

Increasing Group Size Alters Behavior of a Folivorous Primate

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Abstract Group size influences many aspects of mammalian social life, including stress levels, disease transmission, reproductive rates, and behavior. However, much of what is known about the effects of group size on behavioral ecology has come from comparisons across multiple groups of different sizes. These findings may be biased because behavioral differences across groups may be more indicative of how

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environmental variation influences animal behavior, rather than group size itself. To partially circumvent this limitation, we used longitudinal data to examine how changes in group size across time affect the behavior of folivorous red colobus monkeys (*Procolobus rufomitratus*) of Kibale National Park, Uganda. Controlling for food availability, we demonstrated that increasing group size resulted in altered activity budgets, based on 6 yr of data on a group that increased from 57 to 98 members. Specifically, as group size increased, individuals spent less time feeding and socializing, more time traveling, and increased the diversity of their diet. These changes appear to allow the monkeys to compensate for greater scramble competition apparent at larger group sizes, as increasing group size did not show the predicted relationship with lower female fecundity. Our results support recent findings documenting feeding competition in folivorous primates. Our results also document behavioral flexibility, an important trait that allows many social mammals to maximize the benefits of sociality (e.g., increased vigilance), while minimizing the costs (e.g., increased feeding competition).

Keywords Behavioral plasticity · Dietary diversity · Fertility · Red colobus · Scramble competition · Sociality · *Procolobus rufomitratus*

Introduction

Group size affects many aspects of social organization and behavior (Janson and Goldsmith 1995; Pulliam and Caraco 1984). The size of social groups has been implicated in the stress levels of individuals (Pride 2005; Snaith *et al.* 2008; Takeda *et al.* 2003), disease susceptibility (Cote and Poulin 1995; Davies *et al.* 1991; Loehle 1995; Nunn and Heymann 2005; Rifkin *et al.* 2012), reproductive and developmental rates (Borries *et al.* 2008; Creel and MacDonald, 1995; Mann *et al.* 2000), and individual and group behavior (Brown and Brown 1996; Carpenter 2007; Griffiths and Magurran, 1997; Koenig 2002; Nunn *et al.* 2009). Inter- and intraspecific variation in group sizes has been documented across broad spatial and temporal scales (Holmes and Price 1986; Poulin 1995; Weldon *et al.* 2004), and the causes and impacts of this variation have been the focus of intense study (Brown and Brown 1996; Croft *et al.* 2008; Elgar 1989; Ezenwa 2004; Griffin and Nunn 2012).

Among the numerous explanations proposed to explain the large variation in social systems observed across vertebrates (Elgar 1989; Isbell 1991; Snaith and Chapman, 2007; Sterck *et al.* 1997; Wrangham 1980), the influence of group size on feeding competition between and within groups has been proposed as a major player in the evolutionary ecology of sociality (Eubank *et al.* 2004). A key relationship used in the development of theoretical models of group size determinants was the dependence of the rate of energy intake on the number of individuals in a group (Croft *et al.* 2008; Perkins *et al.* 2009; Pulliam and Caraco 1984; Wrangham *et al.* 1993). The increased nutritional requirements of larger groups are thought to cause larger groups to travel farther to visit more food patches that are depleted more rapidly (Chapman and Chapman 2000; Chapman *et al.* 1995; Janson and Goldsmith 1995; Janson and van Schaik 1988). Thus, individuals in larger groups are predicted to have to increase energy expenditure and travel farther to maintain energy intake (i.e., scramble competition; van Schaik 1989; van Schaik and van Hooft 1983). The increased energetic costs

of living in a large group may be a sensible investment, however, if larger groups experience decreased predation or increased success in intergroup encounters (Croft *et al.* 2008; Perkins *et al.* 2009). Given the pros and cons of increases in group size, there may be an ideal group size that is most appropriate for a given environment where the benefit-to-cost ratio of group living is maximized (van Schaik and van Hooff 1983). Though some groups of animals may have more flexibility to adapt to changes in group size, herbivorous mammals are of particular interest because their fibrous diet, subsequent slow digestion, and large body sizes (Demment and Van Soest 1985) make it difficult to adjust time budgets to changing competitive regimes (Borries *et al.* 2008).

