



Home Range and Frugivory Patterns of Mountain Gorillas in Bwindi Impenetrable National Park, Uganda

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Mountain, western, and Grauer's gorillas exhibit broad differences in ecological patterns with western gorillas eating more fruit and having larger home ranges than their largely folivorous counterparts in the Virunga Volcanoes. We studied the home range and frugivory patterns of one group of Gorilla beringei beringei in the little-studied population of Bwindi Impenetrable National Park, Uganda, to compare with other populations and to investigate whether there was any relationship between patterns of frugivory and home range size. During the 3-year study, the gorillas ate 16 species of fruit on 27% of observation days. There was high variability in frugivory among the 3 years and no consistent seasonal pattern. Annual home range size was ca. 21 km² for Years 1 and 2, and it increased dramatically to 40 km² in Year 3. Home range size varied considerable between months and seasons, but there is no clear relationship between occurrence of fruit-eating and home range size. The group exhibited more fruit-eating and a larger home range size those of the gorillas in the Virunga Volcanoes. Their home range size is comparable to that of western gorillas, though Bwindi gorillas consumed less fruit. Home range size and utilization by all gorillas probably depends on a complex relationship between the distribution and abundance of both fruit and herbaceous vegetation and social factors such as male mating tactics.

KEY WORDS: *Gorilla beringei beringei*; mountain gorilla; home range; frugivory.

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INTRODUCTION

Habitat use is related to many variables, including requirements and constraints according to the species' biology, abundance and distribution of resources, population density, and competition with conspecifics and other species (Dunbar, 1988; McLoughlin and Ferguson, 2000; Oates, 1987). Home range is the area in which an animal normally travels in pursuit of its routine activities (Jewell, 1966). In primates, primarily frugivorous species generally have larger home ranges for their bodily sizes than those of folivorous/herbivorous species (Clutton-Brock and Harvey, 1977; Mace and Harvey, 1983; Nunn and Barton, 2000). This is due to fruit typically being more sparsely distributed than leaves and herbaceous vegetation. The greater energetic gains of fruit relative to herbaceous vegetation make it possible for animals to invest in the travel and search time for fruit. Within species, home range size should also increase as group size increases due to increases in food requirements (Clutton-Brock, 1977; Harvey and Clutton-Brock, 1981; Jansen and Goldsmith, 1995). Additionally, social factors, such as the search for mates or the avoidance of competitors, may also influence primate ranging patterns (Oates, 1987; Steenbeek, 1999; van Schaik, 1996). Understanding home range and dietary patterns is useful not only for models of primate behavioral ecology but also in quantifying the spatial and ecological needs of social groups, which has important implications for the conservation and management of primate populations, especially those found in small, isolated habitats as is the situation for many primates today. In the case of gorillas, given their wide distribution and highly variable ecological conditions across Africa, it is constructive to look for trends in dietary patterns and home range in relation to environment to better investigate the evolution of and variability in their social system (Doran and McNeillage, 1998, 2001).

The long-term studies of feeding ecology at Karisoke Research Center in the Virunga Volcanoes of Rwanda, Uganda, and Democratic Republic of Congo have shown that mountain gorillas feed on abundant evenly distributed herbaceous vegetation and that they eat almost no fruit (McNeillage, 1995, 2001; Watts, 1984; Vedder, 1984). Annual home range size of several groups varied between 3 km² and 15 km² (McNeillage, 1995; Watts, 1998a; Vedder, 1984). In general, groups with more individuals (thus greater biomass) have larger home range sizes than those of smaller groups, but there can be exceptions (McNeillage, 1995; Watts, 1998a). Gorilla groups tend more intensively to use areas of higher food abundance, and core areas usually consist of disproportionately large areas of rich vegetation zones (Watts, 1998a). Trampling of the herbaceous vegetation by mountain gorillas stimulates food plant productivity and the revisitation rates to

particular areas appears to depend on regeneration rates (Watts, 1998b). No seasonal pattern of range use has been detected except for increased use of the bamboo zone during the seasons when shoots are present (Watts, 1998a, Vedder, 1984). However, it should be noted that the Karisoke gorillas in the Virunga Volcanoes live at the highest end of the altitudinal range for gorillas and therefore at the extreme end of the ecological spectrum that gorillas inhabit.

Studies of other subspecies of gorillas have revealed that western and Grauer's incorporate more fruit in their diets and that they have larger home ranges than those of Virunga gorillas, though range size is still quite variable (Grauer's gorillas: Yamagiwa *et al.*, 1994, 1996; western gorillas: Doran and McNeilage, 2001; Goldsmith, 1999; Remis, 1997a; Tutin, 1996). They appear to travel further per day during fruiting or rainy seasons than during poor fruit seasons (Grauer's gorillas: Yamagiwa *et al.*, 1996; Goodall, 1977; western gorillas: Doran and McNeilage, 2001; Goldsmith, 1999; Tutin, 1996;) and they may also use a larger area of the home range during fruiting seasons (Goodall, 1977; Remis, 1997a). Accordingly, the degree of frugivory influences the movement patterns and home range size for gorillas (Remis, 1997a; Doran and McNeilage, 2001).

Home range size and movement patterns also appear to be influenced by male mate acquisition and retention strategies. For example, at Karisoke, gorilla groups have dramatically shifted their home range following intergroup encounters that involved high male-male competition, and lone silverbacks use larger areas than expected based on ecological requirements, presumably because they are searching out other groups (Watts, 1991, 1994, 1998a). Due to the lack of habituated lowland gorillas, the impact of social factors on their ranging patterns has not been investigated.

One problem with making comparisons of home range between different populations is the variability in methodologies used. In particular, it is important to consider the spatial and temporal scale used, and the method used to define home range quantitatively. Different methods have various advantages and disadvantages depending on the focal taxon and field conditions. Studies of primates, and specifically of gorillas, generally use the grid square method to estimate home range size, but unless a study monitors group movements extremely intensively the grid cell method will produce an underestimate of range size because groups will not have been observed in many grids that are within the home range (Chapman and Wrangham, 1993; Harris *et al.*, 1990; Singleton and van Schaik, 2001; Sterling *et al.*, 2000). The size of the grid square also influences the estimate of home range size; in general, the home range size estimates will correspondingly increase with increased grid square size. The minimum convex polygon method (MCP) eliminates the problem of grid squares within the range that are not entered

and is more accurate when the number of data points is low. However, peripheral data points may strongly influence home range size (Harris *et al.*, 1990). Given the pros and cons of differing methods, several authors suggest that more than one method should be used to estimate home range size (Herbinger *et al.*, 2001; Singleton and van Schaik, 2001; Sterling *et al.*, 2000). On the temporal scale, most researches use *ca.* 1–2 years of data to estimate home range size. However, in an examination of long-term habitat use patterns by the Karisoke gorillas Watts (1998a) calculated overall home range size for ≤ 7 years for particular groups and found them to be considerably larger than annual yearly ranges. Either one year or multiyear home ranges can be justified, as long as the same temporal scale is used in comparisons of different groups and different sites.

