

CHAPTER ELEVEN

**Preliminary GIS Analysis
of Range Use by
Sympatric Mountain
Gorillas and Chimpanzees
in Bwindi Impenetrable
National Park, Uganda**

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INTRODUCTION

A central premise of evolutionary theory is that ecological competitors act as important agents of natural selection, molding species into their current phenotype. When two closely related, morphologically similar species occur in the same habitat, it is reasonable to infer that they are different in some critical

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ecological features that have allowed coexistence. It remains for field researchers to identify these ecological differences.

A clear understanding of primate ranging patterns is essential to understanding feeding and foraging behavior and consequently the behavioral ecology of the species. Ranging patterns may be influenced by climate, territoriality, distribution of water resources, location of sleeping sites, distance traveled the previous day, intergroup encounters, competition for food and mates, predation pressure, diet, and other ecological constraints. Spatial and temporal distribution and abundance of food resources are perhaps the most important environmental determinant of primate movements (Milton & May, 1976; Clutton-Brock & Harvey, 1977; Wrangham, 1980; Isbell, 1983; Boinski, 1987). Diet is the most crucial factor suggested to explain the differences in ranging patterns of animals (Mitani & Rodman, 1979) bearing in mind that an animal's energetic needs determine its home range size (Mace & Harvey, 1983).

The degree of frugivory or folivory has been shown to influence primate ranging patterns (Milton & May, 1976; Clutton-Brock & Harvey, 1977; Doran & McNeilage, 1998). Seasonal fluctuations in resource abundance often cause primates to change their feeding behavior and ecology, with frugivores tending to have larger home ranges and longer day ranges for their size than do folivores (van Schaik, 1983; Chapman, 1988; Janson & Goldsmith, 1995).

Previous studies of gorilla ranging behavior indicate that home range areas of Virunga gorillas (Fossey, 1974; Fossey & Harcourt, 1977; Watts, 1984; Vedder, 1984; Yamagiwa, 1987; McNeilage, 1995) are small compared to eastern lowland gorillas (Casimir, 1975; Goodall, 1977; Yamagiwa *et al.*, 1994) and western lowland gorillas (Bai-Hokou: Remis, 1994; Goldsmith, 1999; Lopé: Tutin, 1996). In addition, foraging effort varies more over time for eastern lowland gorillas and western lowland gorillas than with mountain gorillas (Watts, 1996). The distances of the foraging path taken by an animal from dusk to dawn (day range length [DRL]) are longer for eastern lowland gorillas (Goodall, 1977; Yamagiwa & Mwanza, 1994) than for western lowland gorillas (Remis, 1994, Goldsmith, 1996; Lopé: Tutin, 1996). This distance has been shown to increase when gorillas used seasonal fruit crops than when they ate mostly terrestrial herbaceous vegetation (THV) or bamboo (Watts, 1996).

Studies of chimpanzee ranging behavior have tended to be less systematic, because of the logistical difficulties imposed by the chimpanzee social system. While gorillas travel in cohesive groups, chimpanzees travel in temporary

subgroups, or parties, in which membership is highly variable (Goodall, 1986). Because of this fission–fusion system, there is no one direction or distance of group travel. In practice, daily range estimates are based on individual path lengths. Male chimpanzees tend to travel farther (Goodall, 1986) and faster (Wrangham 2000) than females, presumably because of the high cost of female locomotion when carrying offspring, and the tendency for males to travel to home range perimeters to patrol territorial boundaries.

In this chapter, we present preliminary results of a long-term study of range use by sympatric mountain gorillas (*Gorilla gorilla beringei*) and chimpanzees (*Pan troglodytes schweinfurthii*) in Bwindi Impenetrable National park, Uganda. The primary objectives of the study were to (1) map and measure the home range area for one group of gorillas and one community of chimpanzees in Bwindi and (2) measure mean DRL for one group of gorillas. We describe our use of GIS/GPS technology in collecting, analyzing, and presenting ranging data.