The apparent abundance of resources, i.e., leaves, for folivorous primates in tropical forests has led to the suggestion that scramble competition should be limited or absent, and thus not a constraint on group size in folivorous primates (Isbell 1991). This hypothesis has been supported by numerous intergroup comparisons of folivorous primates, which have found little or no evidence of scramble competition (Clutton-Brock and Harvey 1977; Janson and Goldsmith 1995; Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998; Yeager and Kool 2000). In a comparative analysis of primates, however, Janson and Goldsmith (1995) found that folivores exhibited smaller group sizes than similarly sized frugivores in similar areas. This apparent contradiction between theory and empirical data has been coined the “folivore paradox” (Janson and Goldsmith 1995; Snaith and Chapman 2005; Snaith and Chapman 2007; Steenbeek and van Schaik 2001); however, there is mounting evidence that folivores may exhibit significant scramble competition for quality leaf resources. Folivores are resource limited in larger groups (Borries *et al.* 2008); they deplete patches as a function of group and patch size (Snaith and Chapman 2005); their total biomass is predicted by the quality of resources (Chapman *et al.* 2002; Oates *et al.* 1990); and the size of their daily range increases with group size (Snaith and Chapman 2008). These findings suggest that resources are limiting to folivores, and that scramble competition limits group sizes (Borries *et al.* 2008; Snaith and Chapman, 2007, 2008), as it does for frugivores.

In an attempt to resolve these contradictory findings, we conducted a longitudinal analysis of group size, food availability, and behavior in red colobus monkeys (*Procolobus rufomitratus*) of Kibale National Park, Uganda. The mean group size of red colobus across Kibale has increased over the past 15 yr, suggesting high levels of plasticity in this social variable (Gogarten and Chapman *unpubl. data*). Most studies examining the effects of group size on the behavior of social mammals have compared multiple groups with different group sizes, but this method may be problematic if primates adjust group sizes in response to ecological conditions to avoid the costs of scramble competition, or if large groups are in high-quality areas, negating the need to increase day range or modify activity budgets (Snaith and Chapman 2005). Our analysis of a single group through time reduces the number of confounding variables and provides an alternate means of examining the effect of group size on behavior (Symington 1988). We examined how changes in group size affect the behavior of folivorous red colobus, specifically feeding, socializing, traveling, and diet. We predicted that larger group sizes are associated with increased time spent traveling (Koenig 2002; Snaith and Chapman 2008), decreased time spent feeding and socializing (van Schaik *et al.* 1983), higher dietary diversity (Snaith and Chapman 2007, 2008), and lower female fecundity (Beehner *et al.* 2006; Borries *et al.* 2008; Snaith and Chapman

2008). We expected that red colobus spend less time traveling, more time feeding and socializing, and have lower dietary diversity with increased food availability, so we control for variation in this factor in our analysis.

Methods

We collected data from a well-habituated group of red colobus in Kibale National Park, Uganda (Chapman *et al.* 2000, 2010; Gogarten *et al.* 2012a; Struhsaker 1997). Kibale is a 795-km² park consisting of moist, mid-altitude forest located in the western part of Uganda in the foothills of the Rwenzori mountains (0°13'–0°41'N and 30°19'–30°32'E). Rainfall is seasonal with two rainy seasons (1691 mm; data from 1990–2013, Chapman and Chapman *unpubl. data*). Monthly rainfall data were collected immediately adjacent to the group's home range throughout the study.

We collected activity data over 56 mo (July 2006–February 2011). We collected group scan data by randomly selecting 5 adults every 30 min ($N = 35,100$ individual scans, monthly mean = 638 scans, range = 190–969 scans). During these scans, we recorded the individual's identity if known; sex; behavior (feeding, traveling, being social (i.e., grooming, playing), resting; behavioral categories following: Struhsaker 1975), the species and plant part being consumed if feeding, and the group spread. Individuals were classified as adults based on body size (Struhsaker 1975). Data were collected by C. A. Chapman, J. F. Gogarten, and five well-trained field assistants; we conducted an intensive training period to standardize all data collection techniques and minimize interobserver error before data collection.

Counts of the number of individuals in the group were conducted opportunistically when monkeys crossed open areas, facilitating a complete group count ($N_{\text{counts}} = 28$). We estimated group sizes for each month from the available group counts by building a generalized additive model (GAM) with a smoothing spline over the studies' duration, using the R package *mgcv* (Fig. 1; $R^2 = 0.878$, $P < 0.001$; Miyamoto *et al.* 2013; Wood 2011; Zuur *et al.* 2009). We used a GAM model because we were interested in best fitting the available data and did not want to assume a linear relationship between time and group size (Wood 2011; Wood and Wood 2011; Zuur *et al.* 2009). For each group count, we calculated the infant to female ratio as an estimate of group-wide female fertility (Akçakaya *et al.* 1999).