To better understand the determinants of home range size in gorillas and primates in general, information from several populations in a wide range of ecological conditions is needed. Preliminary information on Bwindi mountain gorillas indicates that they exhibit larger home ranges and incorporate more fruit in their diet than Virunga mountain gorillas do (Sarmiento *et al.*, 1996; Achoka, 1993), but no intensive study had been conducted to measure these variables or to examine whether increased fruit eating leads to greater home range size. Via observations of one group of Bwindi gorillas we aimed: a) to report occurrence of fruit eating, b) to report the monthly, seasonal, and yearly home range sizes spanning 3 years using both the grid square and minimum convex polygon method, c) to examine whether there is a correlation between monthly and seasonal home range size and occurrence of fruit eating, and d) to examine other social factors, e.g., intergroup encounters and male mating tactics, that may influence home range size. We compared home range and fruit eating patterns of Bwindi gorillas versus those of other gorilla populations and sought explanations for the variability.

Bwindi Impenetrable National Park (BINP) is only 25 km away from the Virunga Volcano Conservation Area. BINP is an afro-montane forest ranging in elevation between 1160 and 2607 m and it is characterized by extremely rugged terrain of steep-sided hills throughout. The altitudinal range of Bwindi is the same as that in approximately 33% of the area of the Virunga Volcanoes, but the best studied part of the Virungas (around the Karisoke Research Center) occurs at habitat and altitudinal zones (2700–3400m) that are absent in Bwindi.

Bwindi contains *ca.* 300 mountain gorillas (McNeilage *et al.*, 2001, in prep). Despite the close proximity of Bwindi to the Virunga Volcanoes, Sarmiento *et al.* (1996) suggested that Bwindi gorillas should be considered a different subspecies from both Grauer's gorillas and Virunga gorillas, based on limited morphological and ecological measurements. However, genetic analysis showed that the populations are genetically indistinguishable

(Garner and Ryder, 1996; Jensen-Seaman and Kidd, 2001). Bwindi gorillas are currently classified with Virunga mountain gorillas as *Gorilla beringei beringei* but further study may lead to reclassification (Groves, 2001).

METHODS

Study Site and Study Group

Bwindi Impenetrable National Park (BINP) is in the southwest corner of Uganda, Africa (0°53'–1°08'N; 29°35'–29°50'E). The average annual rainfall from 1998 to 2001 was 1326 mm. Observation years started on September 1 and ended on August 31. There are two rainy and two dry seasons per year, which comprise 3-mo wet (March–May and September–November) and dry seasons (June–August and December–February).

Kyagurilo is the study group, which been monitored by the Institute for Tropical Forest Conservation since the late 1980's. At the start of our study in September 1998 they were habituated to humans and could be followed for several hours each day. The size of the group varied between 12 and 14 members (Table I). At the beginning of the study, Kyagurilo comprised 1 adult male/silverback, 2 blackbacks, 5 adult females, 3 juveniles, and 1 infant (per Watts 1990). The blackbacks matured into silverbacks and emigrated separately in November 1999 and November 2000, but one (Rukina) rejoined the group in March 2001 after spending 5 mo as a lone silverback. The 3 juveniles aged into subadults, the infant became a juvenile, and 2 new infants were born. Finally, a subadult female immigrated into the group in 2000.

Estimates of the biomass of the group at the beginning and end of the study are based on published estimates of weight for gorillas in different age/sex classes: 200 kg for adult males/silverbacks, 150 kg for maturing blackback males, 100 kg for adult females, 75 kg for 7–8 year old subadults, 50 kg for 3–6 year old juveniles, and the weight for infants is negligible (McNeilage, 1995; Watts, 1998a). The group biomass did not change significantly during the study (Table I).

Table I. Group composition of the Kyagurilo Group according to age/sex classifications (Watts, 1990) and estimation of group biomass

Year	Adult males	Black backs	Adult females	Sub-adults	Juveniles	Infants	Total	Estimated biomass (kg)
Sept 1998	1	2	5	0	3	1	12	1150
Aug 2001	2	0	5	3	2	2	14	1225

Data Collection

We collected data on home range and fruit eating patterns from September 1, 1998–August 31, 2001. Kyagurilo was tracked and followed by field assistants on a nearly daily basis (5–7 days per week) according to similar methods used in the Virunga Volcanoes (Fossey, 1983). The average length of time gaps when the group was not observed or data was not available or both is 2.5 days, excluding a 40-day halt in data collection in March–April 1999 due to a rebel invasion in the western region of the park. With the exception of this period, there was no monthly or seasonal bias in observations.

The gorillas were contacted between 07:45 and 12:30 h each day and observations lasted *ca.* 4 h per day. The gorillas usually fed for $\geq 50\%$ of observation time (Robbins, unpublished data). During observations, field assistants recorded on daily reports specific names and parts eaten, including fruit, for all plants eaten. While the sampling regime gives only an estimate of fruit eating each day and does not account for the amount of time per day spent eating fruit, it represents adequate sampling of the presence or absence of fruit in their diet on a daily basis. Field assistants also noted if the gorillas interacted with another gorilla group and the location of the event. Any intergroup interaction with the same group that occurred on consecutive days is counted as one interaction.

To determine the location of the gorillas GPS readings were taken at the night nest sites and upon first contact with the gorillas. To allow for relative independence and equal sampling of days, we used only one data point per day for analysis, with preference given to nest site location. Poor GPS satellite coverage coupled with hilly terrain and tree canopy limited the number of days for which GPS readings are available.

Home Range Analysis

We entered the GPS readings for group locations into ArcView GIS software to calculate home range size. We then calculated home range on a monthly, seasonal, and yearly basis via the minimum convex polygon method (MCP; Southwood 1966). We excluded two mo (March and December 1999) from monthly analyses because there were < 10 data points. We also excluded the March–April–May 1999 season from analysis because there were significantly fewer data points than for other seasons.

To determine if we had a sufficient number of points per year to measure home range size accurately and to determine if the increasing number of sampling points in each successive year (Year 1 = 206, Year 2 = 253, Year 3 = 316) would affect yearly home range size comparisons, we plotted

home range size against the number of sampling points, using randomly chosen points per year in intervals of 20 points to determine the number of points needed for annual home range size to reach asymptotes. Asymptotes (90% of overall home range size) were reached after adding 100, 60, and 120 points for each of the 3 years, respectively.

Because the number of points available per month ranged between 12 and 31, we investigated whether the number of points influenced our estimates of monthly home range size. While there is a positive correlation between the number of GPS points per month and monthly home range size for all 3 years combined (Spearman rank correlation, $n = 34$, $r = 0.417$, $p < 0.05$), there is no correlation when each of the 3 years is considered individually (Year 1, $n = 11$, $r = 0.146$, n.s.; Year 2, $n = 11$, $r = 0.123$, n.s.; Year 3, $n = 12$, $r = 0.448$, n.s.). This suggests that the positive correlation across all 3 years is due to an actual increase in home range size in successive years and not because of a greater number of data points with successive years. Nonetheless, we also standardized all monthly home range values by limiting the number of points used to a comparable number for each month (Vedder, 1984). For the months that had >16 data points, we randomly excluded days in blocks of 3 to simulate the average length of gaps in data collection, so that each standardized monthly home range size was based on 14–16 points for all months.

