et al., 2003; *Brachyteles arachnoides hypoxanthus*: Dias & Strier, 2003; *Colobus guereza*: Fashing, 2001; *Ptilocolobus tephrosceles*: Isbell, 1983; Struhsaker & Leland, 1987; 17 species of Asian colobines: Yeager & Kool, 2000]. However, not all of these studies took food availability into account when looking at the relationship between day range and group size. Evidence is now accumulating to support the notion that folivores are

in fact food-limited. Recently, three tests of the ecological-constraints model on folivores have found a relationship between group size, day range, and food availability [*Gorilla beringei beringei*: Ganas & Robbins, 2005; *P. tephrosceles*: Gillespie & Chapman, 2001; *C. vellerosus*: Saj & Sicotte, 2007a,b, this study is discussed below]. In a review, Snaith and Chapman [2007] list other indicators that suggest that food is limiting for folivores, including: (1) group size in red colobus can be predicted from food tree density, forest size, and degree of deciduousness; (2) folivore biomass can be predicted by food availability; (3) folivores have been seen to change their behavior (e.g. displaying fission–fusion behavior) in response to food depletion; and (4) some folivore species show contest competition for food both within and between groups in certain instances [*Semnopithecus entellus*: Koenig, 2000; *C. polykomos*: Korstjens et al., 2002]. The complexity surrounding this issue is in part owing to the false dichotomy between “folivores” and “frugivores.” Most species classified as “folivores” have at least a portion of their diet made up by unripe fruits, seeds, and other high-quality items. It is difficult to say which items represent critical foods that may regulate the expression of food competition [Lambert, 2007].

In this study, we test the ecological-constraints model on five different-sized groups of ursine colobus monkeys (*C. vellerosus*). This species is highly folivorous [diet: 79% leaf parts; Saj & Sicotte, 2007a], varies in group size [Boabeng-Fiema Monkey Sanctuary (BFMS) range: 9–38, mean: 15.0, $n = 15$; Wong & Sicotte, 2006], and shows male and female dispersal [Saj et al., 2007; Teichroeb et al., accepted]; group size thus could fluctuate in response to food availability. Saj and Sicotte [2007a,b] tested whether the observed social system of *C. vellerosus* could be inferred from the distribution of its food resources, and in doing so documented the occurrence of scramble competition and the apparent lack of contest competition for food. This study builds on this work by examining the effect of monthly changes in food availability on ranging in five differently sized groups and by taking into account ingestion rates to further document the behavioral expressions of scramble competition in this population. In addition, in an analysis of activity budgets in *C. vellerosus*, Teichroeb et al. [2003] found that adult females in a large group spent more time feeding than adult males, a relationship not found in a small group. We further examine activity budgets with our larger sample of groups. We hypothesize that if *C. vellerosus* at BFMS are ecologically constrained, the larger groups will either travel further per day to satisfy their food requirements or their ranges will show greater food availability. Individuals in larger groups may also travel or feed more and rest less than those in smaller groups. In this study we deal

only with the effects of group size on behavioral measures of feeding efficiency, while taking food availability into account, although we acknowledge that the threat of infanticide also has an influence on group size in several species [e.g. *C. guereza*: Chapman & Pavelka, 2005; *A. seniculus*: Crockett & Janson, 2000]. Infanticide has been observed in this population of ursine colobus [Teichroeb & Sicotte, 2008a].

METHODS

Study Site and Study Species

Research on *C. vellerosus* has been conducted at the BFMS in central Ghana (7°43'N and 1°42'W) under the direction of P. S. since 2000. This dry semi-deciduous forest is 191.6 ha in size. BFMS contains primary forest, regenerating farmland (secondary forest), and woodland [Fargey, 1991]. Detailed information about the study site can be found in Saj et al. [2005]. The annual rainfall at BFMS during this study (July 2004–June 2005) was within the normal range at 1,329 ml (monthly range: 0.4–227.6 ml) [Fargey, 1991].

Nineteen bi-sexual groups of *C. vellerosus* [B. O. Kankam, unpublished data] and a growing population of Campbell's mona monkeys (*Cercopithecus campbelli lowei*) are protected at BFMS by a hunting ban [Saj et al., 2005]. Births and matings are not seasonal [Teichroeb & Sicotte, 2008b]. Group composition is multi-male and uni-male, with the presence of all-male bands (AMBs) [Saj & Sicotte, 2005; Wong & Sicotte, 2006]. Between-group encounters are usually aggressive, with adult males as the main participants [Sicotte & MacIntosh, 2004].