To estimate the availability of foods, we monitored the phenology of 309 trees representing 33 species each month (for details on tree species and methods, see Chapman *et al.* 2005). We focused our estimate of food availability on young leaves, as young leaves constituted >77.0% of the plant parts observed being consumed across the 56 mo of observation. The remainder of the observed diet consisted of bark (representing 5.9% of time spent feeding), leaf petioles (5.5%), mature leaves (3.5%), unripe fruits (1.3%), leaf buds (1.2%), and flowers (1.2%; for a detailed analysis of the red colobus diet, see Chapman *et al.* 2002; Chapman and Chapman 2002). During each month, we estimated the availability of young leaves on each tree using a 0–4 scale (Chapman *et al.* 2005). If a monitored tree died, it was replaced with another tree of the same species and approximate size to ensure a continuous sample size. As an index of food availability, we used the sum of the 0–4 scores divided by the number of trees monitored that month. Monthly phenology data were available for all months of the

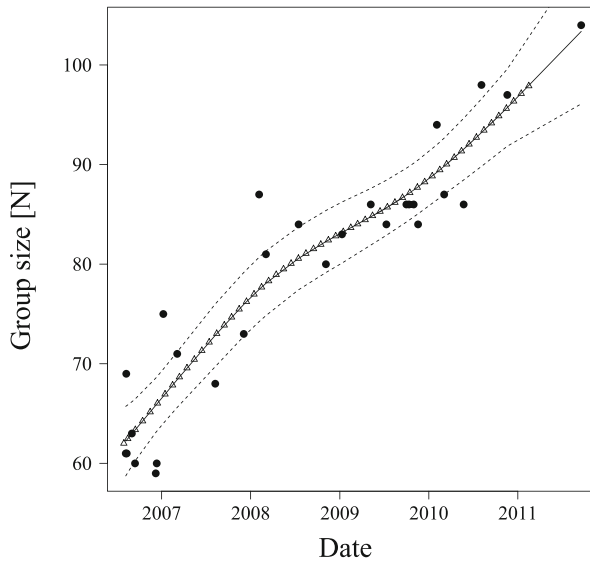


Fig. 1 Size of the focal group of red colobus in Kibale National Park, Uganda between July 2006 and February 2011 (Miyamoto *et al.* 2013). Black circles represent group counts; triangles represent the predicted group size for each month; the solid line represents the generalized additive model predicting group size through time; and the dashed line represents the 95% confidence bands.

study except June 2008, June 2009, June 2010, and October 2010; for these months we used the average of the food availability index of the month before and after the missing month. In addition, though all of the species that we monitored were eaten by red colobus, we constructed a second food availability index consisting of nine of the ten most commonly consumed species, to capture aspects of phenology potentially most relevant to the red colobus (Table 1). These 10 most commonly consumed species made up almost 60% of this group's diet, but we excluded *Newtonia buchannani* because it is a rare, but preferred, species for which phenology data were not available.

When individuals were observed eating during a scan ($N = 15,774$ scans), we recorded the species, age, and plant part being consumed, e.g., *Celtis durandii* young leaves and *Markhamia lutea* leaf petioles of a specific length. Owing primarily to poor visibility, we were unable to identify the plant species being consumed in *ca.* 2% of feeding scans and these scans were excluded from the analysis of dietary diversity. For each month, we calculated the inverse of Simpson's index of diversity (Levins 1968; Simpson 1949) using the vegan package for R (Oksanen *et al.* 2012). We rarified the data to the minimum number of scans during which individuals were observed eating in a given month ($N = 104$) to eliminate any sample size effect (Soetaert and Heip 1990). This index ranges from 1 to a maximum equal to the number of species in the sample, with higher values indicating higher diversity.

Though our behavioral data would ideally be analyzed using generalized linear mixed effects models (GLMMs) with a multinomial response variable and controlling for potential temporal autocorrelation, we are unaware of any current implementation. Thus, we examined the influence of food availability and group size on behavior using three separate GLMMs. Specifically, behavior was treated as a binomial variable (feeding/not feeding, traveling/not traveling, and socializing/not socializing) and we

Table 1 Food species most commonly consumed by the red colobus focal group in Kibale National Park, Uganda between July 2006 and February 2011

Species name	Percent of diet
<i>Albizia grandibracteata</i>	10.5
<i>Trilepsium madagascariense</i> ^a	9.4
<i>Newtonia buchananii</i> ^b	8.7
<i>Celtis africana</i>	5.6
<i>Celtis durandii</i>	4.4
<i>Millettia dura</i>	3.8
<i>Strombosia scheffleri</i>	3.6
<i>Parinari excelsa</i>	3.5
<i>Dombeya mukou</i>	3.3
<i>Macaranga schweinfurthii</i>	3.2
<i>Prunus africana</i>	2.9
Total	58.9

^a Formerly *Bosqueia phoberos*.

