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Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model

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Abstract The ecological constraints model predicts that daily travel distance and home range size of social animals will increase as group size increases in order to meet the dietary needs of additional group members. This theory has been supported more predominantly by studies of frugivorous primate species than by studies of folivorous species. We examined the ranging patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda, who include both herbaceous vegetation and fruit in their diet, to determine how ecological, behavioral, and social parameters influence movement patterns. Data were collected from three groups of gorillas with overlapping home ranges at a low-altitude location (1,450–1,800 m) and one group at a high-altitude location (2,100–2,500 m) in Bwindi from September 2001 to August 2002. We analyzed daily travel distance and home range size in relation to group size, while also considering patterns of frugivory, rainfall, and location (proxy for food availability) within the park. Both daily travel distance and home range size were positively related to group size. In addition, the degree of frugivory positively influenced daily travel distance and home range size, while rainfall negatively influenced daily travel distance only. Finally, groups at the low-altitude location, with higher fruit availability, traveled less than the group at the high-altitude location. These results demonstrate that mountain gorillas in Bwindi provide support for the ecological constraints model, but further studies are needed to determine how fine-scale spatial and temporal availability of food resources influence movement patterns. Ranging patterns of Bwindi gorillas are compared to those observed in other gorilla populations in the context of the ecological constraints model.

Keywords Ecological constraints model · Ranging behavior · Group size · Food availability · *Gorilla beringei beringei*

Introduction

One of the main goals of primate behavioral ecology is to determine the ecological factors that influence the size and structure of social groups (Clutton-Brock and Harvey 1977; Terborgh 1983; van Schaik 1983; Sterck et al. 1997; Chapman and Chapman 2000a; Kappeler and van Schaik 2002). While primates may live in social groups to reduce predation risk, this may come at the cost of increased feeding competition. The ecological constraints model predicts that as group size increases, the amount of food needed collectively by the group also increases, and daily travel distance (DTD) and home range size should expand accordingly (Altmann 1974; Clutton-Brock and Harvey 1977; Chapman and Chapman 2000a). If a growing group is unable to increase travel distance to feed its additional members, food intake per individual may decline, which may lead to lower reproductive success (Dunbar 1988; Janson and van Schaik 1988; van Schaik 1989; Isbell 1991; Janson 1992; Janson and Goldsmith 1995; Sterck et al. 1997; Koenig 2002).

The relationship between group size and DTD is likely to depend on the distribution and abundance of food resources in the environment. A strong, positive relationship between group size, diet, and DTD is expected in frugivorous primates whose food occurs in discrete patches that are more likely to occur at low density, contain limited amounts of food, and be more monopolizable than leaves or herbaceous vegetation (Waser 1977; Chapman et al. 1995; Janson and Goldsmith 1995; Chapman and Chapman 2000a, 2000b). Frugivores may face higher levels of feeding competition than do folivores due to the costs associated with feeding on monopolizable patches (decreased net food intake and increased travel costs), and thus have greater limitations on group size than do folivores (Dunbar 1988; Janson 1992; Janson and Goldsmith 1995). To maintain equal levels of

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frugivory, larger groups would need to travel farther than smaller groups foraging in a habitat of a given level fruit abundance (biomass per unit area). A group in a habitat where fruit abundance is low would then also need to travel farther than a similar-sized group in a habitat with higher fruit abundance to consume the same amount of fruit. Many studies that have examined the relationship between group size and DTD in frugivorous primates have found that larger groups travel farther per day than smaller groups (Waser 1977; van Schaik et al. 1983; Chapman 1990; Wrangham et al. 1993; Chapman et al. 1995; Janson and Goldsmith 1995; O'Brien and Kinnaird 1997).

Folivores can have larger group sizes than frugivores, because leaf-based and herbaceous foods are generally more evenly distributed in space and time, allowing group members to spread out while foraging, thereby reducing travel costs and limiting feeding competition (Altmann 1974; Milton and May 1976; Clutton-Brock and Harvey 1977; Milton 1980; Oates 1987; Isbell 1991; but see Koenig et al. 1998). However, the energy constraints of a leaf-based diet, the avoidance of conspecific threat, predation, and female transfer patterns may limit folivore group size (Janson and Goldsmith 1995; Treves and Chapman 1996; Steenbeck and van Schaik 2001). Many studies of folivorous primates have found no relationship between group size and DTD (Struhsaker and Leland 1987; Yeager and Kool 2000; Fashing 2001; Arrowood et al. 2003; Dias and Strier 2003). However, most primates are neither exclusively frugivorous nor folivorous, but instead have a mixed diet, and group size may be limited by the food sources in their diet that are most easily depleted (Chapman and Chapman 2000b).

An increase in group size is also expected to increase home range size in both frugivores and folivores, although this relationship is less clear (Schoener 1971; Clutton-Brock and Harvey 1977; Isbell 1991). Many studies of both frugivorous and folivorous primates have found a relationship between group size and home range size (Supriatna et al. 1986; Butynski 1990; Ostro et al. 1999; Gillespie and Chapman 2001; Steenbeck and van Schaik 2001; Dias and Strier 2003) while others have not (Struhsaker and Leland 1987; Yeager and Kool 2000; Fashing 2001; Lehmann and Boesch 2003). Not all studies control for differences in food availability in the home ranges of different groups, which may explain the lack of relationship. Additionally, few studies take into account the overall density of conspecifics and/or other species feeding on the same resources in a study area, which may obscure any direct relationship between food availability, home range size, and group size.

Gorillas exhibit inter- and intra-population variation in their degree of frugivory, making them a useful species in which to test the influence of both group size and diet on ranging patterns. Western gorillas (*Gorilla gorilla*) are more frugivorous than most eastern gorillas (*G. beringei*), based on the diversity of fruit in their diets and the percentage of days fruit is consumed, although the actual amount of fruit consumption has not been fully quantified for most populations (Watts 1984; Tutin and Fernandez

1985; Williamson et al. 1990; Yamagiwa et al. 1994, 1996; McNeillage 1995; Remis 1997a; Doran et al. 2002; Cipolletta 2003; Ganas et al. 2004; Nkurunungi 2004). Differences in frugivory between and within gorilla species are likely due to differences in the abundance and distribution of fruiting trees and herbs within their habitats (Doran and McNeillage 1998, 2001). In general, density of fruiting trees is higher and density of herbaceous vegetation is lower in lowland forests inhabited by western gorillas than in the montane forests inhabited by populations of eastern gorillas. Correspondingly, the two gorilla species also show significant variation in ranging patterns, presumably due to these differences in food distribution (Doran and McNeillage 1998, 2001). The average DTD is greater in western gorillas than in eastern gorillas but the size of home ranges is comparable between most populations of the two species (Fossey and Harcourt 1977; Goodall 1977; Vedder 1984; Watts 1991, 1998; Yamagiwa et al. 1992, 1996; McNeillage 1995; Tutin 1996; Remis 1997b; Goldsmith 1999; Cipolletta 2003, 2004; Robbins and McNeillage 2003; Doran-Sheehy et al. 2004; Nkurunungi 2004). In the only population of gorillas where the relationship between group size and ranging patterns has been examined to date, a positive correlation was found between group size, DTD, and home range size (Fossey and Harcourt 1977; McNeillage 1995; Watts 1998). However, this population of mountain gorillas at the Karisoke Research Center, Rwanda is not representative of the genus as a whole because their high-altitude environment (>2,500 m) has the lowest availability of fruit and the highest density of herbaceous vegetation of all gorilla habitats; additionally, they consume almost no fruit, have the shortest DTD, and smallest home range size of any gorillas studied. Doran et al. (2004) found a positive correlation between the degree of frugivory and DTD for one group of western gorillas but not with monthly home range size; however, this study was unable to examine how differences in group size affected ranging patterns.