Study Groups

Data were collected on four groups of *C. vellerosus* (WW, DA, B2, and RT) for 13 months (July–November 2004, January–August 2005). One of these groups (DA) had an influx of at least seven males from an AMB. This led to the dispersal of three females (one adult and two subadult) and the eventual eviction of the three resident adult males; the AMB males then began to evict one another (Table I). Thus, DA spent 6 months at a mean group size of 22 (DA₁) and 6 months at 27 (DA₂). We treat DA as two groups when examining the effect of group size on behavioral variables in this study (Table IV). We present overall values for DA's home-range quality and monthly food availability though as DA₁ and DA₂ had the same range. Each of the 6-month periods for DA included a portion of the rainy and dry seasons and had a similar amount of rainfall (DA₁ rainfall = 712.6 ml; DA₂ rainfall = 793.7 ml).

All individuals in the small study groups (B2 and RT) were recognized by features of the face and tail. All adult males and some adult females (DA, $n = 5$; WW, $n = 8$) were recognized in the larger study groups. Counts of individuals in RT and B2 could be done easily during follows; counts of the larger DA and WW groups were done opportunistically when they were crossing a narrow gap in the canopy or a road. At least one good group count was obtained per month. Group composition and number of study days for each group are presented in Table I. We were in contact with groups for 2,406 hr during 202 follow days. Focal-animal samples totalled 433.3 hr (RT: 106.5 hr; B2: 102 hr; DA₁: 50.3 hr; DA₂: 49.5 hr; WW: 125 hr).

Behavioral Data Collection

Each study group was followed for two, 2-day periods per month from dawn to dusk (6:00 am–6:00

TABLE I. Group Size, Group Composition, and Diet for Each Study Group

	RT	B2	DA ₁	DA ₂	WW
Group size	13	13–17	21–23	23–31	28–33
Adult/subadult group size (w/o juv. and inf.)	7	7–12	15–18	16–26	20–30
Adult males	1	1–3	3–4	3–8	6–10
Subadult males	1	2–4	3–5	3–5	2–6
Adult females	5	4	9	9–10	10–11
Subadult females	1	0–1	1	1–3	2–3
Juveniles/infants	5	4–5	4–5	4–5	2–5
# Full-day follows	48	48	22	26	58
Diet					
% Young leaves/buds	35.1	47.2	50	26.5	53.0
% Mature leaves	36.3	31.7	31.1	55.5	25.9
% Leaves (undetermined age)	7.8	5.8	2.7	3.4	2.5
% Fruit	11.6	5.1	6.1	0.8	2.1
% Flowers/flower buds	2.8	1.0	0.2	4.5	5.0
% Seeds/seed pods	5.1	4.2	0.08	5.6	9.2
% Other	1.3	5.0	3.3	0.08	2.3

pm) by J. A. T. and a research assistant. Behavioral observations were done using 10-min focal samples [Altmann, 1974] that were alternated among adult and subadult individuals. At least 1 hr was left between focal samples on the same individual. In WW and DA, the observer moved around the group, alternating focal samples between known and unknown animals to insure this rule. Scan samples were taken every 30 min during follows to record all trees occupied by the group relative to 50 × 50 m quadrats on a map of the field site.

The activity budget was broken into four behavioral categories: (1) feed—the manipulation and ingestion of food items; (2) move—all travel; (3) social behavior—grooming, play, copulations, and aggression; and (4) rest—all times when the individual was stationary and not involved in any other category. Within focal samples, the distance (in meters) that the animal travelled during moving bouts was estimated using tail length as a guide [tails average slightly under a meter in length, 730–930 mm; Jeffrey, 1975]. The mean rate of travel (m/sec) between feeding bouts (within food patches; defined as a single tree) could then be estimated and compared for different groups. The diet of the study groups was determined as the proportion of feeding time spent on different species and plant parts during focal samples.

Food intake was also assessed during focal samples. When the monkey's face was visible during feeding, the number and identity of the plant parts fed upon in each bite were recorded and timed for as many bites as possible, recording whether petioles and mid-ribs were eaten. Up to 30 samples (mean = 27, min = 4) of the identical plant parts were collected from the tree or the ground and weighed to obtain a mean fresh weight of food items consumed in each bite [following Chivers, 1998]. All bites recorded in focal samples were used to calculate that focal's mean grams of fresh weight consumed per second. The mean ingestion rates for adult females in groups of different size were lumped and the mean scores for the groups were compared. Between-group variance for intake rate (g/sec) was 0.014 and was higher than within-group variance for all groups except B2 (RT: 0.011; B2: 0.026; DA₁: 0.009; DA₂: 0.003; WW: 0.013). Although in some species ingestion rates may differ for females of different social statuses [Janson & van Schaik, 1988], this is unlikely to be the case in ursine colobus where displacements over food are rare and female dominance hierarchies seem to be lacking [Saj & Sicotte, 2007b].