^b Phenology data were not available for this species as it was very rare but preferred, so it was not included in the food availability index.

fitted models with a binomial error distribution, included monthly rainfall as a factor to control for aspects of environmental variability beyond food availability, and included month as a random factor. To account for temporal autocorrelation of months, as evidenced by moderate patterning in the residuals of these models, we used an AR1 correlation structure in our models (Zuur *et al.* 2009). Models were implemented in the *nlme* (Pinheiro *et al.* 2012) and *MASS* R packages (Venables and Ripley 2002) using the *glmmPQL* function, which implements GLMMs with a penalized quasi-likelihood. To test whether the estimation of group size in months, rather than actual counts, impacted our analysis, we created three reduced GLMMs including only data from those months where group counts were available.

Because the GLMMs did not allow us to simultaneously analyze behavioral differences across categories, we built separate models to explain variance in each of feeding, traveling, and social behaviors. Unfortunately these models do not allow the inclusion of random effects or temporal autocorrelation, so results should be interpreted with caution. Given that individuals had a choice between any number of behaviors at any given time, we analyzed behavior as a nominal response to group size in a multinomial baseline-category logit model (Agresti 2002), implemented in the *nnet* R package (Ripley 2011; Venables and Ripley 2002). We predicted that the behavior of an adult would be a function of group size, food availability, and rainfall. We included resting behavior in this multinomial baseline-category logit model to have a baseline behavior against which to compare our three behaviors of interest (Agresti 2002). These four behaviors represented 97.8% of the scans.

We tested the influence of food availability, rainfall, and group size on dietary diversity using multiple regression. In addition, to test specifically for the effect of group size on dietary diversity, we constructed a simple linear model to explain

variance in dietary diversity as a function of group size. To test whether the infant to female ratio, an indicator of female fecundity (Fedigan 1986; Gogarten *et al.* 2012b; van Schaik 1983), was influenced by group size, we constructed a linear model explaining variance in the infant to female ratio as a function of group size. We examined the influence of group size and food availability on group spread using a GLMM with a Poisson error distribution and included monthly rainfall as a factor to control for aspects of environmental variability beyond food availability, with month as a random factor. As for the analysis of the behavioral data, we used an AR1 correlation structure to control for temporal autocorrelation in the data (Zuur *et al.* 2009). All statistical analyses were conducted in R version 2.14.2 (R Development Core Team 2012).

Ethical Considerations

This work conforms to the legal requirements of Canada and Uganda and was conducted under appropriate ethics and legal clearances. Specifically, permission to conduct this research was given by the National Council for Science and Technology, the Uganda Wildlife Authority, and the McGill Animal Care Committee.

Results

Group size increased from 57 to 98 individuals over 56 months (Fig. 1). Subjects spent most of their time feeding (45.8%), followed by resting (37.7%), traveling (7.9%), and socializing (6.4%) behaviors. The monthly food availability index ranged from 0.852 to 2.041 (mean = 1.673, $\sigma = 0.247$). The food availability index for the 10 top red colobus foods ranged from 1.298 to 2.430 (mean = 1.898, $\sigma = 0.229$), while monthly rainfall ranged from 34.7 to 376.3 mm (mean = 142.71, $\sigma = 84.85$).

The percentage of time spent feeding ranged from 32.9 to 59.8% across months, the percentage of time spent traveling ranged from 0.7 to 23.3%, and the percentage of time spent socializing ranged from 1.5 to 13.2%. Monthly variation in behavior was best explained by variation in group size. Increasing group size was associated with a decreased percentage of time spent feeding and socializing, and an increased percentage of time spent traveling (Table II). Controlling for changes in food availability and rainfall, as the observed group size increased (by $N = 41$ individuals), red colobus were 77% less likely to be observed feeding during a scan, 82% less likely to be observed socializing, and 239% more likely to be observed traveling. Increasing food availability was associated with an increase in the proportion of time spent feeding, while the relationships to time spent socializing (positive) and traveling (negative) were not significant (Table II). Comparing the maximum to minimum food availability observed, while controlling for changes in food availability and rainfall, individuals were 111% less likely to be observed traveling, 54% more likely to be observed feeding, and 59% more likely to be socializing. Rainfall did not predict any behavior. Similar results were found between food availability based on the 10 most commonly consumed foods and group size: feeding was predicted by group size and food availability, but not rainfall; socializing was predicted by group size, but not food availability or rainfall; and