METHODOLOGY

The study area covers approximately 25 km² of Afromontane forest in the Ruhija section of Bwindi Impenetrable National Park in southwestern Uganda (from approximately 0°53′–1°08′ S and 29°35′–29°50′ E). The study site is of rugged, wet terrain, with an elevational range from 2000 to 2300 m. The forest is quite heterogeneous, with at least 163 tree species recorded (Butynski, 1984). Bwindi possesses a complex floristic composition that includes eight botanical communities, among which *Parinari*-dominated forest, *Chrysophyllum*-dominated upland forest, *Newtonia*-dominated forest, swamp, and a small bamboo zone are the most widely distributed (Howard, 1991; Bitariho, 1999). Unlike the Virunga Volcanoes, where more than 50% of gorilla habitat is bamboo forest (Bitariho, 1999), the bamboo zone in Bwindi covers no more than 1–2% of gorilla habitat, located primarily in the highest elevations of the park (outside the study site) between 2400 and 2600 m (Bitariho, 1999). Annual rainfall averages 1100–2400 mm (Butynski, 1984), and the climate is characterized by two dry seasons lasting from about May to July and from late December to February.

Gorillas in Bwindi Impenetrable National Park number approximately 300, or about 1/km² (McNeillage *et al.*, 1998). Mitochondrial DNA studies have shown them to be virtually indistinguishable from their sister population in the

Virunga Volcanoes (Garner & Ryder, 1996; Jensen-Seaman & Kidd, 2001) with which they occupied continuous forest until 400–500 years ago (Hamilton *et al.*, 1986; Stanford, 2001). Little was known about the Bwindi chimpanzee population before the present study was begun. Research on Bwindi chimpanzee–gorilla sympatry began in late 1996 and is ongoing. Until 1999, the research was carried out at two sites: Nkuringo in the southwestern corner of the park, and Ruhija, in the eastern section. Political instability forced closure of the Nkuringo site and the suspension of data collection in Ruhija in early 1999. In January 2000, the project started again in Ruhija. The data presented in this paper were collected in Ruhija, primarily from January to December 2000.

The study population was the Ruhija chimpanzee community and one gorilla group, the habituated Kyagurilo “research” group. One of us (JBN) plus field assistants have studied the gorilla group since 1997. The animals are habituated and individually identified; both direct observational and indirect data were collected. During the study period, the group consisted of 13 animals (1 silverback male, 1 blackback male, 5 adult females, 6 immatures) and was monitored daily by research staff of the Institute of Tropical Forest Conservation. The Ruhija chimpanzee community is partially habituated; many of its members tolerate approach by observers to within 25 m when feeding in trees, but animals cannot be followed or watched at close range on the ground. This community consists of at least 25 individuals, including at least 5 adult males whose identities and dominance ranks are known. CBS and three field assistants collected data on this community.

Using GIS Technology for Range Use Analysis

A recently emerged key technology that can be used to study habitat use patterns in primates is geographic information systems (GIS) technology. Using handheld global positioning system (GPS) units, which interface with orbiting satellites, researchers can precisely map the locations of animals, nests, feeding sites, and other habitat features. Although this technology has been available for more than a decade, its use has been limited in primate field studies by the lack of digitally mapped field sites onto which GPS coordinates could be plotted. In Uganda, conservation-oriented GIS research has been carried out since the 1990s, and many of the conservation areas in the country have been mapped from Landsat images.

A contour map of Bwindi Impenetrable National Park in southwestern Uganda, converted to a digitized image, is used for ecological monitoring purposes by research staff at the Institute for Tropical Forest Conservation, a nongovernmental conservation organization. This map is analyzed using Arcview GIS software application, and contains features such as elevation contours, stream drainage, vegetation type, trails, and political boundaries. We gather chimpanzee and gorilla ranging data by obtaining coordinates with handheld GPS units wherever known animals are observed, and wherever nests are found within the known home range. These coordinates are downloaded from the units onto the Arcview image of the study site, where they can be sorted and analyzed by date, location, and a number of other variables.

GPS readings were obtained with handheld Garmin 2+ units, often facilitated by using 2-m remote antennas suspended overhead. One GPS recording for gorillas and one for chimpanzees was chosen per day for home range mapping and analysis. Readings were normally taken from gorilla nest sites, and from either fresh chimpanzee nests or feeding sites. Poor reception under thick vegetation or on cloudy and rainy days sometimes made it impossible to obtain GPS readings.