Home ranges and day ranges were determined from 4,950 location scans during follows (RT: 1,181 scans; B2: 1166; DA₁: 583; DA₂: 630; WW: 1,390). The home range of each group was defined as all 50 × 50 m quadrats entered during follows. Day ranges were determined during full-day follows by recording the approximate center of mass of

the group every 30 min in relation to the trees on a map of the field site [Waser, 1974]. Straight-line measurements between these points were used to estimate the distance moved by the group from dawn until dusk. Group spread estimates were taken at the end of focal samples when the location of >75% of the group was known. The trees that represented the widest distance between individuals were recorded and later the distance between the boles was measured on a map of the field site, then half the distance of the crown diameter of these trees was added to get an estimate of group spread [Saj & Sicotte, 2007b]. During group spread scans the "group activity" was recorded and defined as the activity of at least 75% of the group in the categories of feeding, resting, moving, or socializing. If no group activity could be discerned at the time of the scan (i.e. an estimated 50% of the group was feeding and 50% was resting), none was recorded.

Home-Range Quality Assessment

The tree species composition of each groups' range was determined by a large-tree survey and a quadrat survey. The large-tree survey consisted of measuring (diameter at breast height (DBH), crown diameter, height, crown shape) and mapping every tree ≥40 cm DBH in the home range of each group. During the quadrat survey every tree ≥10 cm DBH was counted in randomly placed quadrats that made up at least 10% of the home range of each group. Phenology surveys were conducted on the day before or after each 2-day follow. Samples of up to five randomly selected individuals of each food tree species were monitored to calculate the proportion of trees with colobus food items. In total 207 trees were monitored biweekly (122 trees in WW and DA's overlapping ranges and 85 trees in B2 and RT's overlapping ranges). The percentage of crown cover and maturity of leaves, floral parts, fruits, and seeds were determined on this scale: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%, with each category summing to 4 when the plant parts were present [Sun et al., 1996]. The phenology of climbers was not measured as they do not make up a large portion of the diet (<7%).

The food available to each group on each 2-day follow was assessed for the quadrats that they entered [following Gillespie & Chapman, 2001]. Food species comprising ≥5% of the group feeding time for that follow were identified and the stem density (#/ha) and basal area (m²/ha) of those trees (measuring ≥40 cm) that were in a food phenophase were calculated for the quadrats entered. Only large trees were used because *C. vellerosus* at BFMS use these trees most often for feeding (78.5% of food trees are ≥40 cm DBH) [Saj & Sicotte, 2007a]. Only the species constituting at least 5% of the diet were used in food availability estimates because, as was found

by Gillespie and Chapman [2001], the use of the entire diet leads to numbers that are erroneously high and difficult to compare. Species comprising at least 5% of the diet represented from 50.4 to 65.4% of the study groups' total diet (Table III). Data collection methods were compliant with the University of Calgary's Animal Care Committee and with the laws of Ghana.

Data Analyses

To investigate whether the groups' home ranges differed in quality, we compared their overall measurements for tree diversity, density, and basal area (Table II). Monthly food availability (mean density of trees in a food phenophase in the quadrats entered) for each group was compared using a one-way analysis of variance. We next investigated whether there were any differences in diet and ingestion rate between the groups. A Spearman correlation was run on the mean ingestion rates for adult females at different group sizes. The relationship between group size and ranging behavior was examined using Spearman correlations between group sizes for mean home-range size, day range, and group spread while feeding. Within each group, mean monthly group spreads were compared when the "group activity" was resting compared with when it was feeding using Wilcoxon tests. The effect of group size on activity budgets and rate of travel for adult females within food patches was determined using Spearman correlations between the groups for mean travel rate (m/sec) and proportion of the day feeding, resting, moving, and socializing.