The main goal of this study was to test the ecological constraints model by examining the relationship between group size and both DTD and home range size in mountain gorillas of Bwindi Impenetrable National Park, Uganda, while also investigating how levels of frugivory, rainfall amount, and study location (as proxy for measure of food availability) influenced these variables. The study was conducted using three groups of gorillas with overlapping home ranges at a low-altitude site (Buhoma: 1,450–1,800 m) and one group at a higher altitude site (Ruhija: 2,100–2,500 m). Fruit-eating by gorillas and fruit availability in Bwindi differ markedly inter- and intra-annually and thus provide a good opportunity to test how frugivory influences movement patterns (Robbins and McNeillage 2003; Ganas et al. 2004; Nkurunungi et al. 2004). First, we predicted that larger groups would have both longer DTDs and larger home range sizes than smaller groups. Second, we predicted that DTD and home range size, on a biweekly and monthly basis respectively, would increase with increased levels of frugivory, because fruit patches are temporally available and more widely dispersed than herbaceous vegetation (Nkurunungi et al. 2004).

Food availability is an important variable influencing movement patterns of primates (Vedder 1984; Bennett 1986; Strier 1987; Olupot et al. 1997; Isbell et al. 1998; Chapman and Chapman 2000a; Li et al. 2000; Gillespie and Chapman 2001; Kaplin 2001). The density of herbaceous vegetation and fruit availability differ between locations in Bwindi. The density of herbs eaten by gorillas was lower at the low-altitude site (4.33/m² in Buhoma) than at the high-altitude site (10.6/m² in Ruhija), and it was unlikely to vary seasonally at either location (Nkurunungi et al. 2004; personal observation). Additionally, on both a monthly and yearly scale, fruit availability was greater in Buhoma than Ruhija (Nkurunungi et al. 2004). Finer measurements of the spatial and temporal availability of the gorillas' food resources were not available. Therefore, third, we used location as a proxy to represent the differences in food availability between the two study sites (assuming that the three groups with overlapping home ranges had the same availability). Assuming the patchy distribution and availability of fruit has a stronger influence on the gorillas' ranging than the evenly abundant herbs, we predicted that the group with lower fruit availability (high-altitude site) would have longer DTDs and larger monthly home ranges than the three groups at the low-altitude location.

Last, we predicted that rainfall would reduce DTD and home range size because of thermoregulatory constraints if it is correlated with decreased temperature (Kleiber 1961; Whittow 1971). Rainfall has been shown to influence the movements of lar gibbons (*Hylobates lar*), siamangs (*H. syndactylus*), and red colobus monkeys (*Procolobus badius*) (Raemaekers 1980; Isbell 1983). Additionally, rainfall is sometimes used as a proxy for food abundance

(Vedder 1984; Lehmann and Boesch 2003). Vedder (1984) found that a mountain gorilla group at the Karisoke Research Center, Rwanda increased monthly home range size with decreasing rainfall although this was attributed to the relationship between rainfall and food abundance. Goldsmith (1999) found that gorillas at Bai Hokou, Central African Republic traveled farther during the rainy season, but a correlation between food abundance and rainfall was not verified.

To determine how group size, frugivory, rainfall, and location (food availability) affected DTD and home range size, we compared these variables on a biweekly and monthly basis between groups in a multiple linear regression. We then compared our results with those from other populations of gorillas in the context of the ecological constraints model.

Methods

Study location and study animals

This study was conducted at two locations separated by 18 km within Bwindi Impenetrable National Park (0°53'–1°08'N; 29°35'–29°50'E) in southwestern Uganda between September 2001 and August 2002. Bwindi is an afro-montane rainforest, 331 km² in size, ranging in altitude from 1,160 to 2,607 m, characterized by steep-sided hills, peaks, and narrow valleys (McNeilage et al. 2001).

Data on DTD and home range size were collected from 4 habituated gorilla groups, ranging in size from 7 to 24 individuals, excluding infants (Table 1). Two groups, Mubare

Table 1 For each gorilla group, the location they ranged in, the number of individuals in each group (including and excluding infants), the sex/age class composition of each group (following Watts 1990b), annual mean daily travel distances (DTD), mean biweekly

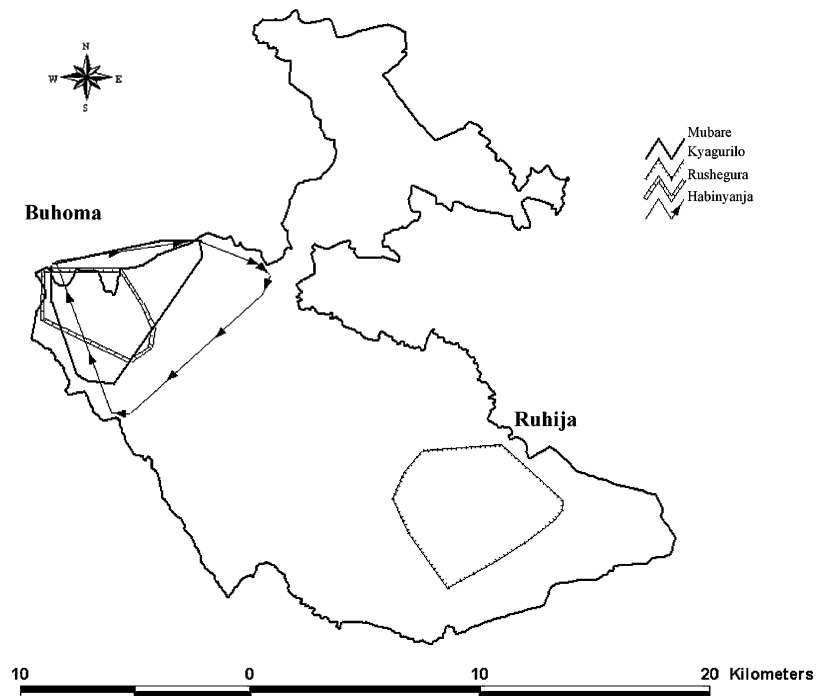
DTD, biweekly DTD ranges, yearly home range size [calculated using both minimum convex polygon (MCP) and grid square methods], monthly home range ranges (calculated using only the MCP method), and mean monthly home range

	Mubare	Habinyanja Pre-fission	Habinyanja Post-fission	Rushegura ^a	Kyagurilo
Location of group	Buhoma	Buhoma	Buhoma	Buhoma	Ruhija
Group size	12	30	22	8	14
Group size w/o infants	11	24	17	7	12
Silverbacks	1	2	1	1	2
Blackbacks	0	2	2	0	0
Adult females	6	13	8	5	5
Subadults	0	2	2	0	3
Juveniles	4	5	4	1	2
Infants	1	6	5	1	2
Mean annual DTD	547 m	847 m	978 m	633 m	1034 m
Mean biweekly DTD	550 m	863 m	953 m	643 m	1032 m
Range of Biweekly DTD	222–1053 m	553–1284 m	628–1203 m	265–1030 m	637–1720 m
Yearly home range MCP	22.9 km ²	37.6 km ²	**	13.7 km ²	31.3 km ²
Yearly home range grid	16.25 km ²	22.25 km ²	**	11.25 km ²	24.75 km ²
Monthly home range range	1.2–10.3 km ²	3.72–9.13 km ²	0.89–6.94 km ²	1.99–7.88 km ²	1.66–11.11 km ²
Mean monthly home range	3.58 km ²	6.76 km ²	4.59 km ²	3.43 km ²	4.78 km ²

^aData from the Rushegura group are only for a six and a half month period.