In addition to MCP, we also used the grid cell (500-m) method to estimate seasonal and yearly home range size and yearly core area for comparisons with other studies of home range in gorillas. However our sampling regime of using only a single GPS per day limited how we could use the method. For example, when using only one GPS point per day, by default the maximum number of 250-m \times 250-m grid cells that could be entered in one month is 31. Therefore, the largest area covered would be only 1.9 km². Similarly, using 500-m \times 500-m grid squares would limit monthly home range values to 7.5 km². However, using successively larger grid squares leads to larger overestimates of home range. We defined core areas by selecting grid squares that contained the highest frequency of group location points until 75% of the points were included (Watts, 1998a).

We calculated home range overlap and core area overlap between all pairs of years to examine site fidelity over time. We calculated overlap as the percent of area used commonly between 2 time periods divided by the total area used during them. We calculated home range overlap via both the MCP and 500-m grid square estimates, but due to our method of estimating core area (Watts, 1998a), we calculated core area overlap via only the 500-m grid square estimate.

We used Spearman rank (non-parametric) correlations to investigate the relationship between fruit-eating and home range size on seasonal and monthly bases.

RESULTS

Fruit-eating

Fruit-eating occurred on 27% of all observation days (Table II, Figure 1, 2). There was high variability in the occurrence of fruit eating among years (Year 1 = 23.8%, Year 2 = 43.2%, Year 3 = 15.6%; Figure 1), among seasons ($n = 11$, $x = 17.0\%$, range 2.9–70.3%, $SD = 20.0\%$), and among months ($n = 34$; $x = 27.3\%$; range 0–100%, $SD = 27.3\%$).

The gorillas ate 16 different species of fruit (trees only; Table II). The gorillas ate 0–6 species of fruit per month and 1–9 species per season. However, they ate only 6 species on >20 days, and we refer to them major fruit species (Figure 2). Therefore, over half of the fruit species eaten play a small dietary role. Among the major fruit species, the gorillas ate *Myrianthus* and *Maesa* across the greatest number of mo with the least obvious seasonal patterns (Figure 2). They ate other fruits, for example *Chrysophyllum*, during roughly the same time of the year for >1 yr (Figure 2).

The only consistent seasonal patterns in fruit eating are that the lowest fruit eating times were September through December for Years 1 and 3, during which time fruit eating occurred only ≤ 3 days each mo (Table III). Higher fruit eating months occurred between January and June, again with high variability between years. The highest fruit-eating period of the entire study occurred between February and June of 2000 (Year 2).

Table II. Fruit species eaten by Kyagurilo between September 1998 and August 2001. % days eaten and % fruit days eaten total >100% because more than one fruit was eaten on certain days

Species	# days observed eaten	% occurrence of all fruit	% days eaten	% fruit days eaten	Months eaten	Years eaten
<i>Myrianthus holstii</i>	70	22.73	9.03	30.17	17	3
<i>Chrysophyllum albidum</i>	58	18.83	7.48	25.00	12	3
<i>Teclea nobilis</i>	33	10.71	4.26	14.22	6	2
<i>Maesa lanceolata</i>	28	9.09	3.61	12.07	12	2
<i>Syzigium guineense</i>	26	8.44	3.35	11.21	9	3
<i>Olea welwitschii</i>	20	6.49	2.58	8.62	5	2
<i>Olinia usambarensis</i>	15	4.87	1.94	6.47	4	3
<i>Drypetes gerrardii</i>	15	4.87	1.94	6.47	3	1
<i>Mystroxydon aethiopica</i>	14	4.55	1.81	6.03	2	2
<i>Ficus spp.</i>	9	2.92	1.16	3.88	7	3
<i>Allophyllus macrobotrys</i>	8	2.60	1.03	3.45	5	3
<i>Xylamos monespora</i>	6	1.95	0.77	2.59	2	2
<i>Podocarpus milanjanus</i>	3	0.97	0.39	1.29	2	2
<i>Symphonia globulifera</i>	1	0.32	0.13	0.43	1	1
Unknown tree species	1	0.32	0.13	0.43	1	1
<i>Strombosia sp.</i>	1	0.32	0.13	0.43	1	1

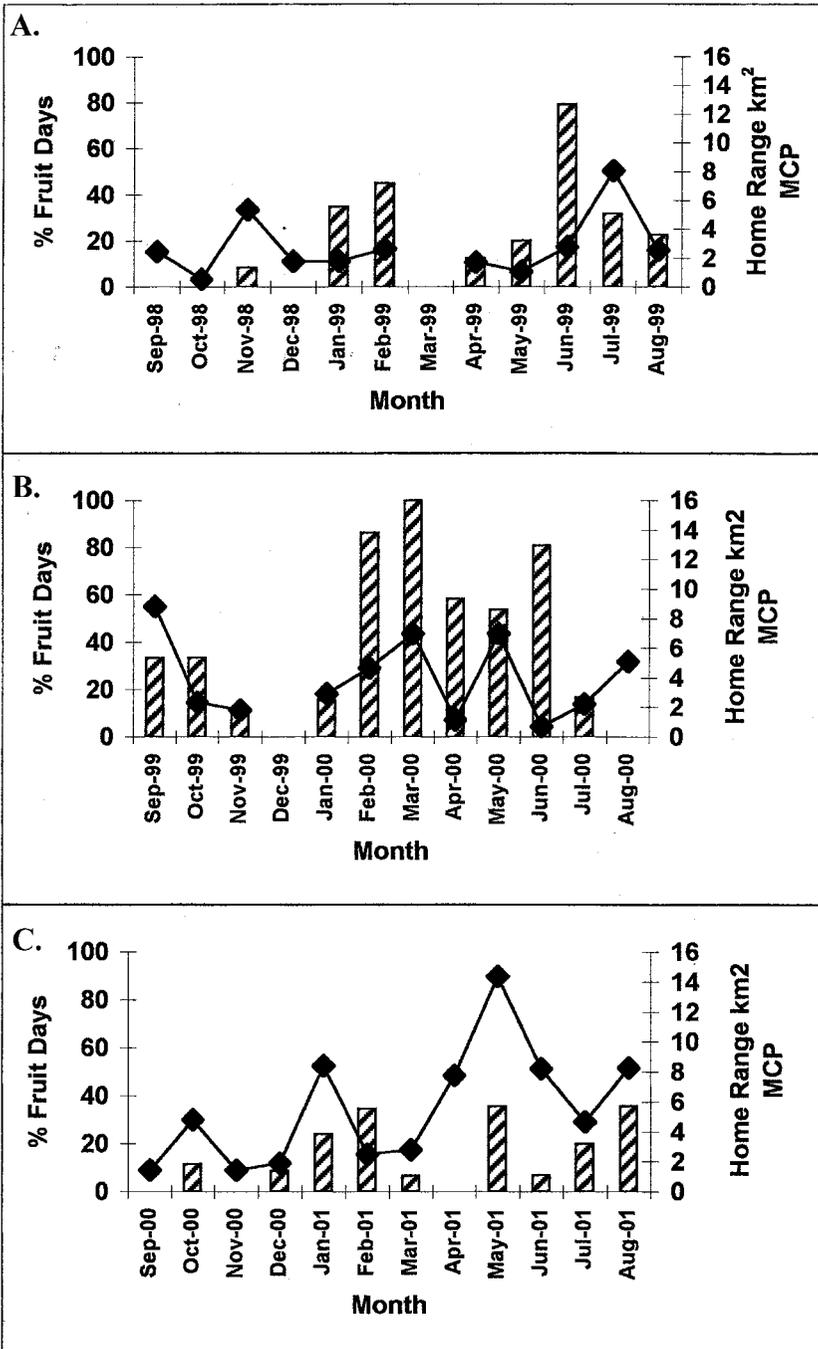


Fig. 1. Monthly home range size (connected diamonds; MCP method) and % of days the gorillas ate fruit per month (dashed columns). A. Year 1 B. Year 2 C. Year 3.