We then performed an overall test of the significance of the ecological-constraints model by combining a series of independent tests using Fish-

er's log-likelihood method [Sokal & Rohlf, 1995]. We chose several variables that each have a predicted relationship with group size under the model: (1) home-range size (ha); (2) mean day range (m); (3) the proportion of time spent feeding; (4) the mean rate of travel (m/sec) for adult females within a food patch; and (5) the mean ingestion rate for adult females (g/sec). The *P* values from the Spearman correlations for these variables and group size were combined into the Fisher's log-likelihood method that uses them to determine the overall probability of rejecting the null hypothesis and accepting the predictions of the ecological-constraints model [Sokal & Rohlf, 1995]. All statistics were two-tailed and were done using SPSS 14.0 for Windows. An α level of 0.05 was set for significance.

RESULTS

Home-Range Quality Comparisons

The quadrat survey showed that no single group had an obviously better quality home range (Table II). DA's home range showed the highest measurements for stem density but the lowest for basal area, indicating that it contained a large number of small trees. As small trees are used less often than large trees for feeding by *C. vellerosus* [≥ 40 cm DBH; Saj & Sicotte, 2007a], this suggests that DA group had the lowest quality home range. There was, however, no difference in monthly food availability (mean monthly density of trees in a food phenophase in the quadrats entered) between any of the groups ($n = 49$, $F = 0.67$, $df = 3, 45$, $P = 0.57$) (Fig. 1).

Diet and Ingestion Rates

Despite having overlapping home ranges, the study groups showed some variation in the species composition of their diets (Table III) owing to the heterogeneous forest composition at BFMS. Notwithstanding this variation in food species, the plant part composition of their diets (Table II) was quite similar. DA₁ and DA₂ vary from each other, particularly in the proportion of young leaves, which tend to flush seasonally. The mean ingestion rates for adult females showed little increase with group size (Table IV) and a Spearman correlation between groups at different group sizes was not significant ($n = 5$, $r_s = 0.2$, $P = 0.37$) (Table V).

Ranging and Group Size

Mean day-range length ($n = 5$, $r_s = 0.98$, $P = 0.01$) and mean group spread while feeding ($n = 5$, $r_s = 0.9$, $P = 0.04$) increased with group size and there was a trend for home-range size to increase with group size ($n = 5$, $r_s = 0.82$, $P = 0.09$) (Tables IV and V, Fig. 1).

We compared within-group differences in group spread in the same month when the group activity

TABLE II. Ecological Characteristics* of Each Group's Home Range

	RT	B2	DA	WW
Tree species diversity				
Total stems	126	175	381	330
Number of species	29	48	54	53
Number of food species	21	26	24	30
Density (stems/ha)				
Total tree density	168	116.7	217.7	220
Food species density	117.3	56	126.9	78.7
$\geq 5\%$ species density ^a	18.7	17.3	44.6	4.7
Basal area (m ² /ha)				
All species basal area	28.1	24.6	18.8	33.1
Food species basal area	19.2	14.5	9.2	20.9
$\geq 5\%$ species basal area ^a	12.9	10.6	4.8	9.3

DBH, diameter at breast height.

*Calculated from a quadrat survey measuring all trees ≥ 10 cm DBH in at least 10% of each group's range (RT: 3 quadrats, 11.1% of the range; B2: 6 quadrats, 11.8% of the range; DA: 7 quadrats, 11.1% of the range; WW: 6 quadrats, 10.7% of the range).

^aSpecies that represent $\geq 5\%$ of the diet.