**“Habinyanja” and “post-fission Habinyanja” are the same group when considering yearly home range size.

Fig. 1 Map of Bwindi Impenetrable National Park, Uganda and the two study locations, Buhoma (1,450–1,800 m) and Ruhija (2,100–2,500 m). The total home range for each gorilla group was calculated using the minimum convex polygon method



and Habinyanja, ranged around Buhoma (1,450–1,800 m), in the western section of the park (Fig. 1). Halfway through the study (Feb. 2002), the Habinyanja group fissioned, and eight gorillas jointly emigrated to form another group, Rushegura. For the purposes of analyzing the influence of group size on ranging patterns, we divided the Habinyanja group into “pre-fission” and “post-fission” and treated them as two independent groups. Because these groups in Buhoma are used for an ecotourism program, the Uganda Wildlife Authority seeks to keep human disturbance to these gorillas to a minimum. Therefore we were not permitted to conduct direct observations on the gorillas. The fourth group, Kyagurilo, ranges near Ruhija (2,100–2,500 m), in the eastern section of the park (Fig. 1) and is habituated for research purposes. While direct observations were made on this group, we consistently used indirect methods to measure ranging and dietary patterns with all groups.

Daily Travel Distance (DTD)

We measured the distance traveled each day by each gorilla group by first locating their night nests. Every night, all weaned individuals of a group make nests in close proximity to one another to form a night nest site. We measured the distance between two consecutive night nest sites along the gorillas’ path, an obvious trail caused by bent vegetation, discarded food items, and dung, using a topofil (hipchain, which measures the distance traveled). These trails are easy to follow with the assistance of experienced trackers, and this method is commonly used in studies of ranging patterns of gorillas. We chose the largest main path, and although not all gorillas in the group use the same path, the group moves as a cohesive unit and therefore this is the best estimator for measuring DTD of goril-

las when indirect methods are used (Watts 1991; Yamagiwa et al. 1992; McNeilage 1995; Tutin 1996; Goldsmith 1999). Because the gorillas are monitored daily, we could consistently follow the trails only 1 day behind the gorillas and follow each group simultaneously to ensure that we were not following old trails or confusing one group’s trail with another. We calculated both a yearly and a biweekly mean DTD. DTD was not recorded in the month of April for the Kyagurilo group because contact was lost with the group for two and a half weeks following an intergroup encounter. On average, we measured 18 DTDs per month per group (Mubare: mean=18, range=14–24, SD=3.06; Kyagurilo: mean=21, range=15–28, SD=4; pre-fission Habinyanja: mean=16, range=6–21, SD=5.97; post-fission Habinyanja: mean=15, range=11–19, SD=2.88; Rushegura: mean=19, range=17–21, SD=1.79).

Home range

To determine the gorillas’ home ranges, we took a Global Positioning System (GPS) measurement daily at each group’s night nest site. When the nests were not located, we recorded a point when the gorillas were first contacted. For all groups, we used only one GPS point per day, when we entered the GPS coordinates into ArcView software and calculated yearly home ranges using both the minimum convex polygon (MCP) method and the grid cell method (500 m×500 m) (Southwood 1966). The grid square method may underestimate home range size, by using only one GPS datum point per day, or overestimate it if only a small portion of the entire grid square is used. The MCP method may overestimate home range size, but because both methods are used by researchers studying the home range size of primates, it is useful to

calculate sizes using both methods for comparisons with other studies (Herbinger et al. 2001; Singleton and van Schaik 2001; Lehmann and Boesch 2003; Robbins and McNeilage 2003). We also calculated monthly home ranges but using only the MCP method, because the grid square method biases towards an underestimation in monthly size estimates due to the small number of points (Robbins and McNeilage 2003). Due to the fission of the Habinyanja group in February, for this month there are fewer than 14 data points each for the pre-fission Habinyanja, post-fission Habinyanja, and Rushegura groups, and we did not calculate these monthly home ranges. Furthermore, because the Rushegura group formed mid-study, we have only six and a half months of data for this group. On average, we recorded a GPS datum point 24 days per group per month (Mubare: mean=24, range=19–30, SD=2.76; Kyagurilo: mean=28, range=14–30, SD=4.62; pre-fission Habinyanja: mean=22, range=10–26, SD=6.05; post-fission Habinyanja: mean=22, range=14–25, SD=3.79; Rushegura: mean=23, range=6–27, SD=7.48).

Measures of frugivory

To distinguish between days when the gorillas ate fruit versus days when they did not, we collected fecal samples from the gorillas' night nests (<48 h old), and recorded whether fruit seeds were present in the dung and recorded the number of species present (see Ganas et al. 2004 for detailed methods). We considered the presence of seeds in the dung 2 days after the DTD was measured, based on gut passage rates recorded from captive-gorilla studies (Remis 2000), as an indication the gorillas ate fruit that particular day. While captive-primate digestion trials have shown that retention time of food varies (Dierenfeld et al 1992; Lambert 2002; Remis and Dierenfeld 2004), any error in our method of estimating constant gut passage time would have been consistent across all study groups. Second, although some primates have been observed to spit or drop fruit seeds while feeding (Corlett and Lucas 1990; Kaplin and Moermond 1998; Lambert 1999), which would contribute to an underestimation of frugivory, Bwindi gorillas have not been observed to spit seeds during over 1,500 h of observation (M.M. Robbins, personal observation). Finally, although dung beetles may be present in Bwindi and remove animal dung and thus seeds, neither author has seen dung beetles removing seeds from gorilla feces in Bwindi. Each day was categorized based on whether: (1) the gorillas ate fruit from trees, (2) they ate fruit from any plant sources (herb, shrub or tree), or (3) they did not eat fruit. We distinguished between tree fruits and fruit from any plant source because tree fruits may influence movement patterns more strongly than herb or shrub fruits due to the possible greater fruit-crop sizes associated with most trees. As another measure of frugivory, we also calculated: (1) the number of fruit species eaten from trees, and (2) the number of fruit species eaten from any plant sources (following Goldsmith 1999; Cipolletta 2003; Doran-Sheehy et al. 2004). All unknown fruit species were classified

as “non-tree fruits” ($n=6$ species, 1 species occurred on 6 days, 5 species were found on only 1 day each throughout the study). Based on the presence of seeds in the feces, there was no significant difference among the groups in the percent of days that they consumed fruit (the range was 65.6–82.1% of observation days across the year, excluding partial data for the Rushegura group; Ganas et al. 2004).