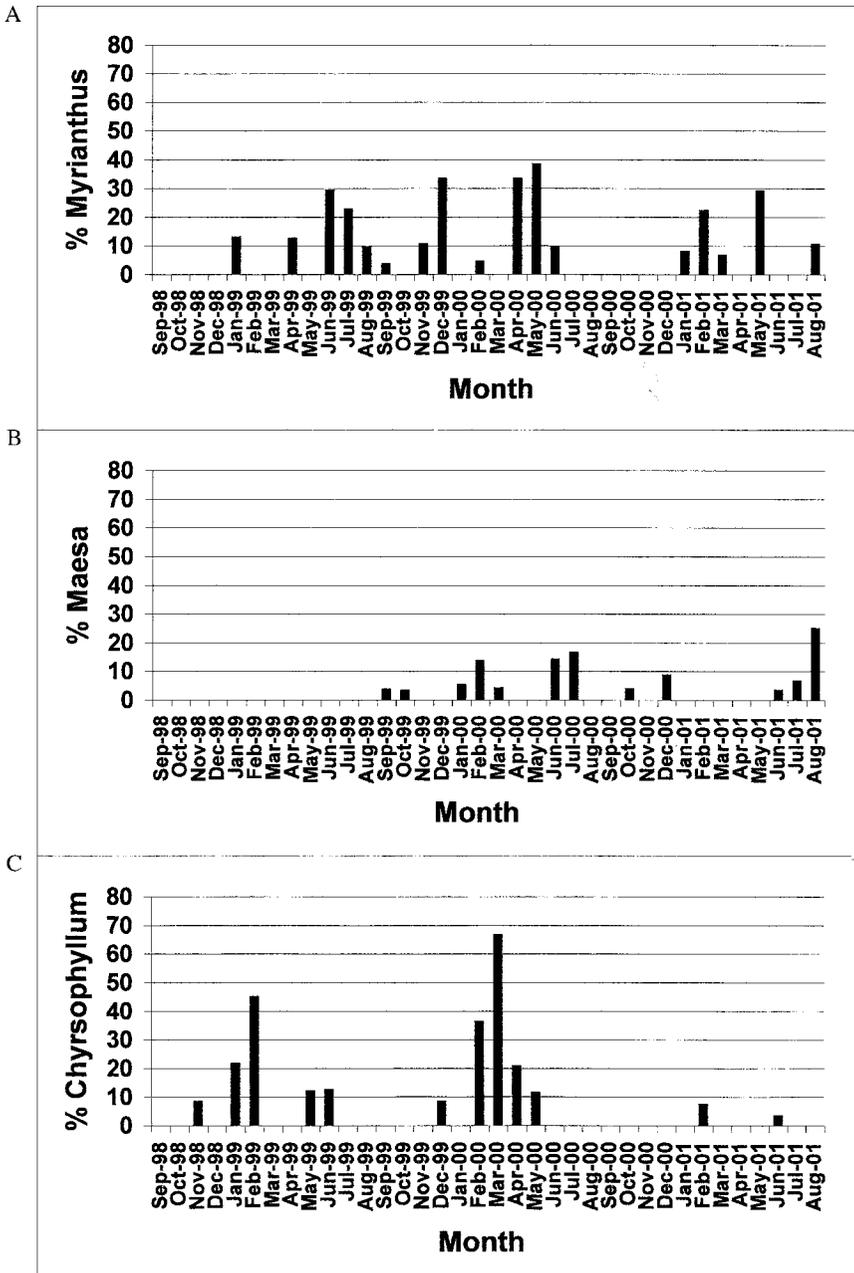


Fig. 2. Percent of observation days the gorillas ate the 6 major fruit species across the 3 years of the study. A. *Myrianthus holstii* B. *Maesa lanceolata* C. *Chrysophyllum albidum* D. *Syzgium guineense* E. *Olea welwitschii* F. *Teclea nobilis*.

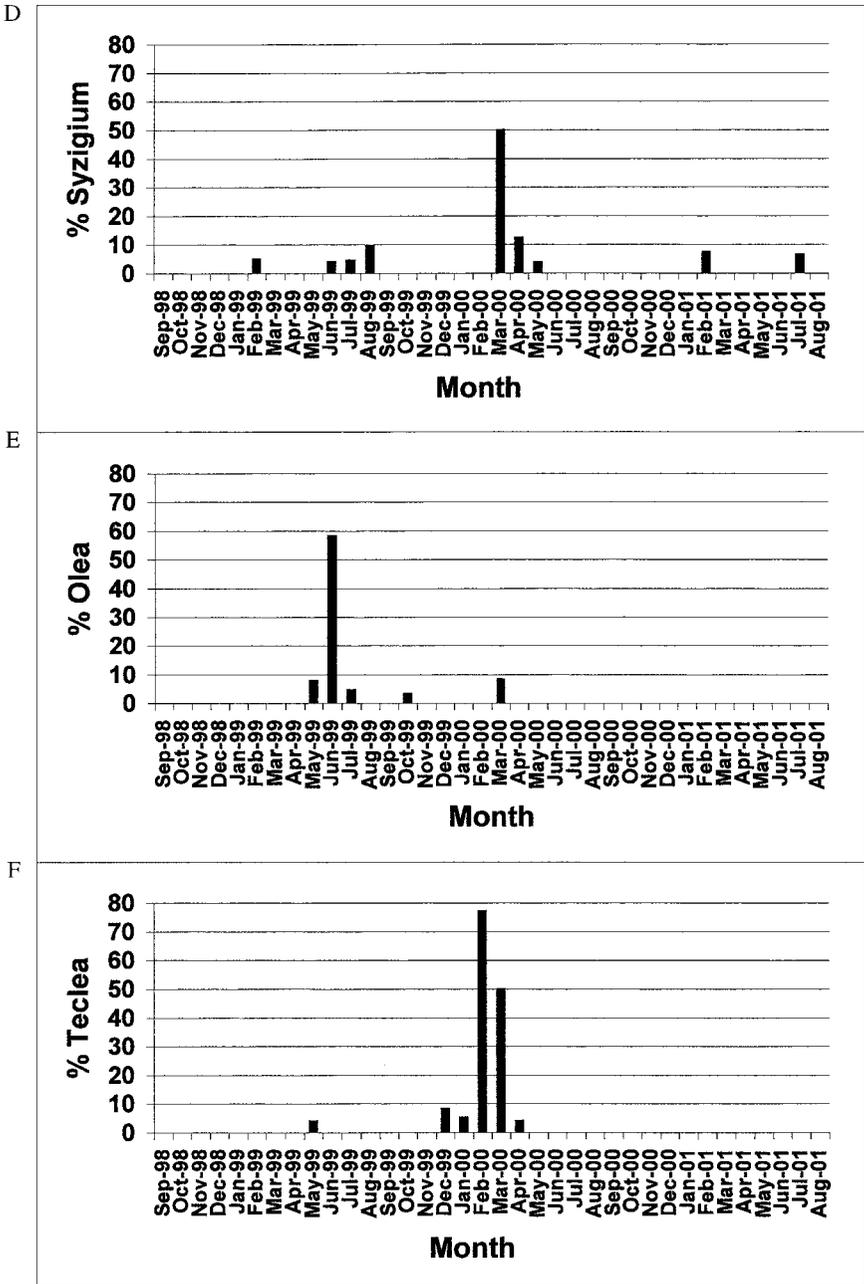


Fig. 2. (Continued.)