Table II Generalized linear mixed models explaining variance in probability that individual red colobus in the focal group in Kibale National Park, Uganda were socializing, feeding, or traveling at a given scan between July 2006 and February 2011

Dependent variable	AR1 Phi	Independent variables								
		Group size		Rainfall		Food availability				
		Effect (SE)	t	P-value	Effect (SE)	t	P-value			
Proportion of time spent socializing	0.087	-0.0200 (0.00702)	-3.912	< 0.0001	-0.000589 (0.000708)	-0.832	0.409	0.498 (0.309)	1.609	0.114
Proportion of time spent feeding	0.409	-0.0188 (0.00389)	-4.819	< 0.0001	0.000183 (0.000398)	0.460	0.648	0.537 (0.175)	3.067	0.0035
Proportion of time spent traveling	0.153	0.0583 (0.0108)	5.392	< 0.0001	0.000898 (0.00110)	0.818	0.417	-0.932 (0.492)	-1.894	0.0639

P-values in bold indicate significant results ($\alpha = 0.05$). AR1 Phi represents the estimated autocorrelation between consecutive months for the model. The df for all presented t-values = 51.

traveling was predicted by group size and food availability, but not rainfall (Table III). Results of the reduced models, including only months where group counts were available, are qualitatively extremely similar (Table IV), although in models explaining variance in traveling and socializing behavior, group size was no a longer significant predictor, likely due to small sample size. The effects of previously significant predictors remained in the same direction as in the full models (i.e., the effect of previously positive predictors remained positive and previously negative predictors remained negative).

From results of the multinomial logit model, behavior was most affected by group size (likelihood ratio $\chi^2 = 873.04$, $df = 3$, $P < 0.001$), followed by food availability (likelihood ratio $\chi^2 = 204.23$, $df = 3$, $P < 0.001$), and rainfall (likelihood ratio $\chi^2 = 11.59$, $df = 3$, $P = 0.009$). Increasing group size was associated with an increased probability that individuals were traveling and a decreased probability that they were socializing or feeding (Table V; Fig. 2A and B), while increasing food availability was associated with an increased probability of individuals feeding and socializing and a decreased probability of traveling (Table V; Fig. 2C). Similar results were observed using the availability of the most commonly consumed foods: behavior was best predicted by group size ($\chi^2 = 840.58$, $df = 3$, $P < 0.001$), followed by food availability ($\chi^2 = 132.61$, $df = 3$, $P < 0.001$) and rainfall ($\chi^2 = 15.14$, $df = 3$, $P = 0.002$).

Increasing group size was associated with higher dietary diversity ($R^2 = 0.23$, $F_{[1,53]} = 16.6$, $P < 0.001$; Fig. 3). This relationship was also observed in the multiple regression analysis, explaining variance in dietary diversity as a function of group size, food availability, and rainfall ($R^2 = 0.24$, $F_{[3,51]} = 5.42$, $P < 0.005$), where food availability ($t = 0.470$, $P = 0.640$) and rainfall ($t = 0.074$, $P = 0.941$) were not significant factors in the model, but group size was ($t = 2.279$, $P < 0.01$). Increasing group size had no effect on the female to infant ratio ($R^2 = 0.045$, $F_{[1,26]} = 1.22$, $P = 0.279$). Though neither food availability ($t = -0.730$, $df = 51$, $P = 0.470$) nor rainfall ($t = 1.012$, $df = 51$, $P = 0.316$) was a significant predictor of group spread, increasing group size was associated with increasing group spread (AR1 Phi = 0.765, $t = 2.380$, $df = 51$, $P < 0.001$).