Rainfall

Data on rainfall were collected daily from stations in Buhoma and Ruhija monitored by the Uganda Wildlife Authority and the Institute of Tropical Forest Conservation. Both locations experienced two wet seasons (Sept. to Nov. 2001 and March to May 2002) and two dry seasons (Dec. 2001 to Feb. 2002 and June to Aug. 2002). Rainfall varied between locations with a total of 1,924 mm (monthly range: 28–365 mm) at Buhoma and 1,313 mm (monthly range: 6–277 mm) at Ruhija during the study period.

Data analysis

We used a multiple linear regression to assess the effects of ecological (study location/food availability, rainfall), behavioral (frugivory), and social variables (group size) on DTD and home range size. Fruiting patterns in Bwindi are variable both within and between study locations, and often fruit availability for particular species is limited to a short time period (J. Ganas and M.M. Robbins, personal observation). Therefore, to examine the relationship between frugivory and DTD, we calculated all variables as biweekly means (starting at the beginning of each month, following Gillespie and Chapman 2001). We tested travel distances with the following variables: tree fruit and any plant fruit source-eating days, calculated as percentages of days fruit was eaten per biweekly period, and the mean number of tree and any plant fruit species eaten per day, calculated as biweekly means. We also included the number of gorillas in each group (excluding infants), biweekly rainfall amount, and location (Buhoma or Ruhija, as a dummy coded variable that allows a categorical variable to be used in a linear regression). Only days in which DTD had corresponding fecal samples were used for DTD calculations.

For home range size, we tested monthly home range sizes against the previously mentioned variables, but with monthly percentages and means. We calculated monthly home ranges rather than biweekly home ranges because the number of points in a biweekly period (one point per day) would not provide an accurate estimate of home range size (Robbins and McNeilage 2003).

The four fruit variables (percentage of days fruit was eaten from trees, percentage of days fruit was eaten from any plant sources, the number of tree-fruit species eaten, and the number of total fruit species eaten) were significantly correlated with each other ($r=0.455-0.9$, P -values between 0.001 and 0.005). Therefore, we ran four separate analyses each for DTD and home range, with one of the

frugivory variables together with remaining independent variables and chose the best model based on the highest adjusted r^2 . After the first analysis was completed (for DTD and home range), we removed the non-significant independent variables and ran the regressions again, to be able to attribute more of the variance to the significant variables. We present the results from these tests. We used an ANOVA to test for interactions between two independent variables together with the remaining variables. To evaluate the importance of the significant independent variables, we calculated two measures of effect size, the partial η^2 and the regression coefficient, β . The partial η^2 value is the amount of variance explained by an independent variable once all other variables are held constant. The standardized regression coefficient, β , is used to compare the magnitude of effect of different variables that were measured in different ways. It describes the change in the dependent variable (expressed in SD units) caused by an increase in one unit (in SD) of the independent variables, while all other independent variables are held constant. The unstandardized β describes the actual change in the independent variable with an increase of one unit in the dependent variable. Tests were two-tailed. SPSS version 11.0 statistical software was used.

Results

Daily Travel Distance

The yearly mean DTD varied between 547 m and 1,034 m for the four groups. See Table 1 for the mean DTD and biweekly ranges for each group. Considering the frugivory variables, the best model of the linear regression for biweekly DTD included the percentage of days gorillas ate fruit from any plant sources. The regression model revealed that all variables (group size, frequency of frugivory, rainfall, and location) significantly influenced DTD and there was no interaction effect between the variables (Table 2). The biweekly DTD average was longer in larger groups. Furthermore, the percentage of days gorillas ate fruit from any plant source also positively influenced DTD (Fig. 2). The group at the high-altitude location (lower fruit avail-

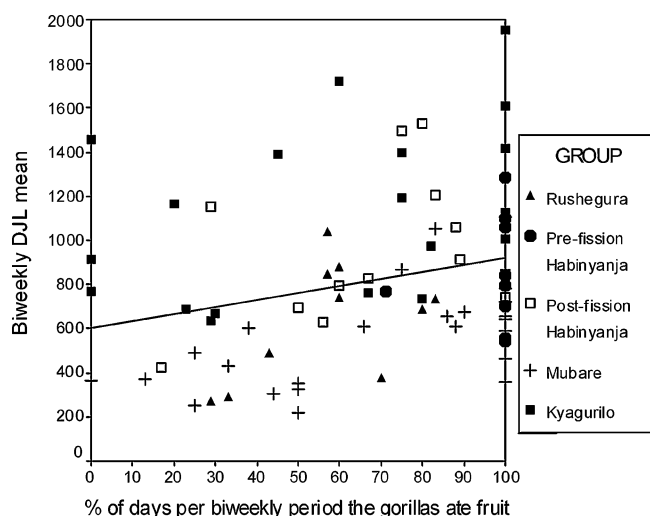


Fig. 2 The relationship between frugivory and average biweekly DTD for four gorilla groups

ability) traveled farther than the groups at the low-altitude location (Fig. 2; Table 2). Lastly, an increase in rainfall was related to a decrease in DTD. Comparing the partial η^2 and the regression coefficient β , location (our proxy for food availability) had a considerably stronger effect on DTD than the other independent variables, followed by the degree of frugivory, group size, and rainfall amount. To eliminate the differences in locations, we also repeated the analysis with only the three groups at the low-altitude site, but the results did not change.

Home range

Annual and monthly home range sizes varied considerably within and between groups (Table 1). For the three groups with 1 year of data, Mubare, Habinyanja, and Kyagurilo, the size of groups' home ranges reached an asymptote (when >90% of current home range size is reached) between 10 and 11 months, indicating that an estimate of these groups' annual home range sizes could be determined at this time.

Table 2 Linear regression test results of the ecological and social variables influencing DTD and monthly home range size. See Methods for explanation of η^2 and β values

Dependent variable	Independent variable	F value	n	df	Adjusted R ²	t value	P value	Partial η^2	Stand. β	Unstan. β
Day journey length	All fruit days	12.589	71	4,72	0.379	2.749	0.008	0.095	0.264	3.143
	Group size					2.130	0.037	0.059	0.205	15.835
	Rainfall					-2.089	0.040	0.057	-0.192	-1.224
	Location					-5.516	0.001	0.297	-0.515	-427.3
Monthly home range size	No. of total fruit species	4.053	34	4,35	0.194	2.078	0.045	0.110	0.371	0.344
	Group size					2.094	0.044	0.111	0.316	0.165
	Location					-2.296	0.028	0.131	-0.400	-2.389

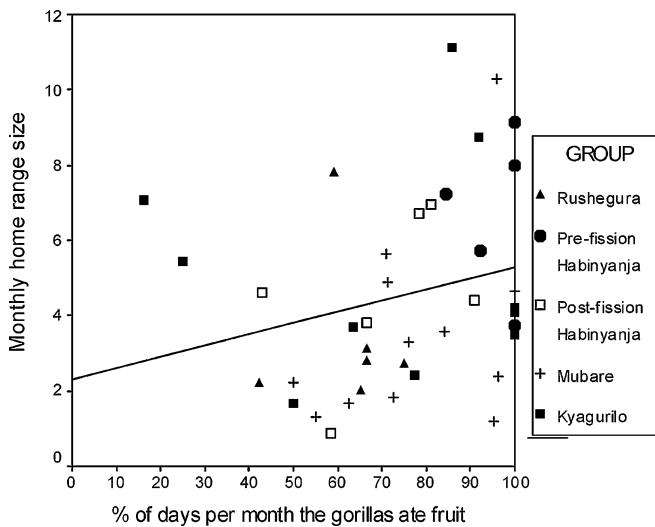


Fig. 3 The relationship between frugivory and monthly home range for four gorilla groups