A major problem in studying chimpanzee ranging patterns is the uncertainty whether nests in border areas of the known range were made by the Ruhija or a neighboring community. For this reason there is some bias in the chimpanzee range sampling toward samples taken within the estimated core area of the range. A total of 264 GPS points in 2000 for gorillas and 483 for chimpanzees were recorded for use in range analysis.

To map home range area, GPS readings were downloaded into Arcview software application (version 3.1) and analyzed at both the GIS laboratory at Makerere Institute of Environment and Natural Resources and the Jane Goodall Research Center at the University of Southern California. The GPS points were overlaid onto Bwindi Impenetrable National Park database of CARE-DTC map 1997 (adapted from Cahusac, 1958). The total home range during 2000 was mapped to show the area size and location of nest and contact sites and superimposed over the vegetation map of Bwindi Impenetrable National Park. The map was also divided into two blocks, Kagyembagyembe (K) and Nyaruchundura (N), on the basis of vegetation characteristics of the gorillas' home range.

Gorilla home range was computed in two ways. First, the peripheral GPS points for the entire period of study were connected to yield the total home

range area. In addition, the peripheral GPS points for each year were connected to show inter-annual variation in home range area. This is the minimum convex polygon (MCP) method and was used for home range estimates for mountain gorillas in the Virungas (McNeilage, 1995). The MCP method does not take into account the empty spaces that the animals will not have visited, thus overestimating the home range size. In addition, it gives no indication of how the range is utilized, and is subject to bias by both small sample sizes and extreme outlying locations (Hooge *et al.*, 2000).

Using a second method, the map was divided into 1-km² quadrats. The number of quadrats with GPS points was then counted and used to estimate home range. The grid method has been used for mountain gorillas in the Virungas (Vedder, 1984; Watts, 1997), although without GPS data. It is the most suitable method for animals with irregular-shaped home ranges or home ranges with several areas of concentrated use, which was the case with gorillas. In this study, both methods were used to avoid bias.

RESULTS

Figure 1 shows the distribution of chimpanzee and gorilla nesting sites from GPS points collected during 2000. The gorilla group used various vegetation types within their home range. They avoided the large swamp, dividing their range into two forest blocks. The frequency of quadrat use varied significantly among core, regularly, and frequently used areas (Kruskal–Wallis test $H(2, n = 34) = 27.9, P < 0.001$). Overall, quadrat use ranged from 0.2 to 12.7%, with lower percent frequencies towards the periphery of the home range. Only 7 km² of the total home range was used more intensively (core area), accounting for 20.6% of the total home range area. Ten square kilometers of the remaining area (29.4%) was regularly used and most of the remaining area (50% of the total home range) was less frequently used. Range use by both species varied widely by month, and range use appears to diverge (note that chimpanzee ranging data in July 2000 were not available). Chimpanzee and gorilla ranges showed extensive overlap at a broad scale, but in only 2 months (March and October) did nest sites overlap extensively. In other months, gorilla nests were tightly clustered in distribution, while chimpanzee nests were found in a more scattered pattern that fell entirely or almost entirely outside the range of gorilla nests. Chimpanzee and gorilla range use was similar, but overlapped little, despite their tendency to feed on the same fruit resources (Stanford &