Discussion

Our results demonstrate that changes in group size impact the behavior of a folivorous primate above and beyond the variance explained by environmental factors, such as rainfall or food availability. With increasing red colobus group size, group spread increased and individuals spent less time feeding and socializing and more time traveling. This is likely a result of increases in patch depletion and scramble competition (caused by higher intragroup competition), necessitating an increased proportion of time spent traveling to meet the group's nutritional demands. Similarly, dietary diversity increased with group size, suggesting that intragroup competition forces individuals to eat less preferred foods. Taken together, these results suggest that there are increasing costs of intragroup competition associated with increasing group size, including the energetics of travel, quality of the diet, and time available for sociality. This finding is in accord with a growing body of evidence that scramble competition in folivores limits group sizes (Borries *et al.* 2008; Harris *et al.* 2010; Snaith and

Table III Generalized linear mixed models explaining variance in probability that individual red colobus in the focal group in Kibale National Park, Uganda were socializing, feeding, or traveling at a given scan between July 2006 and February 2011, using a food availability index based only on the top 10 red colobus foods

Dependent variable	AR1 Phi			Independent variables			Food availability ^a		
	Effect (std. err.)	t	P-value	Effect (SE)	t	P-value	Effect (SE)	T	P-value
Proportion of time spent socializing	0.087	-2.661	0.010	-0.000613 (0.000735)	-0.834	0.482	0.380 (0.295)	1.285	0.205
Proportion of time spent feeding	0.408	-4.353	< 0.0001	0.000146 (0.000417)	0.350	0.728	0.430 (0.168)	2.563	0.0134
Proportion of time spent traveling	0.153	5.679	< 0.0001	0.00110 (0.00113)	0.975	0.334	-0.890 (0.462)	-1.927	0.0595

P-values in bold indicate significant results ($\alpha = 0.05$). AR1 Phi represents the estimated autocorrelation between consecutive months for the model. The df for all presented t-values = 51.

^a Models built using food availability index based on the 10 most commonly consumed red colobus foods.

Table IV Reduced generalized linear mixed models explaining variance in probability that individual red colobus in the focal group in Kibale National Park, Uganda were socializing, feeding, or traveling at a given scan between July 2006 and February 2011

Dependent variable	AR1 Phi		Independent variables								
			Group size		Rainfall		Food availability				
	Effect (SE)	<i>t</i>	Effect (SE)	<i>t</i>	Effect (SE)	<i>t</i>	Effect (SE)	<i>t</i>	<i>P</i> -value		
Proportion of time spent socializing	0.083	-0.0133 (0.01116)	-1.139	0.271	0.271	-0.00201 (0.00123)	-1.638	0.120	0.243 (0.457)	0.532	0.602
Proportion of time spent feeding	0.412	-0.0211 (0.00605)	-3.484	0.0028	0.00131 (0.000642)	2.035	0.0578	0.588 (0.243)	2.419	0.0271	
Proportion of time spent traveling	0.134	0.0208 (0.0228)	0.915	0.3728	-0.000154 (0.00239)	-0.0643	0.950	0.0321 (0.928)	0.0346	0.973	

We included only data from those months where group counts were available. *P*-values in bold indicate significant results ($\alpha = 0.05$). AR1 Phi represents the estimated autocorrelation between consecutive months for the model. The df for all presented *t*-values = 19.

Table V Estimated parameters in the multinomial logit model for red colobus behavior in Kibale National Park, Uganda between July 2006 and February 2011, with resting as the baseline category

Logit	Intercept	Effect of group size	Effect of food availability	Effect of rainfall
$\log(\pi_f/\pi_r)$	0.442 (0.106)	-0.0169 (0.00145)	0.649 (0.0650)	0.000251 (0.000149)
$\log(\pi_s/\pi_r)$	-0.939 (0.204)	-0.0290 (0.00277)	0.934 (0.126)	-0.000384 (0.000291)
$\log(\pi_t/\pi_r)$	-5.445 (0.224)	0.0589 (0.00294)	-0.694 (0.123)	0.000688 (0.000271)

SE values in parentheses. These parameters are combined to describe the log odds of performing a given behavior instead of resting as a function of group size, food availability, and rainfall, e.g., the odds of feeding over resting is $\log(\pi_f/\pi_r) = 0.442 - 0.0169 * \text{group size} + 0.649 * \text{food availability} + 0.000251 * \text{rainfall}$. f = feeding; r = resting; t = traveling; s = socializing.

Chapman 2005, 2007). In fact, in the current study the impact of this scramble competition apparent at larger group sizes causes greater shifts in the activity budget than seasonal fluctuations in food availability or rainfall.