The home range size for Rushegura group, with only six and a half months of data, did not reach an asymptote, and therefore the annual home range of the Rushegura group is likely to be larger than what we recorded. The best model of the linear regression selected included the total number of fruit species eaten. In the multiple regression, all variables except for rainfall significantly influenced the monthly home range size and there was no interaction effect between the variables (Table 2). Larger groups had larger monthly home ranges; the total number of fruit species eaten positively influenced monthly home range size (Fig. 3), and the group at the high-altitude location (with lower fruit availability) had larger monthly home ranges than the groups at the low-altitude location. Of the three significant variables, location had the strongest effect on home range size, followed by the total number of fruit species eaten, and group size, but no single variable had a noticeably stronger effect than the other (Table 2). As with the analysis of DTD, repeating the analysis for home range using data only on the three low-altitude groups did not change the results.

Discussion

Our results provide support for the ecological constraints model, which asserts that as group size increases, both DTD and home range size should also increase to accommodate the greater foraging requirements of additional group members. In Bwindi mountain gorillas, larger groups travelled farther per day and had larger home ranges than smaller groups. Second, biweekly DTD and monthly home range size varied positively with the amount of fruit in the diet. Furthermore, the group that ranged at the higher-altitude location with the lower amount of fruit availability had both a longer DTD and monthly home range size than the groups at the lower-altitude location. Location (proxy for food availability) had a much stronger effect on the DTD results than the home range results (based on partial ETA^2

values). Lastly, rainfall negatively influenced DTD but it did not influence monthly home range size.

Group size positively influenced both DTD and home range size for Bwindi mountain gorillas, whose diet consists primarily of herbaceous vegetation but includes fruit. Folivorous primate species in which group size was positively related to DTD and home range size include red colobus (*Procolobus badius*, Gillespie and Chapman 2001), Thomas's langurs (*Presbytis thomasi*, Steenbeck and van Schaik 2001), northern muriquis (*Brachyteles arachnoides hypoxanthus*, Dias and Strier 2003, but home range only), and mountain gorillas at the Karisoke Research Center (when comparisons were between groups but not when the same group changed size over time; Watts 1991, 1998; McNeilage 1995). However, there are both frugivorous and folivorous primate species in which an increase in group size did not lead to an increase in DTD (patas monkeys, *Erythrocebus patas*; Chism and Rowell 1988, blue monkeys, *Cercopithecus mitis*; Butynski 1990, northern muriquis; Dias and Strier 2003), home range size (western chimpanzees, *Pan troglodytes verus*; Lehmann and Boesch 2003), or either variable (red colobus; Struhsaker and Leland 1987, black and white colobus, *Colobus guereza*; Fashing 2001, and several Asian colobine species; Yeager and Kool 2000). An option for animals whose food sources are relatively densely distributed is to increase group spread while foraging as an alternative to increasing DTD. This, in fact, may also be occurring in mountain gorillas, as was given as an explanation for the stepwise fashion in which DTD increased with group size for Karisoke mountain gorillas (Watts 1998), and could be possible in Bwindi as well. Our results and these examples suggest that whether an increase in group size also leads to an increase in DTD and/or home range cannot be determined only by whether a species predominantly eats fruit or leaf-based foods. In particular, the distribution, density, size, and quality of food resources within a primate groups' range likely plays a stronger role (Chapman 1988; Isbell 1991; Chapman et al. 1995; Isbell et al. 1998; Chapman and Chapman 2000b; Gillespie and Chapman 2001). Food availability and distribution also significantly influence home range size in social carnivores such as lions (*Panthera leo*) and red foxes (*Vulpes vulpes*) (Macdonald 1983; Lucherini and Lovari 1996; Spong 2002).

We observed that gorilla groups travelled further per day with an increasingly frugivorous diet (Fig. 2), which is consistent with studies on western gorillas (Goldsmith 1999; Doran-Sheehy et al. 2004). Our results also showed that monthly home range size increased with increasing frugivory (Fig. 3). In Bwindi, fruit species eaten by the gorillas are not continuously available throughout the year (Nkurunungi et al. 2004). These results suggest that when fruit is unavailable, the gorillas concentrate on eating the more evenly distributed and readily available herbs, traveling shorter distances, and using smaller areas more intensively. As fruit becomes available, Bwindi gorillas travel further and increase their home range size to exploit patchily distributed fruit. This foraging strategy of energy minimization, reducing travel in the face of a reduction

in food availability, is employed by other primate species such as western chimpanzees (Doran 1997) and woolly monkeys (*Lagothrix lagotricha poeppigii*; DiFiore 2003). Interestingly, our results differ from a previous study of the Kyagurilo group, which found no significant relationship between monthly home range size and frugivory over a 3-year period (DTD not measured; Robbins and McNeilage 2003). Our results suggest that when considering the Kyagurilo group alone, only a weak relationship between both DTD and home range size with frugivory exists (Figs. 2, 3). In contrast to our results, Doran-Sheehy et al. (2004) found an inverse correlation between degree of frugivory and monthly home range size for one group of western gorillas, suggesting that one would not expect an increase in home range size with increased frugivory if the fruits preferred by gorillas at this site were highly clumped and revisited often. These studies emphasize the complex relationship among availability of both fruit and leaf-based foods, degree of frugivory and ranging patterns. When no fruit is available, gorillas reduce travel costs by focusing on herbaceous vegetation and minimize travel distance and range; when a little fruit is available, gorillas travel further to get it, and when a lot of fruit is available, the gorillas would not need to travel so far, or utilize a larger area.

The differences in DTD and home range sizes between the gorilla groups at the two locations in Bwindi may have been influenced by differences in food density, availability, and distribution (Isbell et al. 1998). The location variable, used as a proxy for food availability, had the strongest effect in all analyses. Based on higher fruit availability at the low-altitude location, we predicted that groups here would move shorter distances than the group at the high-altitude location, which was observed. The group with a lower fruit availability traveled longer distances to maintain approximately the same frequency of fruit consumption as the groups in the other location. While all the gorilla groups examined consumed fruit at a similar frequency, they consumed different species of fruit at each location (due mainly to availability; Ganas et al. 2004). Variability in the distribution of fruit and/or patch sizes in the two locations may also account for why the group with the lower fruit availability traveled further than the other groups. However, the density of herbaceous vegetation, which is consumed in large amounts by Bwindi gorillas, may also impact the gorillas' ranging patterns, but the gorillas in the location with the higher herb density (high altitude) had longer DTD and larger home range size. Overall, our results suggest that the gorillas' movement patterns were more strongly influenced by the distribution and abundance of fruit than that of herbaceous vegetation, but both food resources are likely to play a role.