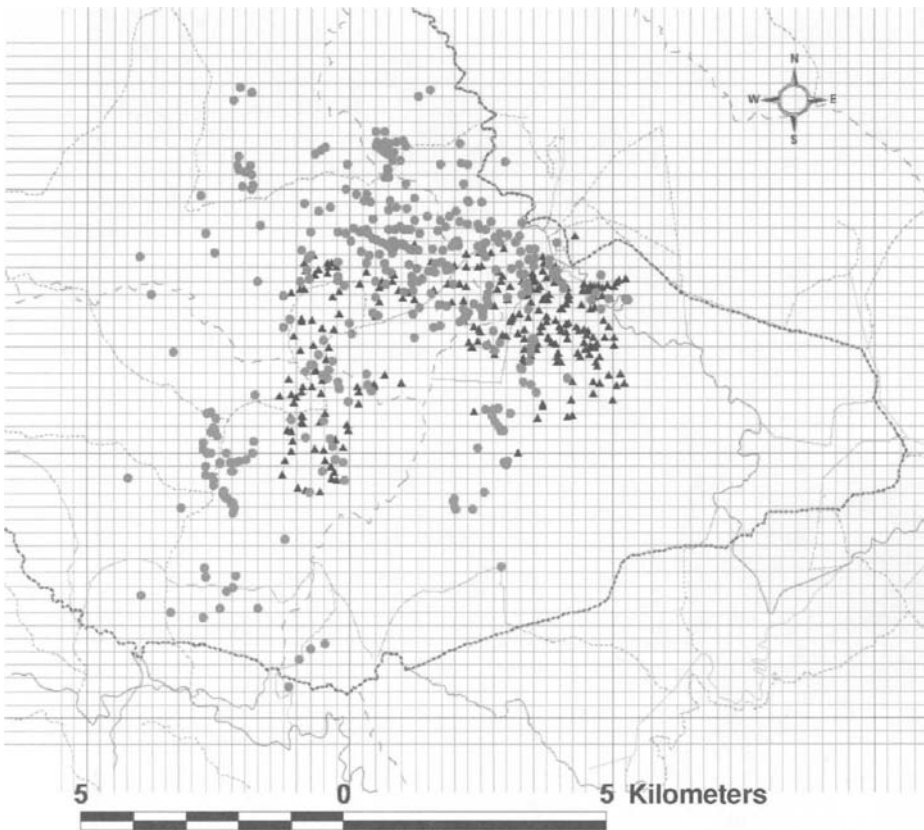
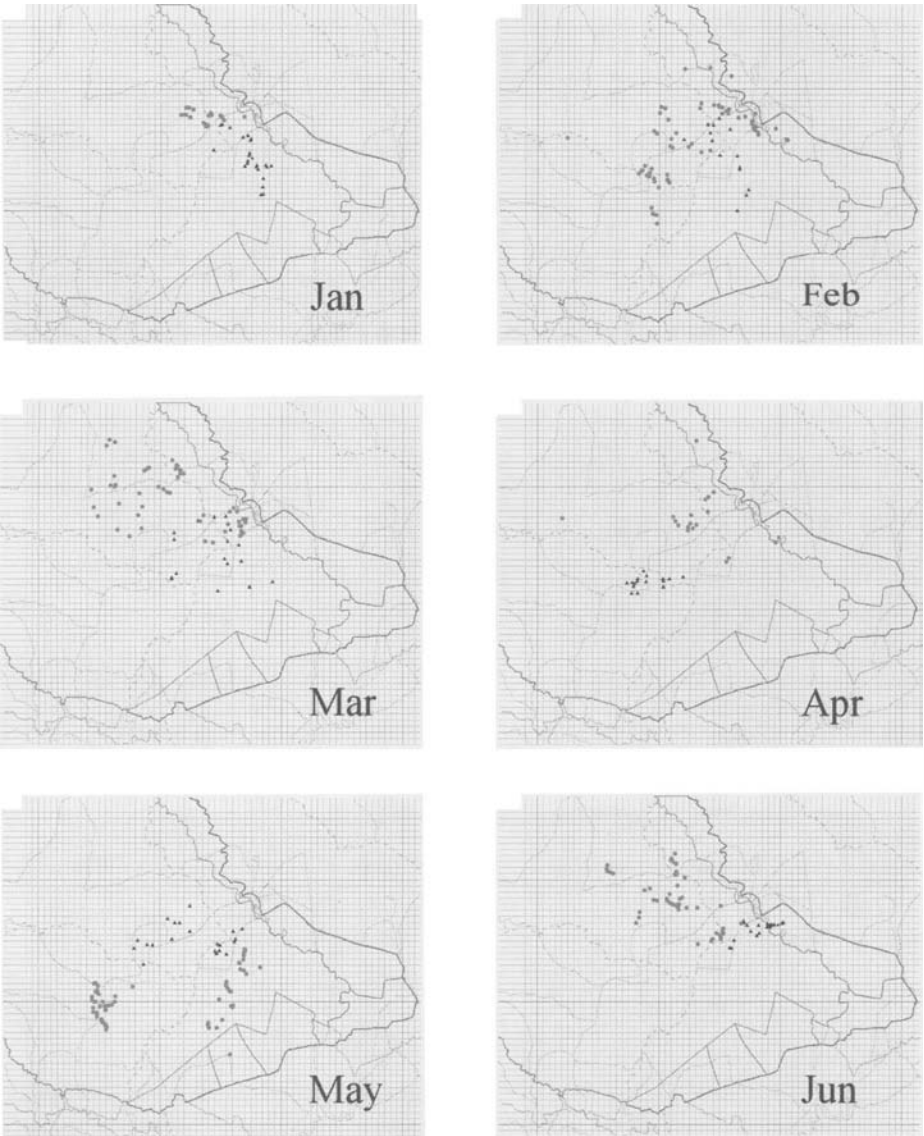