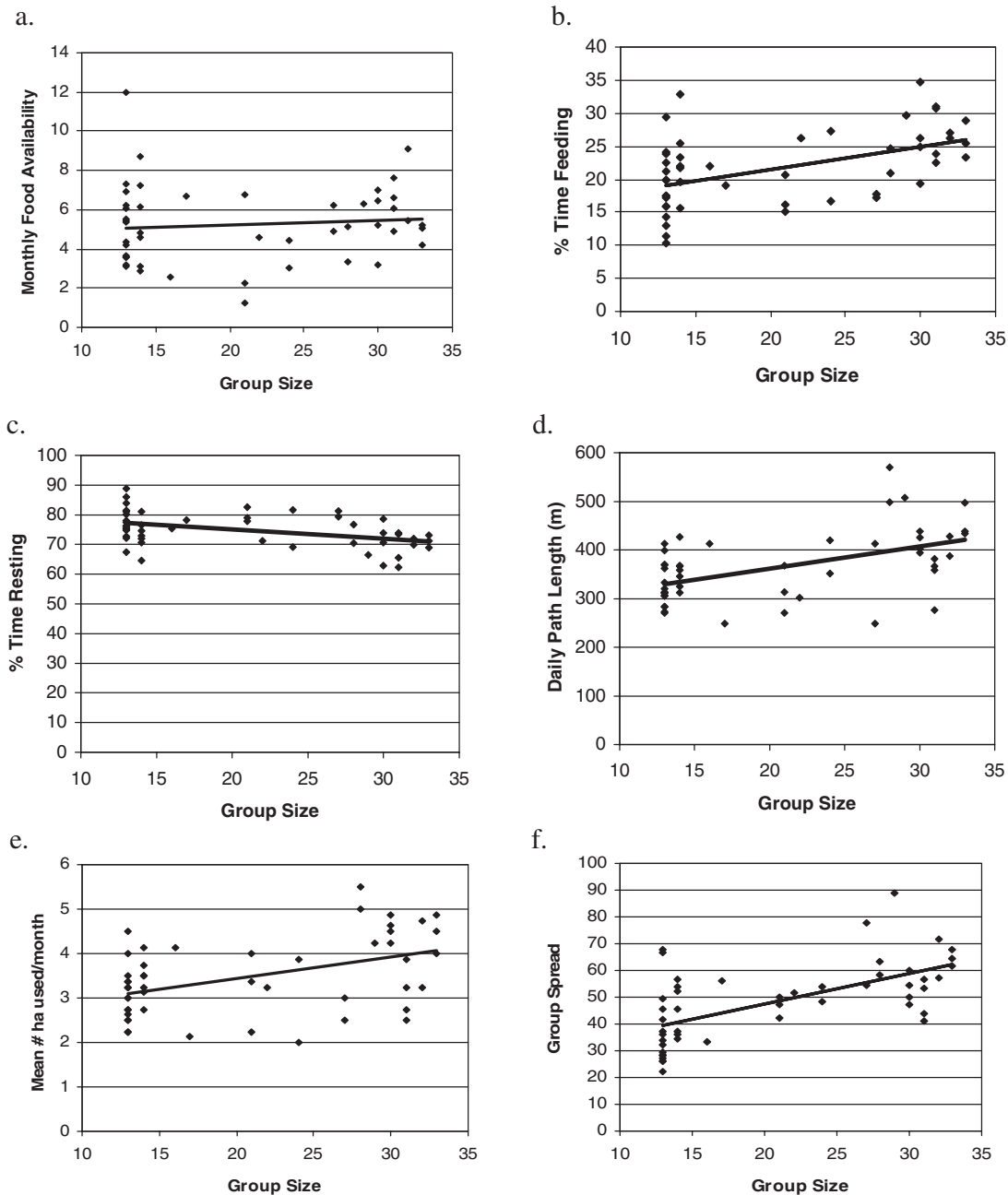


Fig. 1. Scatterplots with trend lines for the monthly values for habitat quality, activity budget, and ranging variables in relation to group size for the five study groups. (Each point represents group size during a particular month.) (a) Monthly food availability (mean density of trees in a food phenophase). (b) Mean percent of day feeding. (c) Mean percent of day resting. (d) Mean day range. (e) Home-range use (mean number of hectares entered each month). (f) Mean group spread.

was “feeding” compared with when it was “resting” in order to test whether interindividual distances increased when feeding. Increased group spread when feeding was found in DA₂ and a trend was found in WW, the two largest groups (RT: $n = 11$, $W = 14$, $P = 0.55$; B2: $n = 11$, $W = -14$, $P = 0.55$; DA₁: $n = 6$, $W = -13$, $P > 0.05$; DA₂: $n = 6$, $W = 19$, $P < 0.05$; WW: $n = 12$, $W = 48$, $P = 0.06$).

Activity Budgets, Rate of Travel, and Group Size

The activity budgets of the groups are presented in Table IV. The percentage of time spent feeding increased with group size ($n = 5$, $r_s = 0.9$, $P = 0.04$) (Table V, Fig. 1). Time spent resting ($n = 5$, $r_s = -0.7$, $P = 0.19$), moving ($n = 5$, $r_s = 0.36$, $P = 0.55$), and socializing ($n = 5$, $r_s = -0.62$,

TABLE III. Plant Species Comprising $\geq 5\%$ of the Annual Diet for Each Study Group