Rainfall negatively influenced DTD in Bwindi gorillas, which is probably due to the fact that the gorillas were trying to avoid getting wet, which would cause them to get cold and lose energy. The lack of relationship between rainfall and home range size is not unexpected considering thermoregulatory constraints are likely to be short-term responses (DTD) rather than long term (home range size).

Dunbar (1992) noted that baboons encounter thermoregulatory constraints in relation to temperature. We found no significant correlation between daily temperature and rainfall at both sites. However, this is not surprising since a temperature decrease may occur only during the part of the day when it rained, especially if associated with cloud cover, and not the entire day. Some studies have found a relationship between rainfall and DTD, which was attributed to a positive correlation between rainfall and food availability (Post 1982; Vedder 1984; Bronikowski and Altmann 1996; Hill et al. 2003), but the relationship between plant productivity and rainfall is not necessarily linear (Janson and Chapman 1999). During our study period, there was no correlation between rainfall and phenology patterns (Nkurunungi et al. 2004), so rainfall was not an indicator of fruit availability. Although we have no data on how rainfall influences the availability of herbaceous vegetation in Bwindi, the species most commonly eaten by the gorillas are available throughout the year so the impact is likely to be small. Thus, we suggest that the thermoregulatory constraints of traveling in the rain diminish travel distances. Alternatively, rain may limit visibility and thus make it more difficult to detect other groups of gorillas or predators and thereby reduce travel.

Habitat use by gorillas can be also influenced by social variables such as male mating strategies and interactions between neighboring groups. Males pursuit of females and a group's responses to these pursuits can temporarily override ecological factors influencing habitat use, and cause abrupt home range shifts (Watts 1991, 1994, 1998; Cipolletta 2004). Mountain gorillas at the Karisoke Research Center traveled farther on days after interactions with solitary males, and have shifted their range in response to these interactions (Watts 1998). In contrast, Doran-Sheehy et al. (2004) found that inter-group interactions had no effect on DTD or monthly home range size. While inter-group interactions occurred during our study, they were too infrequent to be incorporated into our overall model.

The positive relationship between group size and DTD found in this study suggests that feeding competition among individuals may increase with group size in Bwindi mountain gorillas (Janson and Goldsmith 1995; Steenbeck and van Schaik 2001). In Karisoke mountain gorillas, larger groups engaged in more agonistic interactions involving food than smaller groups (Watts 1985), and an increase in group size also led to an increase in foraging time (Watts 1988), suggesting that there are greater levels of feeding competition as group size increases and individuals alter their behavior to compensate. Furthermore, Watts (1990a) suggested that the reproductive output of females may decrease as group size increases, but analysis using a larger sample size is needed to test this hypothesis. While rates of feeding competition are higher when Bwindi gorillas forage on fruit versus herbaceous vegetation, the overall rate of agonistic interactions while foraging is comparable to that of Virunga mountain gorillas (M.M. Robbins, unpublished work; Watts 1985).

Table 3 Average DTD, home range size, and degree of frugivory (based on the percentage of dung samples containing seeds/feeding time devoted to fruit) for three eastern and three western gorilla study sites and whether studies on these groups found frugivory to positively influence either day journey length or home range size

Gorilla species	Study location	Daily Travel Distance	Home range size	Degree of frugivory	Herb density	Frugivory positive influence?	
						DTD	HR size
Mountain gorillas (<i>Gorilla beringei</i>)	Karisoke Research Center, Rwanda	570 m ^a	3–15 km ^{2a,b,c}	<1% of time spent eating fruit ^d	8.8 stems/m ^{2d}	–	–
	Bwindi Impenetrable National Park, Uganda	547–1034 m ^e	*16.25–28 km ^{2e,f}	65.6–82.1% dung samples contained seeds ^g	4.33–10.6 stems/m ^{2h}	Yes ^e	Yes ^e /No ^f
Grauer's gorillas (<i>G. b. graueri</i>)	Kahuzi-Biega Kahuzi location ⁱ	1800–3300 m	23–31 km ²	96.5% of dung samples contained seeds	Not calculated	–	–
	Kahuzi-Biega Itebero location ^l (both DRC)	2155 m	23–31 km ²	89% of dung samples contained seeds	Not calculated	–	–
Western gorillas (<i>G. gorilla gorilla</i>)	Lope, Gabon	1105 m ^j	21.7 km ^{2j}	98% of dung samples contained seeds ^j	1.87 stems/m ^{2k}	**Yes ^j	–
	Mondika, CAR	2014 m ^l	15.75 km ^{2l}	99–100% of dung samples contained seeds ^m	0.78 stems/m ^{2m}	Yes ^l	No ^l
	Bai Hokou, CAR	1717 m–2.6 km ^{2n,o}	18.3–22.9 km ^{2n,o,p}	99% of dung samples contained seeds ^{n,o,q,s}	0.82 stems/m ^{2p}	Yes ^{o,r} /No ⁿ	No ⁿ

^aWatts (1991); ^bVedder (1984); ^cMcNeilage (1995); ^dWatts (1984); ^eThis study; ^fRobbins and McNeilage (2003); ^gGanas et al. (2004); ^hNkurunungi et al. (2004); ⁱYamagiwa et al. (1992, 1994, 1996); ^jTutin (1996); ^kTutin et al. (1991); ^lDoran et al. (2004); ^mDoran et al. (2002); ⁿCippolletta (2003); ^oGoldsmith (1999); ^pRemis (1997a); ^qRemis (1997b); ^rCippolletta (2004).

*Home range size is represented by the grid square method to facilitate comparisons between sites; **based on gorilla fruit availability in environment, not degree of gorillas' frugivory.

Implications for social structure of gorillas

Recent studies have suggested that western gorillas may face greater constraints on group size than mountain gorillas due to less abundant herbaceous vegetation and a greater availability of fruit, which leads to a more frugivorous diet (Doran and McNeilage 1998, 2001; Parnell 2002, Table 3). While the mean group size in western and eastern gorillas appears to be the same (Parnell 2002), very large groups of over 20 individuals have been observed in several eastern gorilla populations (McNeilage et al. 2001; Yamagiwa and Kahekwa 2001; Kalpers et al. 2003) but in only one western gorilla population with a high density of herbaceous vegetation (Bermejo 1999; Magliocca et al. 1999). In general, the positive relationship between DTD and both increased fruit availability and decreased availability of herbaceous vegetation lends support to the idea that western gorillas have more constraints on group

size. If ecological conditions place stronger constraints on group size for western gorillas, this could have implications for variability in reproductive strategies and the social system exhibited by different gorilla populations. In particular, foraging constraints and feeding competition may influence female dispersal patterns and, in turn, male dispersal patterns (Watts 1990b; Stokes et al. 2003; Robbins et al. 2004). Further research on the spatial clumping and patchiness of food resources, group spread while feeding on different food resources, intragroup feeding competition, and the influence of these variables on female reproductive success will help explain if the distribution and availability of fruit and herbaceous vegetation constrain group size in both Bwindi gorillas and western gorillas.