Table III. Seasonal values of fruit-eating and home range size via MCP and 500-m grid square estimates

Season	% fruit days	# of fruit species	# of major fruit species	Home range MCP (km ²)	Home range 500-m grid (km ²)
Sept, Oct, Nov 98	2.94	1	1	15.08	8.75
Dec, Jan, Feb 98/99	27.87	5	3	5.34	6.75
Mar, Apr, May 99	16.67	4	4	5.22	4.0
Jun, Jul, Aug 99	42.86	6	4	20.57	9.75
Sept, Oct, Nov 99	27.63	6	3	13.13	7.25
Dec, Jan, Feb 99/00	50.94	7	4	7.85	5.75
Mar, Apr, May 00	70.27	9	5	13.56	8.25
Jun, Jul, Aug 00	27.50	4	2	12.28	8.25
Sept, Oct, Nov 00	3.95	3	1	18.51	7.75
Dec, Jan, Feb 01	22.67	5	4	12.33	8.25
Mar, Apr, May 01	14.44	3	1	29.94	13.5
Jun, Jul, Aug 01	21.00	7	4	38.03	11.75

Home Range Size

Annual

Annual home range size was 21.8 km², 21.1 km², and 40.1 km² for years 1, 2, and 3, respectively, via the minimum convex polygon method (Figures 3, 4). Home range for the 3 years combined was 40.2 km². Via the 500-m × 500-m grid square method, annual home range size was 17 km², 16.3 km², and 28.0 km² for years 1, 2, and 3, respectively (Table IV; Figure 4). The values are 70–78% of the home range values via the MCP method.

Home range overlap via the MCP estimates is 70.1% between Years 1 and 2, 54.1% between Years 1 and 3, and 52.6% between Years 2 and 3. Via the 500-m grid square estimates, home range overlap is 44.6% between Years 1 and 2, 35.6% between Years 1 and 3, and 42% between Years 2 and 3.

Seasonal

The size of home range for 3-mo seasons varied between 5.2 km² and 38.0 km² (Table III; $x = 17.0$ km²; $SD = 9.6$ km²) via MCP method. In most seasons the group used ≥50% of their annual home range. The 500-m × 500-m grid square method produced seasonal home range values of 4.0 km² and 11.8 km² which range from 30.1% to 126.4% of the MCP values. Because the maximum seasonal home range value via 500-m × 500-m grid square

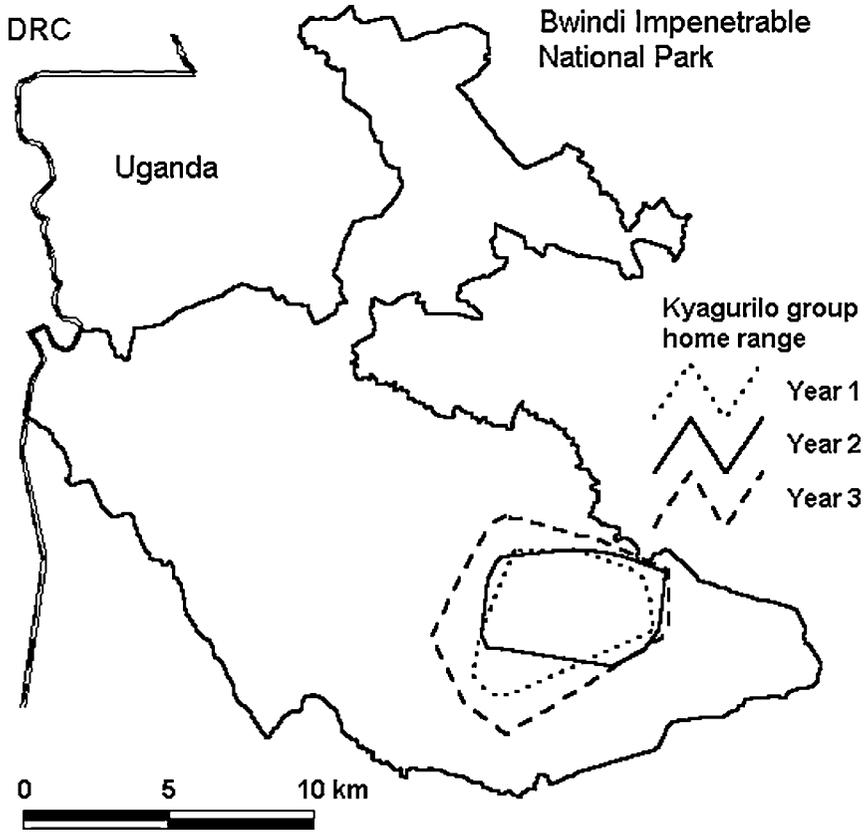


Fig. 3. Home range of Kyagurilo Group during three years.

method is only 22.5 km², it was impossible for all seasonal MCP values to be reached.

Monthly

Monthly home range size varied between 0.96 and 15.7 km² (n = 34, x = 4.8 km², SD = 3.8 km²) based on all points from the MCP method. The standardized monthly home range values, standardizing so all months had 14–16 points varied between 0.53 and 14.35 km² (n = 34, x = 4.14 km², SD = 3.18 km²). For the 29 mo that had standardized MCP, average monthly home range is 84.6% of the home range size without any points removed (range = 53–99.4%, SD = 11.9%).