RT		B2		DA		WW	
Species	% Diet	Species	% Diet	Species	% Diet	Species	% Diet
<i>Antiaris toxicaria</i>	22.5	<i>Antiaris toxicaria</i>	14.1	<i>Aubrevillea kerstingii</i>	37.5	<i>Aubrevillea kerstingii</i>	18.6
<i>Morinda lucida</i>	9.6	<i>Khaya grandifoliola</i>	14.1	<i>Gmelina arborea</i>	8.4	<i>Milicia excelsa</i>	7.7
<i>Albizia coriaria</i>	6.2	<i>Adansonia digitata</i>	9.2	<i>Ceiba pentandra</i>	8.3	<i>Distemonanthus benthamianus</i>	6.9
<i>Celtis zenkeri</i>	5.4	<i>Ceiba pentandra</i>	6.9	<i>Milicia excelsa</i>	5.8	<i>Triplochiton scleroxylon</i>	6.4
<i>Adansonia digitata</i>	4.9	<i>Pouteria alnifolia</i>	6.5	<i>Celtis zenkeri</i>	5.4	<i>Pterygota macrocarpa</i>	5.8
<i>Khaya grandifoliola</i>	4.9	<i>Bombax buonopozense</i>	5.5			<i>Trilepisium madagascariense</i>	5.0
		<i>Albizia coriaria</i>	5.5				
Total	53.5		61.8		65.4		50.4

TABLE IV. Ranging Variables and Activity Budgets for the Study Groups at Different Sizes

	RT	B2	DA ₁	DA ₂	WW
Mean group size	13	15	22	27	30.5
Mean day range (m)	331 (<i>n</i> = 47 days)	336 (<i>n</i> = 47)	336 (<i>n</i> = 22)	339 (<i>n</i> = 22)	453 (<i>n</i> = 57)
Range of daily travel (m)	131–547	202–639	101–573	164–698	222–712
Mean resting group spread (m)	31 (<i>n</i> = 109 scans)	49 (<i>n</i> = 123)	51 (<i>n</i> = 52)	51 (<i>n</i> = 50)	62 (<i>n</i> = 143)
Range of resting group spread (m)	9–93	12–119	14–101	16–121	22–152
Mean feeding group spread (m)	35 (<i>n</i> = 60 scans)	49 (<i>n</i> = 40)	47 (<i>n</i> = 28)	57 (<i>n</i> = 25)	62 (<i>n</i> = 99)
Range of feeding group spread (m)	9–89	13–100	25–78	19–111	9–120
Home-range size (ha)	6.75	12.75	10.25	12.75	14
Rate of travel for females in food patches (m/sec)	0.9 (<i>n</i> = 100 bouts)	0.73 (<i>n</i> = 66)	1.12 (<i>n</i> = 16)	1.05 (<i>n</i> = 39)	0.92 (<i>n</i> = 98)
Ingestion rate (g/sec)	0.1 (<i>n</i> = 53 focals)	0.11 (<i>n</i> = 33)	0.13 (<i>n</i> = 12)	0.05 (<i>n</i> = 14)	0.12 (<i>n</i> = 59)
% Time feeding ^a	19.5	20.4	19.7	23.8	26
% Time resting	76.5	76.4	77.6	72.5	71.1
% Time moving	1.2	1.2	1.4	1.0	1.5
% Time socializing	2.8	1.4	1.1	2.2	1.1

^aThese activity budgets are strictly for comparison purposes. They were determined using focal-animal samples that tend to underestimate time spent moving because animals are often lost during follows, leading to sample discard. True activity budgets for a species should be determined using scan sampling as in Teichroeb et al. [2003] for *Colobus vellerosus*.

TABLE V. Fisher’s Log-Likelihood Method for Independent Tests of the Ecological-Constraints Model Using Ranging and Activity Budget Variables

Variable	Expected relationship with increased group size	Correlation coefficient ^a (<i>N</i> = 5 groups)	<i>P</i> value	ln <i>P</i>
Home-range size (ha)	Positive	0.82	0.089	−1.0506
Mean day range (m)	Positive	0.98	0.005	−5.2983
Proportion of the activity budget spent feeding	Positive	0.9	0.037	−3.2968
Mean rate of travel for adult females within a feeding patch (m/sec)	Positive	0.5	0.391	−0.939
Ingestion rate for adult females (g/sec)	Positive	0.2	0.747	−0.2917
Total				−10.8764 ^b

^aCorrelation coefficients were determined using Spearman correlations.

^bFisher’s log-likelihood method: $\chi^2 = -2 \sum \ln P = -2(-10.8764) = 21.75$; *df* = 2*k* = 2(5) = 10. Critical value for χ^2 at *P* = 0.02 is 21.16; 21.75 > 21.16; therefore, we reject the null hypothesis. The ecological-constraints hypothesis is supported.