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References

- Altmann SA (1974) Baboons, space, time, and energy. *Am Zool* 14:221–248
- Arrowood HC, Treves A, Mathews NE (2003) Determinants of day-range length in the black howler monkey at Lamanai, Belize. *J Trop Ecol* 19:591–594
- Bennett EL (1986) Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos*. *Folia Primatol* 47:26–38
- Bermejo M (1999) Status and conservation of primates in Odzala National Park, Republic of the Congo. *Oryx* 33:323–331
- Bronikowski AM, Altmann J (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav Ecol Sociobiol* 39:11–25
- Butynski TM (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low- density subpopulations. *Ecol Monogr* 60:1–26
- Chapman CA (1988) Patterns of range use by three species of neotropical primates. *Primates* 29:177–194
- Chapman CA (1990) Ecological constraints on group size in three species of neotropical primates. *Folia Primatol* 55:1–9
- Chapman CA, Chapman LJ (2000a) Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA (eds) *On the move: how and why animals travel in groups*. University of Chicago Press, Chicago, pp 24–42
- Chapman CA, Chapman LJ (2000b) Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *Int J Primatol* 21:565–585
- Chapman CA, Wrangham RW, Chapman LJ (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiol* 36:59–70
- Chism J, Rowell T (1988) The natural history of patas monkeys. In: Gautier-Hion A, Bouliere F, Gautier Gautier JP, Kingdon J (eds) *A primate radiation*. Cambridge University Press, New York, pp 412–438
- Cipolletta C (2003) Ranging patterns of a western gorilla group during habituation to humans in the Dzanga-Nkoki National Park, Central African Republic. *Int J Primatol* 24:1207–1226
- Cipolletta C (2004) Effects of group dynamics and diet on the ranging patterns of a western gorilla group (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Am J Primatol* 64:193–205
- Clutton-Brock TH, Harvey PH (1977) Species differences in feeding and ranging behavior in primates. In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. Academic Press, New York, pp 557–584
- Corlett RT, Lucas PW (1990) Alternative seed-handling strategies in primates: seed-spitting by long tailed macaques (*Macaca fascicularis*). *Oecologia* 82:166–171
- Dias LG, Strier KB (2003) Effects of group size on ranging patterns in *Brachyteles arachnoides hypoxanthus*. *Int J Primatol* 24:209–221
- Dierenfeld ES, Koontz FW, Goldstein RS (1992) Feed intake, digestion and passage of the proboscis monkey (*Nasalis larvatus*) in captivity. *Primates* 33:399–405
- DiFiore A (2003) Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuni National Park, Ecuador. *Am J Primatol* 59:47–66
- Doran DM (1997) Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *Int J Primatol* 18:183–206
- Doran DM, McNeilage A (1998) Gorilla ecology and behavior. *Evol Anthropol* 6:120–131
- Doran DM, McNeilage A (2001) Subspecific variation in gorilla behavior: the influence of ecological and social factors. In: Robbins MM, Sicotte P, Stewart KJ (eds) *Mountain gorillas: three decades of research at Karisoke*. Cambridge University Press, Cambridge, pp 123–149
- Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N (2002) Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *Am J Primatol* 58:91–116
- Doran-Sheehy DM, Greer D, Mongo P, Schwindt D (2004) Impact of ecological and social factors on ranging in western gorillas. *Am J Primatol* 64:207–222
- Dunbar RIM (1988) *Primate social systems*. Cornell University Press, Ithaca, New York
- Dunbar RIM (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 31:35–49
- Fashing PJ (2001) Activity and ranging patterns of Guezeas in the Kakamega forest: intergroup variation and implications for intragroup feeding competition. *Int J Primatol* 22:549–577
- Fossey D, Harcourt AH (1977) Feeding ecology of free ranging mountain gorillas (*Gorilla gorilla beringei*). In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes*. Academic Press, London, pp 539–556
- Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A (2004) Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *Int J Primatol*
- Gillespie TR, Chapman CA (2001) Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. *Behav Ecol Sociobiol* 50:329–338
- Goldsmith ML (1999) Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Int J Primatol* 20:1–23
- Goodall A (1977) Feeding and ranging behaviour of a mountain gorilla group (*Gorilla gorilla beringei*) in the Tshibinda-Kahuzi region (Zaire). In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes*. University of Chicago Press, Chicago, pp 449–479
- Herbinger I, Boesch C, Rothe H (2001) Territory characteristics among three neighboring chimpanzee communities in Tai National Park, Cote d'Ivoire. *Int J Primatol* 22:143–167
- Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP (2003) Day length, latitude and behavioural (in)flexibility in baboons (*Papio cynocephalus ursinus*). *Behav Ecol Sociobiol* 53:278–286
- Isbell LA (1983) Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. *Folia Primatol* 41:34–48
- Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143–155
- Isbell LA, Pruett JD, Young TP (1998) Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behav Ecol Sociobiol* 42:123–133
- Janson CH (1992) Evolutionary ecology of primate social structure. In: Smith EA, Winterhalder B (eds) *Evolutionary ecology and human behavior*. De Gruyter, New York, pp 95–130