Our results suggest that scramble competition is occurring in folivores (Borries *et al.* 2008; Snaith and Chapman 2007, 2008). A remaining question is, given an abundant supply of leaves in tropical forests, why is there still competition over this resource? Possible reasons include variance in resource quality driven by factors such as plant secondary compounds (Cardiff *et al.* 2007; Rothman *et al.* 2009; Schofield *et al.* 2001), available energy (Danish *et al.* 2006; Rothman *et al.* 2011), protein-to-fiber ratio (Chapman *et al.* 2003; Felton *et al.* 2009), lack of nutrients such as sodium (Irwin *et al.* 2010; Reynolds *et al.* 2009; Rode *et al.* 2003; Rothman *et al.* 2006), or overall fiber content (Milton 1979). While the red colobus appear to be able to deal with increasing scramble competition by increasing their dietary diversity and changing their activity budget, individuals in the group may be obtaining lower quality foods as group size increases. A recent study using genetic data from two unequally sized neighboring groups of red colobus demonstrated increased female relatedness within the smaller group, which may suggest that females are less likely to disperse when there is less intragroup competition (Miyamoto *et al.* 2013). Future studies should examine variation in the nutritional content and chemical defenses of less preferred plants, and if individuals in larger group sizes are forced to consume lower quality foods. It is possible that the increasing dietary diversity observed at larger group sizes is simply a result of individuals in larger groups encountering a greater variety of foods owing to increased group spread and potentially larger home ranges (Snaith and Chapman 2008). We found no relationship between the infant-to-female ratio and group size, which suggests that shifts in red colobus diet are not yet great enough to impact female fecundity and that this behavioral flexibility is able to compensate for increased scramble competition. Alternatively, there may be a lag time between the increased levels of competition and resulting changes in energy expenditure and diet, and their effects on female fecundity, which the current study, despite its long-term nature, was unable to capture.

Studying a single group longitudinally, rather than multiple groups in a cross-sectional study, allowed us to control for environmental variation and reduce the

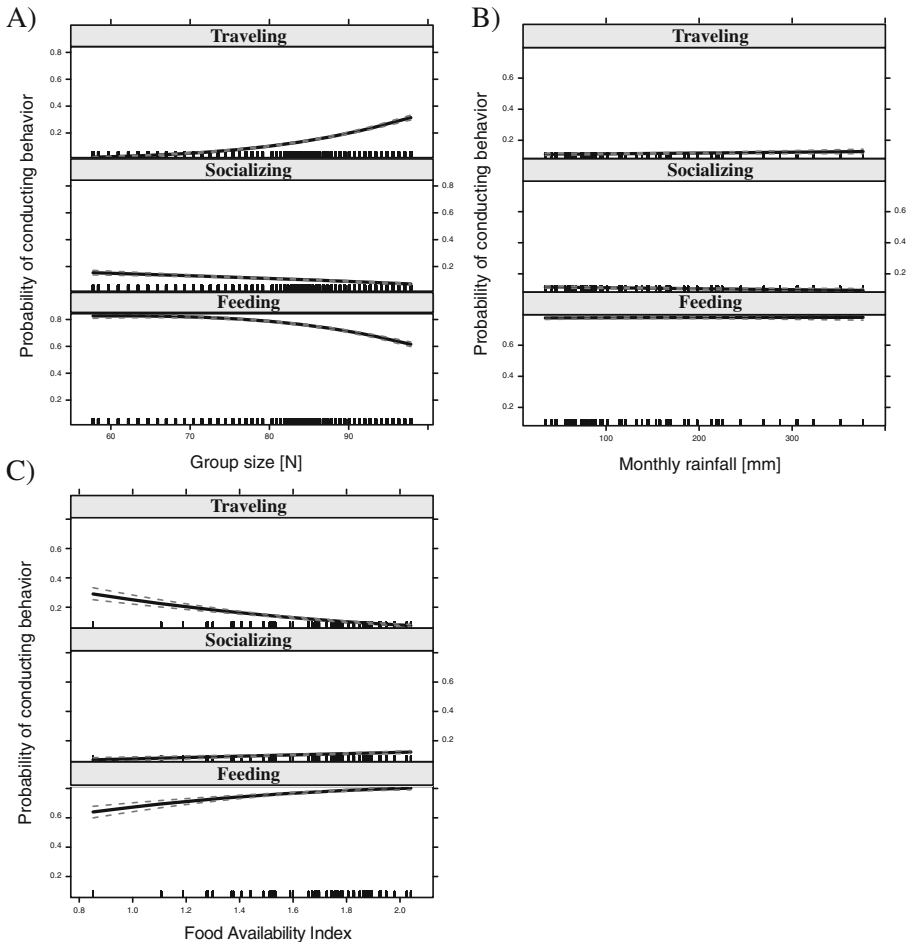


Fig. 2 Fitted probabilities from the multinomial logit model showing the effect of **(A)** group size, **(B)** rainfall, and **(C)** food availability on the probability of conducting different behaviors by the red colobus group studied in Kibale National Park, Uganda between July 2006 and February 2011. Dashed lines indicate 95% pointwise confidence envelope around the fitted probabilities of the model. Tick marks along the *x*-axis represent data used in the construction of the model.