P = 0.27) were not correlated with group size. The rate of travel within a food patch for adult females was not correlated with group size (*n* = 5, *r_s* = 0.5, *P* = 0.39) (Tables IV and V).

The increased time spent feeding for DA₂ compared with DA₁ may have been caused by the increase in group size, but there is an alternative (or possibly complementary) hypothesis. The 6-month

period of data collection on DA₂ corresponded with an increase in mature leaves in the diet. The other groups also showed more time feeding in this period when their diet included more mature leaves (DA shows an increase of 4%, Table IV; the other groups show increases between 2 and 4%; RT: 18.1–21.3%; B2: 18.9–22.2%; WW: 24–28.2%).

Test of the Ecological-Constraints Model

Figure 1 provides a summary of some of the relationships found in this study; ranging and activity budget variables were affected by changes in group size, whereas habitat quality and food availability did not differ significantly. Thus, to test the ecological-constraints model, we used several of the independent correlations for ranging and activity budget above and combined their probabilities using Fisher's log-likelihood method (Table V). All of the chosen variables showed the predicted relationship with group size although the *P* values were not significant for home-range size, rate of travel for adult females within a food patch, or ingestion rate for adult females. Nevertheless, the combined tests were significant ($n = 5$, $df = 10$, $\chi^2 = 21.75$, $P < 0.02$), indicating that the ecological-constraints model is supported by these data.

DISCUSSION

Group Size Effect on Ranging Behavior

Our results support the applicability of the ecological-constraints model to highly folivorous primates. Although home-range quality and food availability were relatively equal for the four groups of *C. vellerosus* at BFMS, these groups showed longer day-range length and a trend for larger home ranges with increased group size (Fig. 1). In addition, group spread in the largest groups tended to be greater when the group activity was feeding compared with when it was resting suggesting that individuals were attempting to avoid overlapping search fields while feeding. These results are consistent with those of Saj and Sicotte [2007b].

Although habitat quality was not consistently different across our groups, the variables that best correlated with increasing group size were the total number of stems and tree density (stems/ha; Table II). The total number of stems is usually predicted to increase with home-range size. In theory, however, this does not have to be the case; in densely treed environments, groups may be able to increase the number of trees in their range with growing group size by only marginally increasing their home-range size. For instance, Dunbar [1987] did not find that group size correlated with home-range size in *C. guereza* at Bole and Lake Shalla, yet group size was correlated with the number of stems of all species in their home range. Dunbar and

Dunbar [1974] estimated that *guereza* groups required a mean of ten trees per individual within the group.

Fission–fusion behavior in several colobine species has been seen in areas of low food availability and has been interpreted as an indication of scramble competition [reviewed in Snaith & Chapman, 2007]. We also observed fission–fusion behavior on two occasions in our largest study group (WW). On September 14, 2004, they formed two, relatively equally sized subgroups that moved 150 m apart, foraging separately for almost 6 hr before reuniting in the same sleeping tree. On July 15, 2005, they also split into two, equally sized subgroups, moving 100 m away from each other in the hour before dark and sleeping separately. It is not known when they reunited, but the group was together when they were recontacted on July 28, 2005.

It is possible that some of the group size effects on ranging that we documented may also have been caused by between-group scramble competition. The largest group (WW) ranged in the middle of the forest where 96% of their home range overlapped with a greater number of other groups than RT, B2, or DA. These latter groups had a portion of their range at the edge of the forest and therefore did not have the same level of overlap (RT: 88%; B2: 67%; DA: 78%). Thus, the largest group may have experienced a more general depletion of resources caused by other groups foraging within their home range and thus a greater level of between-group scramble competition, which could have led to an intensification of the manifestations of within-group scramble competition. Recent censuses indicate that the population size of *C. vellerosus* at BFMS is increasing [B. O. Kankam, unpublished data; Wong & Sicotte, 2006]; therefore, greater habitat-wide depletion of resources may be occurring. The inability to control for home-range overlap within studies of primate food competition is a common problem and one that is difficult to account for. Isbell [1991] suggests that a positive relationship between home-range size and group size is indicative of between-group scramble competition, whereas an increase in day-range length with group size is more suggestive of within-group scramble. If this is indeed the case, then the stronger group size effect on day-range length that we found when compared with home-range size (Table V) may indicate that within-group scramble is more intense in this population than between-group scramble.