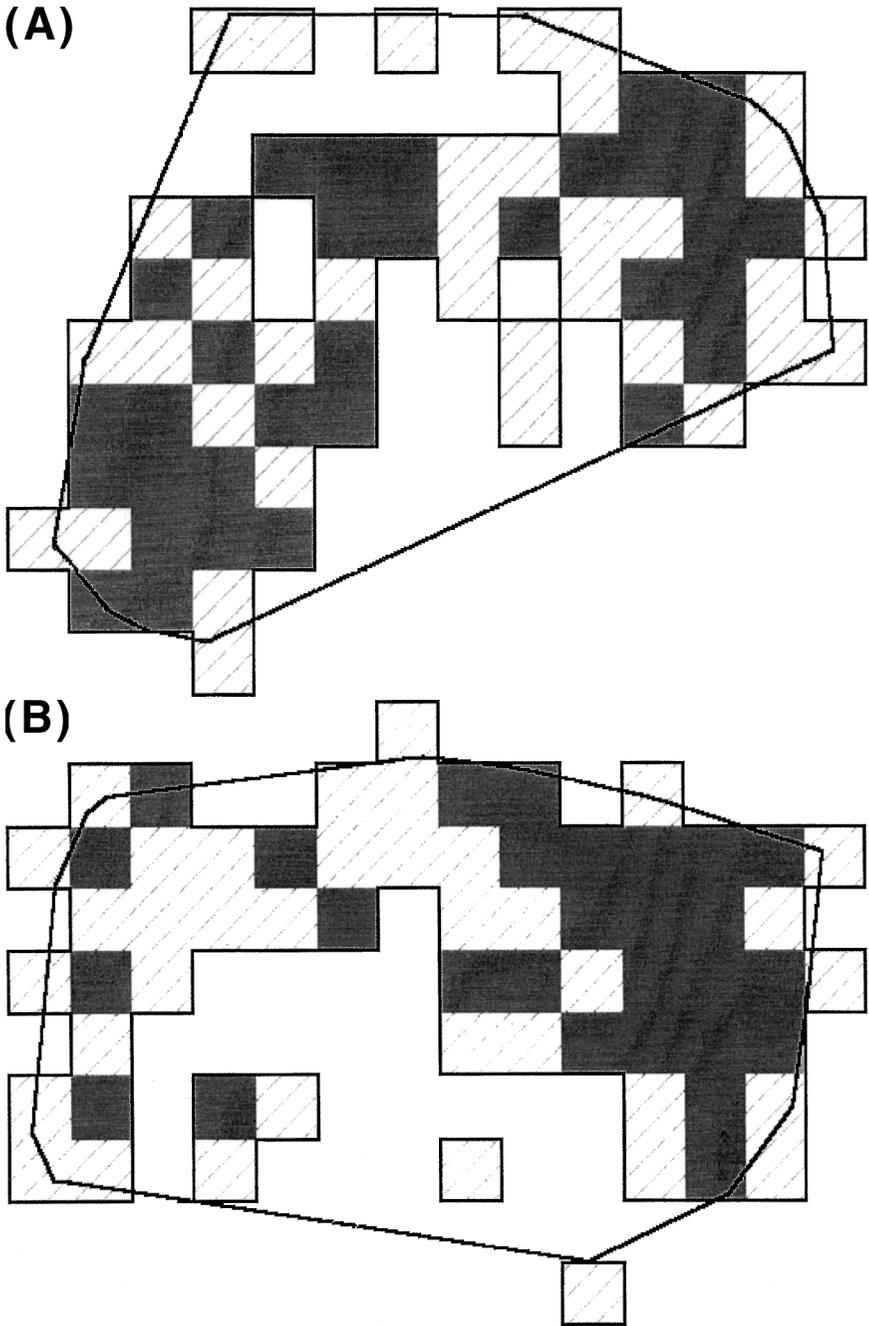


Fig. 4. Home range and core for A. Year 1 B. Year 2 C. Year 3. Outline represents minimum convex polygon (MCP) estimate, hatched squares and grey squares combined represent 500-m grid square estimate, and grey squares represent core area.

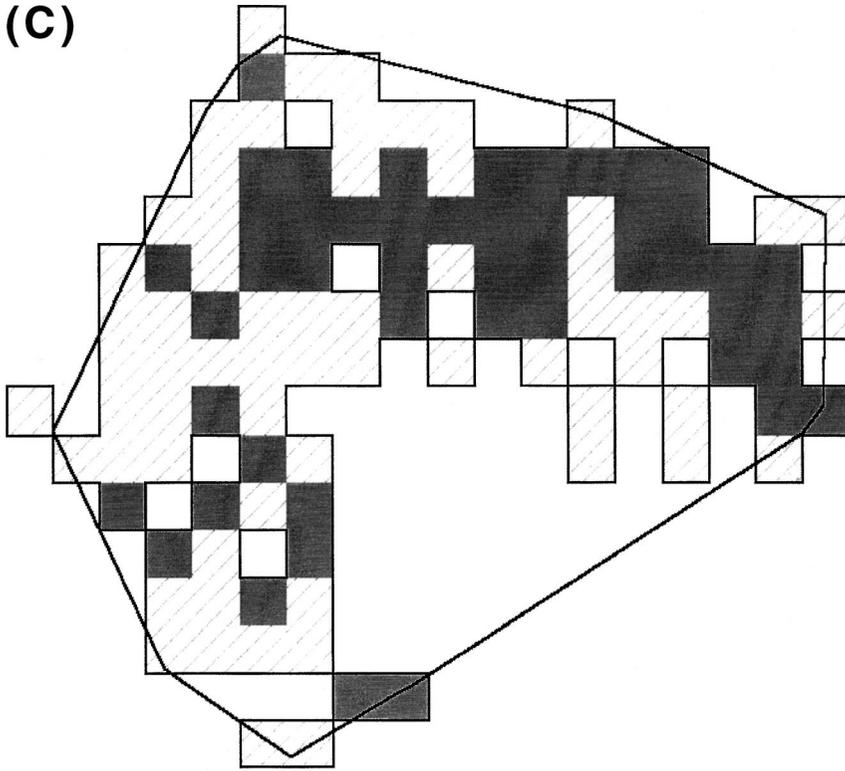


Fig. 4. (Continued.)

Core Area

We estimated annual core area to be between 7.0 and 12.0 km² for the 3 years (Table IV). The values are *ca.* 30–40% of annual home range via the MCP method and 42–50% of annual home range via the 500-m grid square estimate. Via the 500-m grid square estimates, core area overlap is 19.6% between Years 1 and 2, 19.2% between Years 1 and 3, and 24.5% between Years 2 and 3.

Relationship Between Fruit-eating and Home Range

Seasonal

There is no significant correlation between the percentage of days the gorillas ate fruit and seasonal home range size via either MCP or 500-m grid

Table IV. Annual home range size and core area size using different estimation methods

Year	Home range MCP (km ²)	Home range 500-m grid (km ²)	Core area (km ²)	Percentage core area of MCP home range (%)	Percentage core area 500-m grid sq home range (%)
Year 1	21.7	17.0	8.5	39.2	50.0
Year 2	21.1	16.3	7.0	33.2	43.1
Year 3	40.1	28.0	12.0	29.9	42.9
3 Years combined	40.2	34.0	14.0	34.8	41.2

square estimates for all fruit eaten (MCP estimate, $N = 11$, $r = -0.464$, n.s.; 500-m grid square estimate, $N = 11$, $r = -0.431$, n.s.) or if we restrict fruit days to include only the 6 major fruit species (MCP estimate, $N = 11$, $r = -0.255$, n.s.; 500-m grid square estimate, $N = 11$, $r = -0.128$, n.s.). We also examined the 6 major fruit species individually and there is no significant relationship between the amount of any individual fruit species and seasonal home range size.

There is no correlation between seasonal home range size and the total number of fruit species eaten per season (MCP, $N = 11$, $r = -0.092$, n.s.; 500-m grid square estimate, $N = 11$, $r = -0.104$; n.s) or seasonal home range size and the number of major fruit species eaten per season (MCP, $N = 11$, $r = -0.414$, n.s.; 500-m grid square estimate, $N = 11$, $r = -0.337$, n.s.).

Monthly

There is no significant correlation between standardized monthly values of home range size and occurrence of fruit eating for the 3 years combined or each year individually except for Year 3 (3 Years: $N = 34$; $r = 0.200$, n.s.; Year 1: $N = 11$, $r = 0.495$, $p > n.s.$; Year 2: $N = 11$, $r = 0.036$, n.s.; Year 3: $N = 12$, $r = 0.607$, $p < 0.05$). However, the correlation for Year 3 is not statistically significant ($N = 11$, $r = 0.506$, n.s.) when we remove the outlier point of the largest monthly home range value, which is >6 km² larger than any other monthly home range value (May 2001, standardized monthly home range = 14.35 km², percent fruit eating days = 36%).