number of potentially confounding ecological and group-specific variables. However, it is important to acknowledge the limitations associated with studying a single group. It remains possible that the patterns observed in this group are an anomaly, and thus further studies are needed to corroborate these findings in other groups. The costs and time necessary for habituating primates pose significant hurdles to replicating this study, and an alternative powerful approach is combining findings from both longitudinal and cross-sectional studies. The results of the current study closely mirror results from a cross-sectional study of red colobus in Kibale, where individuals in larger groups exhibited increased group spread and spent more time feeding and less time engaged in social behavior (Snaith and Chapman 2008). Further, the changes in group size observed in this group of red colobus are mirrored by changes in group sizes observed across Kibale National Park over the last 15 yr (Gogarten *et al. in review*).

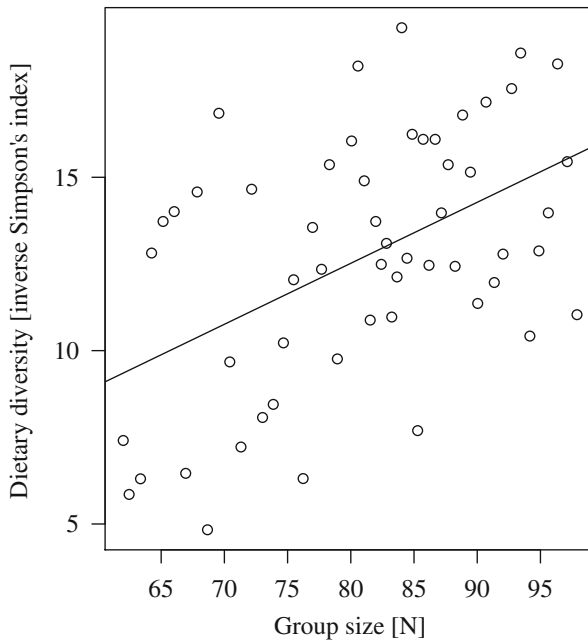


Fig. 3 Dietary diversity as a function of the size of the red colobus study group in Kibale National Park, Uganda between July 2006 and February 2011. Solid line represents the regression explaining variance in dietary diversity as a function of group size.

The factors responsible for these large-scale changes in group size remain unknown; changes in food availability or quality may be playing a role (Gogarten *et al. unpubl. data*), but additional studies are needed. Alternatively, red colobus groups may be recovering from a major disturbance (e.g., disease), which led to smaller than optimal group sizes for the environment, with group sizes only now slowly recovering. Regardless of the causes of the observed changes in group sizes, these changes are modifying the behavior of red colobus, which in turn may impact disease susceptibility, stress, reproductive rates, and ultimately population viability (Borries *et al. 2008*; Griffin and Nunn 2012; Pride 2005; Rifkin *et al. 2012*; Snaith *et al. 2008*).

Socioecological theory suggests that individuals will remain in a group so long as the benefits outweigh the costs, although average group size could rise above the optimum as the benefit for a solitary individual to be a member of a group is greater than the benefit of excluding an individual attempting to join a group (Giraldeau 1988; Purvis *et al. 2000*). Though we found support for the possibility that ecological constraints will limit group size, a number of alternative hypotheses have been proposed, including infanticide (Cardillo *et al. 2005*; Chapman and Pavelka 2005; Steenbeek and van Schaik 2001), disease (Chapman *et al. 2006, 2009*; Godfrey and Irwin 2007; Nunn and Altizer 2006), social memory (Shumway and Stoffer 2000), and predation, the latter of which may limit group size via mortality, especially if larger groups are easier for predators to detect (Hairston *et al. 1960*; Isbell 1994). We have no evidence that infanticide or predation represent significant pressures for this red colobus group, although it has been observed in this species (Struhsaker and Leland 1985, 1987), but the importance of these and other factors in limiting group size is a

continuing focus of our monitoring efforts of this group. The changes in behavior documented here suggest that continued monitoring of this population is critical, as such changes have been shown to impact fitness (Borries *et al.* 2008) and disease susceptibility (Griffin and Nunn 2012) in primate populations.

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