Figure 1. Range use during 2000 by chimpanzees and gorillas in the Ruhija study area. Black triangles indicate GPS locations for gorilla nest sites; grey circles indicate the locations for chimpanzee nests.

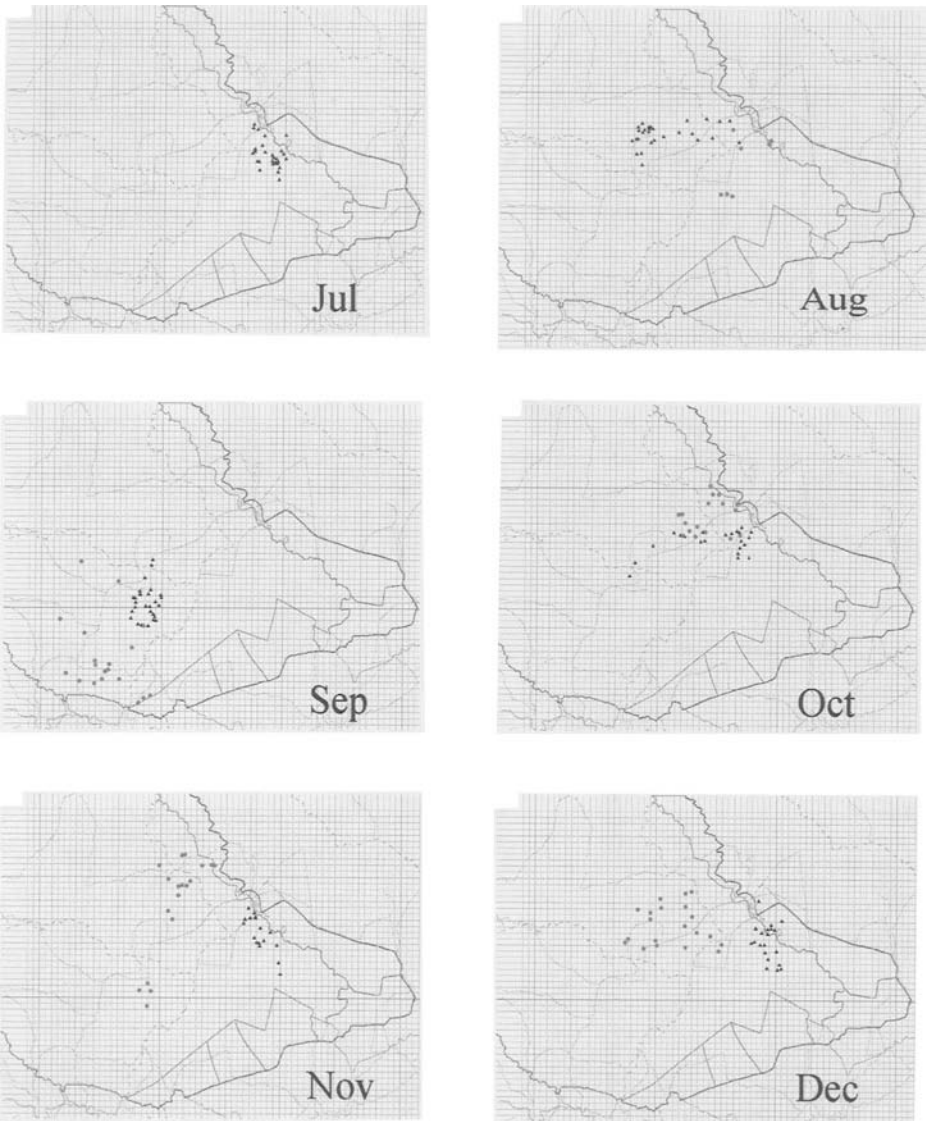
Nkurunungi, 2003). Monthly presence of chimpanzee activity was, however, generally to the east or south of gorilla activity (Figure 2A and B).