There is no relationship between standardized monthly home range size and the percentage of days that the gorillas ate major fruit species per month (3 Years: $N = 34$, $r = 0.146$, n.s.; Year 1, $N = 11$, $r = 0.505$, n.s.; Year 2, $N = 11$, $r = -0.023$, n.s.; Year 3, $N = 12$, $r = 0.430$, n.s.). The total number of fruit species eaten and the number of major fruit species eaten per month also has no relationship with standardized monthly home range size (all fruit: 3 Years, $N = 34$, $r = 0.212$, n.s.; Year 1, $N = 11$, $r = 0.531$, n.s.; Year 2, $N =$

11, $r = -0.055$, n.s.; Year 3, $N = 12$, $r = 0.522$, n.s.; major fruit: 3 Years, $N = 34$, $r = 0.165$, n.s.; Year 1, $N = 11$, $r = 0.437$, n.s.; Year 2, $N = 11$, $r = -0.192$, n.s.; Year 3, $N = 12$, $r = 0.302$, n.s.). There is no significant correlation between standardized monthly home range size for each year or the 3 years combined and the percentage of days on which gorillas ate any of the 6 major fruit species considered individually.

Intergroup Encounters

The number of intergroup interactions per year was 2, 6, and 11 for Years 1, 2, and 3 respectively. Based on nest counts and sightings of the other groups, the intergroup interactions occurred with probably only 2 other groups and 2 lone silverbacks, both of which were the males that emigrated out of Kyagurilo. Ongoing genetic analysis will confirm the identity and number of groups whose home range overlaps with that of the Kyagurilo (Mutebi *et al.*, in prep). While the increased number of interactions in Year 3 corresponds with the large increase in home range size compared to Years 1 and 2, it is not possible to determine if the intergroup encounters caused the group to expand or to shift its range, if the range expansion led to more interactions, or if there is no direct relationship between the two.

DISCUSSION

Frugivory

Kyagurilo ate 16 species of fruit from trees, which is intermediate number between Virunga and western and Grauer's gorilla populations (Table V). Many of the species are the same as those eaten by Grauer's gorillas in Itebero and Kahuzi Biega (Goodall, 1977; Yamagiwa *et al.*, 1992, 1994, 1996), and some are also used by gorillas at the lowest altitude of the Virunga Volcanoes in the Democratic Republic of Congo (McNeillage, personal observation). The number of fruit species eaten by the gorillas depends not only on what they are choosing to eat but also on what is available. The high altitude may be largely responsible for limiting the number of fruiting trees in Bwindi. A greater number of fruit species are consumed by gorillas at lower altitudes within Bwindi despite ranging <20 km from the Kyagurilo home range (Ganas and Robbins, in prep.).

Fruit eating occurred on 27% of observation days across the 3 years of study. While our methodology and those used in other studies does not allow estimates of the percentage diet that is fruit by biomass, it appears that Bwindi gorillas are also intermediate in their fruit consumption between

Table V. Comparison of frugivory, terrestrial herbaceous vegetation density, home range, and core area size in gorilla populations

Population	# of fruit species in the diet	Estimate of fruit in diet	Terrestrial herbaceous vegetation density	Home range size	Core area size
Mountain Gorillas: Karisoke Research Center	1 ^{a,b}	<1% of feeding time spent eating fruit ^d	8.8 stems/m ^{2a}	3–15 km ^{2a,b,c}	1.4–4 km ^{2a,b,c} 30–40% of annual home range
Mountain Gorillas: Bwindi Impenetrable (this study)	16	27% of observation days Approx. 11% of foraging time spent eating fruit Seasonal variation	? (Nkurunungi, in prep)	21–40 km ²	7–12 km ²
Eastern Lowland Gorillas: Kahuzi Biega Highland (1800–3300 m)	20 ^d	96.5% of fecal samples contained fruit remains ^d	Not calculated	23–31 km ^{2a,e,f}	Not calculated
Lowland (600–1300 m)	48	89% of fecal samples contained fruit remains			
Western Lowland Gorillas: Lopé, Mondika, and Bai Hokou	77–115 ^{g,h,i,j}	98% of fecal samples contained fruit remains ^{g,h,i,j,k} Seasonal variation	0.78–1.87 stems/m ^{2k}	7–23 km ^{2h,j}	Not calculated

^aWatts, 1984.^bVedder, 1984.^cMcNeilage, 1995.^dYamagiwa, 1992, 1994, 1996.^eCasimir and Butenandt, 1973.^fGoodall, 1977.^gWilliamson *et al.*, 1990.^hTutin, 1996.ⁱNishihara, 1995.^jRemis, 1997a, 1997b.^kDoran *et al.*, 2002.

Virunga gorillas and western and Grauer's gorillas (Table V). Detailed behavioral observations during the first year of our study suggest that Kyagurilo spent *ca.* 11% of observed foraging time eating fruit, but it will also vary between seasons and years (Robbins, unpublished data).

Fruit consumption varied with time throughout the study period. While there appeared to be neither a distinct fruiting nor non-fruiting season, generally the gorillas consumed fruit less in September through December and more often from January through June. They ate certain species of fruit during distinct periods versus other fruits across all times of the year, which suggests that there is high variability in fruiting patterns among tree species. To best understand fruit eating selectivity patterns of Bwindi gorillas, a direct comparison of fruit eating behavior in relation to fruit availability must be made (Nkurunungi, in prep.) as has been done at other gorilla study sites (Nishihara, 1995; Remis, 1997b; Williamson *et al.*, 1990; Yamagiwa *et al.*, 1996).

Home Range Size

Via the MCP method, the annual home range size of the Kyagurilo was *ca.* 21 km² for each of the first 2 years of the study and then increased to 40 km² in the third year. The estimates for the 3 years via 500-m grid squares are smaller: 16–28 km². The core area used by the Kyagurilo Group was between 7 and 12 km² for the 3 years. It represents *ca.* 30–50% of annual home range size depending on the method of home range estimate and year, which is similar to the percentage of home range used as core area by Virunga gorillas (Watts, 1998a) and indicates that there is selectivity in use of space within the home range. The percent overlap between annual home range estimates for the 3 years range between 35 and 70% depending on the method used and years compared, which shows a moderate degree of site fidelity, but with significant variation in areas used from one year to the next.

The differences in home range size, core area size, and interannual overlap depending on the method of estimation used support previous claims of the pros and cons of each (Harris *et al.*, 1990; Singleton and van Schaik, 2001; Sterling *et al.*, 2000). Grid cells are useful for a representation of patterns of habitat use within home ranges, e.g., core areas, but an outline technique such as MCP is more suitable to calculate home-range area, especially when the number of group location points is low (Harris, *et al.*, 1990). The majority of studies of gorilla home range have used only the grid square method (Fossey, 1974; Goodall, 1977; Remis, 1997a, Vedder, 1984; Watts, 1991, 1994, 1998a, Yamagiwa *et al.*, 1996; except McNeilage, 1995 and Tutin, 1996), but

usually their emphasis of was home range utilization, not just size, which necessitates spatial partitioning. Future students of home range size in gorillas should utilize both methods to estimate of home range. The MCP method should be more appropriate for comparisons across sites because grid cell methods are more likely to be affected by differences in the intensity with which groups are followed and grid size and position (Hansteen *et al.*, 1997).