- Janson CH, Chapman CA (1999) Resources and primate community structure. In: Fleagle JG, Janson CH, Reed KE (eds) *Primate communities*. Cambridge University Press, Cambridge, pp 237–267
- Janson CH, Goldsmith ML (1995) Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326–336
- Janson CH, van Schaik (1988) Recognizing the many faces of primate food competition. *Behaviour* 105:165–186
- Kalpers J, Williamson EA, Robbins MM, McNeilage A, Nzamurambaho A, Lola N, Mugiri G (2003) Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. *Oryx* 37:326–337
- Kaplin BA (2001) Ranging behavior of two species of guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe forest reserve, Rwanda. *Int J Primatol* 22:521–548
- Kaplin BA, Moermond TC (1998) Variation in seed handling by two species of forest monkeys in Rwanda. *Am J Primatol* 45:83–102
- Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. *Int J Primatol* 23:707–740
- Kleiber M (1961) *The fire of life*. Wiley, New York
- Koenig A (2002) Competition for resources and its behavioral consequences among female primates. *Int J Primatol* 23:759–783
- Koenig A, Beise J, Chalise MK, Ganzhorn JU (1998) When females should contest for food-testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behav Ecol Sociobiol* 42:225–237
- Lambert JE (1999) Seed handling in chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *Am J Phys Anthropol* 109:365–386
- Lambert JE (2002) Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). *Int J Primatol* 23:1169–1185
- Lehmann J, Boesch C (2003) Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Cote d'Ivoire. *Behav Ecol* 14:642–649
- Li B, Chen C, Weihong J, Baoping R (2000) Seasonal home range changes of the sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling mountains of China. *Folia Primatol* 71:375–386
- Lucherini M, Lovari S (1996) Habitat richness affects home range size in the red fox *Vulpes vulpes*. *Behav Process* 36:103–106
- Macdonald DW (1983) The ecology of carnivore social behavior. *Nature* 301:379–384
- Magliocca F, Querouil S, Gautier-Hion A (1999) Population structure and group composition of western lowland gorillas in north-western Republic of Congo. *Am J Primatol* 48:1–14
- McNeilage A (1995) Mountain gorillas in the Virunga Volcanoes: ecology and carrying capacity. PhD Thesis, University of Bristol
- McNeilage A, Plumtre AJ, Brock-Doyle A, Vedder A (2001) Bwindi Impenetrable National Park, Uganda: gorilla census 1997. *Oryx* 35:39–47
- Milton K (1980) *The foraging strategy of howler monkeys: a study in primate economics*. Columbia University Press, New York
- Milton K, May ML (1976) Body weight, diet, and home range area in primates. *Nature* 259:459–462
- Nkurunungi JB (2004) The availability and distribution of fruit and non-fruit resources in Bwindi: their influence on gorilla habitat use and food choice. PhD Thesis, Makerere University
- Nkurunungi JB, Ganas J, Robbins MM, Stanford CB (2004) A comparison of two mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda. *Afr J Ecol* 42: 289–297
- Oates JF (1987) Food distribution and foraging behavior. In: Smuts BB, Cheney DL, Seyfarth RM, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 197–209
- O'Brien TG, Kinnaird MF (1997) Behavior, diet, and movements of the sulawesi crested black macaque (*Macaca nigra*). *Int J Primatol* 18:321–351
- Olupot W, Chapman CA, Waser PM, Isabirye-Basuta G (1997) Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *Am J Primatol* 43:65–78
- Ostro LET, Silver SC, Koontz FW, Young TP, Horwich RH (1999) Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belize, Central America. *Biol Conserv* 87:181–190
- Parnell RJ (2002) Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *Am J Primatol* 56:193–206
- Post DG (1982) Feeding behavior of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Int J Primatol* 3:403–430
- Raemaekers J (1980) Causes of variation between months in distance traveled daily by gibbons. *Folia Primatol* 34:46–60
- Remis MJ (1997a) Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. *Am J Primatol* 43:87–109
- Remis MJ (1997b) Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *Am J Primatol* 43:111–133
- Remis MJ (2000) Initial studies on the contributions of body size and gastrointestinal passage rates to dietary flexibility among gorillas. *Am J Phys Anthropol* 112:171–180
- Remis MJ, Dierenfeld ES (2004) Digestive passage, digestibility and behavior in captive gorillas under two dietary regimes. *Int J Primatol* 25:825–845
- Robbins MM, McNeilage AJ (2003) Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *Int J Primatol* 24:467–491
- Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes E (2004) Social structure and life history patterns in western gorillas (*Gorilla gorilla gorilla*) *Am J Primatol* 64:145–159
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369–404
- Singleton I, van Schaik CP (2001) Orangutan home range size and its determinants in a Sumatran swamp forest. *Int J Primatol* 22:877–911
- Southwood TRE (1966) *Ecological methods*. Chapman and Hall, London
- Spong G (2002) Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behav Ecol Sociobiol* 52:303–307
- Steenbeck R, van Schaik CP (2001) Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behav Ecol Sociobiol* 49:100–110
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships. *Behav Ecol Sociobiol* 41:291–309
- Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav Ecol Sociobiol* 54:329–339
- Strier KB (1987) Ranging behavior of woolly spider monkeys, or muriquis, *Brachyteles arachnoides*. *Int J Primatol* 8:575–591
- Struhsaker TT, Leland L (1987) Colobines: infanticide by adult males. In: Smuts BB, Cheney DL, Seyfarth RM, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 83–97
- Supriatna J, Manullang BO, Soekara E (1986) Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan, Indonesia. *Primates* 27:185–190
- Terborgh J (1983) *Five new world primates: a study in comparative ecology*. Princeton University Press, Princeton
- Treves A, Chapman CA (1996) Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. *Behav Ecol Sociobiol* 39:43–53
- Tutin CEG (1996) Ranging and social structure of lowland gorillas in the Lope Reserve, Gabon. In: McGrew WC, Marchant LF, Nishida T (eds) *Great ape societies*. Cambridge University Press, Cambridge, pp 58–70
- Tutin CEG, Fernandez M (1985) Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: some preliminary data. *Int J Primatol* 6:27–43

- Tutin CEG, Fernandez M, Rogers ME, Williamson EA, McGrew WC (1991) Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. *Philos Trans R Soc Lond B* 334:179–186
- van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87:120–144
- van Schaik CP (1989) The ecology and social relationships amongst female primates. In: Standen V, Foley RA (eds) *Comparative socioecology of humans and other mammals*. Blackwell, Oxford, pp 195–218
- van Schaik CP, van Noordwijk MA, de Boer RJ, den Tonkelaar I (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behav Ecol Sociobiol* 13:173–181
- Vedder AL (1984) Movement patterns of a free-ranging group of mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *Am J Primatol* 7:73–88
- Waser P (1977) Feeding, ranging and group size in the mangabey *Cercocebus albigena*. In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes*. Academic Press, London, pp 183–222
- Watts DP (1984) Composition and variability of mountain gorilla diets in the central virungas. *Am J Primatol* 7:323–356
- Watts DP (1985) Relations between group size and composition and feeding competition in mountain gorilla groups. *Anim Behav* 33:72–85
- Watts DP (1988) Environmental influences on mountain gorilla time budgets. *Am J Primatol* 15:195–211
- Watts DP (1990a) Ecology of gorillas and its relation to female transfer in mountain gorillas. *Int J Primatol* 11:21–45
- Watts DP (1990b) Mountain gorilla life histories, reproductive competition, and sociosexual behavior and some implications for captive husbandry. *Zool Biol* 9:185–200
- Watts DP (1991) Strategies of habitat use by mountain gorillas. *Folia Primatol* 56:1–16
- Watts DP (1994) The influence of male mating tactics on habitat use in mountain gorillas (*Gorilla gorilla beringei*). *Primates* 35:35–47
- Watts DP (1998) Long term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 1. Consistency, variation, and home range size and stability. *Int J Primatol* 19:651–680
- Whittow GC (1971) Ungulates. In: Whittow GC (ed) *Ungulates: comparative physiology of thermoregulation*, vol 2. Mammals. Academic Press, New York, pp 191–281
- Williamson EA, Tutin CEG, Rogers ME, Fernandez M (1990) Composition of the diet of lowland gorillas at Lope in Gabon. *Am J Primatol* 21:265–277
- Wrangham RW, Gittleman JL, Chapman CA (1993) Constraints on group size in primates and carnivores: population density and dayrange as assays of exploitation competition. *Behav Ecol Sociobiol* 32:199–209
- Yamagiwa J, Kahekwa J (2001) Dispersal patterns, group structure, and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In: Robbins MM, Sicotte P, Stewart KJ (eds) *Mountain gorillas: three decades of research at Karisoke*. Cambridge University Press, Cambridge, pp 90–122
- Yamagiwa J, Mwanza N, Yumoto T, Maruhashi T (1992) Travel distances and food habits of eastern lowland gorillas: a comparative analysis. In: Itoigawa N, Sugiyama Y, Sackett GP (eds) *Topics in primatology*, vol 2. Behavior, ecology and conservation. University of Tokyo Press, Tokyo, pp 267–281
- Yamagiwa J, Mwanza M, Yumoto T, Maruhashi T (1994) Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* 35:1–14
- Yamagiwa J, Maruhashi T, Yumoto T, Mwanza N (1996) Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In: McGrew WC, Marchant LF, Nishida T (eds) *Great ape societies*. Cambridge University Press, Cambridge, pp 82–98
- Yeager CP, Kool K (2000) The behavioral ecology of colobine monkeys. In: Whitehead PF, Jolly CJ (eds) *Old world monkeys*. Cambridge University Press, Cambridge, pp 496–521