The Ruhija chimpanzee community ranges over roughly the same area as the Kyagurilo gorilla group, although DRL of the gorilla group (~ 800 m) is shorter than that of most chimpanzee parties (>1.0 km; Stanford & Nkurunungi, 2003). Chimpanzee ranging patterns as recorded during 2000 should be regarded as the minimum known range area for the Ruhija community. Because of the fission–fusion community structure, individuals and small parties frequently go undetected and may travel well outside the known range of the community. In addition, some nests recorded within the known community range could have been made by members of neighboring communities rather than the study community. However, the likelihood of serious



(A)

Figure 2. (A) Monthly range use by chimpanzees and gorillas in the Ruhija study area, based on GPS data (January–June 2000). (B) Monthly range use by chimpanzees and gorillas in the Ruhija study area, based on GPS data. (July–December 2000). Black triangles indicate GPS locations for gorilla nest sites; grey circles indicate the locations for chimpanzee nests.



(B)

Figure 2. (Continued)

Location	Nyarucundura (17 km ²)			Other (4 km ²)	Kagyembagyembe (13 km ²)			
9883000	0.6	1.7	2	1.1	3.3	2.9	0.2	
9882000	0.9	2.2	2.9	3.3	5.5	12.7	7.2	
9881000	1.5	5.5	1.3	1.7	2.9	8.7	7	
9880000	5.2	3.7	1.3	1.1	1.3	1.5	2.6	
9879000	3.1	4.6	0.6			0.2		
9878000	0.6	0.4						
9876000								
Coordinates	803000	804000	805000	806000	807000	808000	809000	810000

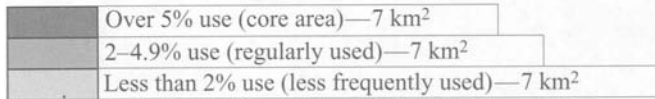


Figure 3. Differential use of 1-km² quadrats over a 2-year period ($n = 544$ GPS nest/feeding sites). The values shown are percent frequencies of nest/feeding sites for each quadrat.

error in this regard is low owing to the highly territorial nature of chimpanzee communities.

Figure 3 shows the distribution of gorilla nest/feeding sites during 1997–2000. The gorillas were recorded 264 times in 2000, and in 37 quadrats total (= 37 km² from 1997 to 2000). By connecting the peripheral points and assuming that all complete quadrats within the boundary were 1 km² each and all the incomplete quadrats were halved, the total area was 26 km², close to that determined from Arcview. Thus from quadrat estimates, the home range was between 26 and 37 km², which is similar to range estimates obtained using Arcview computations (25.8 and 34.7 km²). Using the same assumptions for Ruhija chimpanzees, we estimate a minimum home range size during 2000 of 17 km².

Both ape species nested on the ground as well as in trees. Unlike gorillas in the nearby Virungas Volcanoes, Bwindi gorillas sometimes nest in trees. When

gorillas nested in trees, they nearly always used the same species, *Alcornea floribunda* (Euphorbiaceae). *A. floribunda* is a common understory tree species in Bwindi. These nests were easily identified by their large size and by the presence of gorilla dung in and around them. Nkurunungi (2003) found that approximately 22% of all gorilla nests during 1997–2000 were made in trees.

Chimpanzees nested in trees most (but not all) nights during 2000, but their use of nest trees was more varied. In the northern sector of Bwindi, outside the study area, approximately 6% of all chimpanzee nests were recorded on the ground. These appeared to be night nests rather than day nests, according to the style of construction (Maughn & Stanford, in press). Within the study area, ground nests were found only 10 times in 2000. Whether ground nesting is an adaptation to local conditions or a cultural tradition as seen in many other chimpanzee behaviors, is unknown.

DISCUSSION

The total home range size measured in this study was larger relative that for groups in the Virungas (Fossey, 1974; Fossey & Harcourt, 1977; Vedder, 1984; McNeilage, 1995). However, it appeared to be larger than for *G. g. gorilla* (Jones & Sabater-Pi, 1971; Remis, 1997; Tutin, 1996) and comparable to *G. b. graueri* at Kahuzi-Biega (Casmir and Butenandt, 1973; Yamagiwa *et al.* 1994). Even within Bwindi, there were variations in home range size. Achoka (1993), using a different method and a limited number of nest sites, estimated only slightly smaller home range sizes for two other groups in Bwindi.