Some studies have used increases of group spread with group size as a potential indicator of scramble competition [e.g. Gillespie & Chapman, 2001; Saj & Sicotte, 2007b]. In this study group spread increased with group size during feeding and resting (Table IV), but this effect was expected simply based on the presence of a larger number of individuals. When group spread was compared

between groups while taking the number of individuals per group into account (group spread divided by the number of adults and subadults—an approximate measure of the amount of space taken up by a single individual) this effect disappears. We thus conclude that for *C. vellerosus* at our site group spread is not a useful indicator of scramble competition.

Group Size Effect on Activity Budget

We found increases in time spent feeding with increasing group size in this study. Teichroeb et al. [2003] and Saj and Sicotte [2007b] also found activity budget differences between two differently sized *C. vellerosus* groups at BFMS. Their results indicate that scramble competition was occurring in WW group at this time. Our results on a greater number of groups confirm that group size has an effect on activity budget in this species. It appears that more time has to be spent feeding with increasing group size. Our analyses also suggest that an increase in mature leaves in the diet is associated with an increase in time spent feeding.

There remains at least one competing hypothesis that we cannot rule out, however. If vigilance is related to predator protection [Pulliam, 1973], as opposed to avoidance of conspecifics [Treves, 1998], then time spent scanning for predators is predicted to decrease with increasing group size. As we do not present data on vigilance here, we are unable to say at this time whether an increase in feeding in the larger groups was simply allowed for because they spent less time scanning for predators than individuals in the smaller groups.

Ingestion Rates

Using activity budgets to gauge food competition can be problematic because feeding time is not a very good estimation of food intake [Hladik, 1977; Zinner, 1999] and may not show differences between groups if ingestion rates vary or the chemical composition of food differs. Of these two factors, research suggests that ingestion rates may be more useful in determining energy gain than the chemical composition of food items [Nagy & Milton, 1979; Nakagawa, 1997; Schülke et al., 2006] although it is still not an ideal measure [Koenig, 2002]. In this study, pooled ingestion rates for adult females did not show a correlation with increasing group size as predicted by the ecological-constraints model. The lack of a group size effect on ingestion rates suggests that increasing food intake per unit of feeding time may not be a strategy used to deal with food competition in this species, perhaps because there is an upper limit to increases in food intake given the morphological limitations of mouth size and chew rate. However, we cannot come to a definite conclusion as of yet, as one would need ingestion rates for

individual females to assess if all females in larger groups have relatively equal feeding rates.

The Strength of Scramble Competition for *C. vellerosus* at BFMS

C. vellerosus in larger groups at BFMS spend more time feeding and range further than smaller groups. Increased travel and feeding may allow females in larger groups to meet their nutritional requirements, but these females nevertheless have to exert more energy in order to travel further each day. Increased travel may not be excessively costly, but it is unknown at what point energy expenditure will reach levels that cannot be compensated for by greater feeding time, though it is certainly species- and habitat-specific. It may be telling that group size at BFMS has never been seen to exceed 38 individuals and that forced female emigrations occur in larger groups [Teichroeb et al., accepted]. Behavioral compensation for food competition only likely occurs up to the point where reproductive success becomes affected.

Owing to the difficulty of showing when a folivorous diet is limiting, researchers have up until now focused on detecting the presence or absence of within-group scramble competition, but we may now be at the point with some populations where we can comment on the strength of within-group scramble, even in the absence of long-term data on energy gain and reproduction. For instance, if a population (like that of *C. vellerosus* at BFMS) is showing several of the behavioral indicators of scramble competition, such as a group size effect on day range, home-range size, and time spent feeding, plus occasional fission–fusion behavior in larger groups [Snaith & Chapman, 2007], perhaps these behaviors indicate that scramble competition is stronger in this population compared with a population in which only one behavioral strategy is being used to compensate for food competition. It is possible though that the ecological factors at certain sites limit the behavioral strategies that the population can use to deal with scramble competition. For instance, a high predation rate may limit a group's ability to use a fission–fusion strategy to deal with competition. Thus, the maximum tolerable group size for a certain area is limited by a host of local ecological factors that dictate the coping mechanisms individuals can use to contend with scramble competition.

CONCLUSIONS

The results of this study indicate that larger groups of *C. vellerosus* at BFMS use several behaviors to compensate for increased scramble competition for food in larger groups, highlighting the effectiveness of the ecological-constraints model for detecting food competition in highly folivorous primates. It is still to be determined if birth rates are

decreased in larger groups at BFMS owing to a decrease in female nutritional condition brought on by food competition, an effect that may be currently masked by infanticide at this site [Teichroeb & Sicotte, 2008].

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