Variability in Home Range

The size of the home range of Kyagurilo varied considerably on monthly, seasonal and yearly bases. Our study revealed several interesting findings: a) despite considerable variation in home range size on a monthly and seasonal basis, there is no clear relationship between occurrence of fruit eating and the size of the home range area used; b) there was a drastic increase in home range size in Year 3 versus to Years 1 and 2; and, c) while patterns of frugivory of Bwindi gorillas are intermediate between those of the Virunga gorillas and western and Grauer's gorillas, home range size is larger than that of Virunga gorillas and comparable to that of other gorillas.

There are several possible explanations for the lack of relationship between home range size and frugivory on a monthly or seasonal basis. The gorillas might feed only opportunistically on fruit, in which case fruit consumption would not have an impact on ranging patterns. However, our observations strongly suggest that the gorillas regularly move considerable distances to reach fruiting trees.

If fruit eating has an impact on gorilla movement patterns, and yet there is no clear relationship between home range size and fruit eating, the relationship must be more complicated than a simple increase in home range sizes when more fruit is eaten. A heterogeneous or patchy distribution of fruit trees could be a more important determinant of range size than whether the gorillas are eating fruit or not. Increased levels of fruit-eating in a particular month or season could cause increased or decreased home range size, depending on the distribution and abundance of the fruits eaten. Day journey length might increase when fruit is being consumed (Goldsmith, 1999; Yamagiwa *et al.*, 1992, 1994) if the gorillas criss-cross a particular area more frequently, but this might not result in an increase in overall home range area. Also, the lack of a clearly defined fruit season for each year of the study may also obscure any relationship between seasonal variation in frugivory and home range size.

To better understand the patterns of home range utilization in relation to fruit availability, we need to quantify the distribution and abundance of fruit trees overall and for individual species on both temporal and spatial scales.

Similarly, the degree of interannual home range overlap and site fidelity will be dependent on social factors, such as male mating competition, and ecological factors, such as seasonal and annual variation in food availability and regeneration time for herbaceous food resources (Watts, 1998a, 1998b). Bamboo, the only seasonally available gorilla food in the Virunga Volcanoes, does not occur in the home range of Kyagurilo. Analysis of fruit and terrestrial herbaceous vegetation distribution and abundance in the study area is underway (Nkurunungi, in prep), but it is probable that home range utilization will be influenced by both types of resource (Doran *et al.*, 2002; McNeillage, 2001; Watts, 1984, 1998a, 1998b; Vedder, 1984).

In addition to ecological factors, social factors are also likely influence gorilla ranging patterns. While home range size in Year 3 nearly doubled versus Years 1 and 2, there was no large change in group size or biomass, there appeared to be no obvious change in food availability or distribution, and fruit consumption was lower than in previous years. There was no change in the level of human induced risk or disturbance, nor was there an overt change in the influence that neighboring groups had on Kyagurilo's ranging patterns.

One social factor that may have led to the large increase in home range size in Year 3 is the return of a silverback male, Rukina, to Kyagurilo. Rukina emigrated out of Kyagurilo in November 2000 and rejoined the group in March 2001. We were unable to monitor his movements during the 5 mo he was not with Kyagurilo. Following his return, there were high levels of aggressive conflict between the 2 silverbacks as he challenged the dominant male for alpha position. Frequently, to avoid confrontation, when Rukina approached within <20 m, the dominant silverback followed by the females and immatures moved away, which resulted in decreased resting time and increased in travel time (Robbins, unpublished data). While this does not definitively explain why the group moved into areas not explored in the first 2 years of our study, it is possible that Rukina's pressure on the dominant silverback was, in fact, driving the group into new locations. Of the 15-km² home range size increase compared to Years 1 and 2 combined, 95% of it in Year 3 occurred after Rukina's return.

Regardless of the estimation method or year, the home range of the Kyagurilo was considerably larger than has been measured for Virunga groups (McNeillage, 1995; Vedder, 1984; Watts, 1998a), and it appeared to be more similar to those of Grauer's and western gorillas (Yamagiwa *et al.*, 1992, 1994, 1996; Casimir and Butenandt, 1973; Goodall, 1977; Tutin, 1996; Remis, 1997a; Table V). This pattern may be explained by the fact that Virunga gorillas live in a habitat with exceptionally high herbaceous food densities and include very little fruit in their diet, which leads to small home range size. Conversely, western gorillas consume significant quantities of fruit and often

live in habitats with low and or patchy herbaceous foods (Remis, 1997b; Doran and McNeilage, 1998, 2001; Doran *et al.*, 2002; Table V). It is possible that fruit eating induces Bwindi gorillas to use a larger area overall than they hypothetically would do if they did not eat fruit because of the distribution of fruiting trees and because fruit-eating occurred during most months of the study. Similarly, given our findings on ranging behavior, we predict that the density of terrestrial herbaceous vegetation in Bwindi is intermediate between habitats of the Virunga and western gorillas.

CONCLUSIONS

Large home range size in Bwindi mountain gorillas could have implications for conservation management. If Bwindi gorillas utilize more habitat and occur at a comparable density to Virunga gorillas (*ca.* 0.85 gorilla/km²; Kalpers *et al.*, in press; McNeilage *et al.*, 2001), there may be implications for the potential for the population increase, though we would need to know more about habitat quality and home range overlap before we could draw firm conclusions on carrying capacity. Extrapolation from the Virungas should be done with caution because Bwindi gorillas use different resources and show different ranging patterns. Ranging patterns need to be taken into account when planning park zoning and when addressing conflicts that arise when gorillas range outside of park boundaries and raid crops in surrounding fields.

The large home range of Bwindi gorillas also has implications for our understanding of the variability of the social system of gorillas. On a population level, the density of gorillas and degree of home range overlap in an area in relation to resource utilization are more meaningful variables to consider than simply the home range size of specific social groups. The variables will determine the use by all gorillas in an area, rather than the use of space by particular groups. Given that Bwindi gorillas occur at a similar density to Virunga gorillas and have larger home ranges, one would expect more overlap between groups, potentially a greater degree of inter-group resource competition, and possibly an increased rate of intergroup encounters, which would lead to greater opportunities for female transfer (Yamagiwa, 1999).

Results of this and other studies reveal that the relationships between home range, dietary patterns, and social factors in gorillas and other primates are complex. In general, we might expect annual home range to be primarily related to food resources with social factors adding an additional layer of complexity (Watts, 1998a). Effects of food resources should be most evident vis-à-vis the time scale of regeneration of the resources after use by gorillas, while social factors might operate on any time scale. In order to fully

understand ranging patterns of gorillas it is necessary to consider the home range size on different time scales, as well as the variability in the actual areas used (or conversely the site fidelity) over time in relation to ecological and social factors. As our knowledge of gorillas continues to grow, future comparative studies of the socioecology of all subspecies of gorillas should include investigating links between feeding ecology, ranging patterns, and social behavior on the individual, social group, and populational levels.

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