These results are not surprising given that one of the factors that influence home range size is the availability and distribution of food resources. In Bwindi, fruit trees and food resources are patchily distributed compared to the more uniform habitat in the Virungas, where preferred foods are abundant and widely distributed (Watts, 1984). This supports the observation that frugivores tend to have larger home ranges than folivores (Milton & May, 1976). Virunga gorillas are strict folivores, presumably because they inhabit an area lacking in fruit tree species compared to Bwindi.

There are likely costs involved for gorillas traveling long distances in search of fruit. First, gorillas are large-bodied animals, and using a large range would be energetically costly. They may therefore eat nonherbaceous foods, which are more readily available and less temporarily distributed, as an adjustment to fruit scarcity. Second, a larger home range could influence the rates of encounter with other groups, perhaps leading to intergroup male agonism. For example,

Watts (1998b) argued that close proximity to other social units can strongly affect short-term movements in mountain gorillas and a group moved farther on days of and after interactions with other groups or lone males than on other days. Although gorilla encounters may lead to female transfer, they often result in fierce agonistic behaviors. Evidence of fights has been observed between groups in this area. There is also a risk of male infanticide from other groups when groups interact.

Finally, longer DRL may lead to competition with other gorillas or other animals for food. There are other groups of wild gorillas in the study site, which are the most likely intraspecific competitors. Chimpanzees are also possible food competitors, which show considerable dietary overlap with gorillas (Stanford & Nkurunungi, 2003). Our research has shown substantial dietary overlap between the two ape species (Stanford & Nkurunungi, 2003), and at least one bout of aggressive interspecific food competition.

Watts (1998b) and Yamagiwa *et al.* (1996) point out that even where gorilla groups and chimpanzee communities share the same area of forest, the two species exploit resources differently. Gorilla groups tend to use small parts of their home range each month, covering the entire home range only over the course of an annual cycle. Chimpanzees, on the other hand, forage widely for fruit on a daily basis, covering large portions of their home range in a shorter time period. When important chimpanzee foods are scarce, the community disperses into small subgroups, with larger foraging parties forming mainly when ripe fruit is abundant (Goodall, 1986). These divergent foraging strategies may also allow the two species to avoid feeding competition for fruit when sympatric. It has been hypothesized that since there is a greater seasonal abundance of fruit in Bwindi than in the Virungas (Butynski, 1984), Bwindi gorillas should be more frugivorous, and should travel further each day, than those in the Virungas. Since fruit resources tend to be more widely and ephemerally distributed, gorillas in Bwindi are expected to respond to fruit in their diet by increasing their home range size and daily ranging behavior. Consequently, gorillas at Bwindi are expected to have bigger home ranges, longer day ranges than their Virunga relatives. Achoka (1993) and Sarmiento *et al.* (1996) suggested that gorillas in Bwindi exhibited larger home ranges and traveled farther than their counterpart subspecies in the neighboring Virungas. Bwindi gorillas, however, have DRLs only slightly longer (800 m; Goldsmith *et al.* 1999; Nkurunungi, 2003) than those in the Virungas, despite a seasonal pattern of foraging for ripe fruit. It is not clear why Bwindi gorillas do not travel

longer distances each day than they do. Goldsmith and Moles (2003) found no correlation between terrain and travel distance, but their study was of gorillas that traveled outside the forest for lengthy periods and reflected abnormal, human-influenced foraging patterns and DRLs.

A future goal of the study made possible by the use of GIS is to test whether the range use pattern of one ape species influenced that of the other. This should be possible once a larger database of GPS readings over multiple seasons and annual cycles is available. For example, range use of areas within the overall home range by one ape might be nonrandomly correlated, either positively or negatively, with range use of the same area by the other species. A positive correlation in use of an area would suggest that one species was drawn to the same food resource and was attracted to the area by the presence of the other, perhaps through detection of food calls. A negative correlation would imply avoidance, either mutual or by one species of the other. Range use patterns may detect patterns of the relationship between the two species that dietary studies do not, provided a fine-grained level of detail were available.

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