



Behavioral Ecology of Sympatric Chimpanzees and Gorillas in Bwindi Impenetrable National Park, Uganda: Diet

Craig B. Stanford¹ and J. Bosco Nkurunungi²

Received March 29, 2002; revision June 17, 2002; accepted January 22, 2003

*Via a field study of chimpanzees (*Pan troglodytes schweinfurthii*) and gorillas (*Gorilla gorilla beringei*) in Bwindi Impenetrable National Park, Uganda, we found that their diets are seasonally similar, but diverge during lean seasons. Bwindi chimpanzees fed heavily on fruits of *Ficus* sp., which were largely ignored by the gorillas. Bwindi gorilla diet was overall more folivorous than chimpanzee diet, but was markedly more frugivorous than that of gorillas in the nearby Virunga Volcanoes. During 4 mo of the year Bwindi gorilla diet included more food species than that of the chimpanzees. Three factors in particular—seasonal consumption of fibrous foods by gorillas, interspecific differences in preferred fruit species, and meat consumption by chimpanzees—contributed to dietary divergence between the two species. When feeding on fruits, gorillas ate *Myrianthus holstii* more frequently than chimpanzees did, while chimpanzees included more figs in their annual diet. Chimpanzee diet included meat of duikers and monkeys; gorilla frequently consumed decaying wood.*

KEY WORDS: Chimpanzees, gorillas, sympatry, diet, *Pan troglodytes*, *Gorilla gorilla*.

¹Jane Goodall Research Center, Department of Anthropology, University of Southern California, Los Angeles, CA 90089-0032; e-mail: stanford@usc.edu.

²Department of Zoology, Makerere University, Kampala, Uganda; e-mail: nkurunungi@yahoo.com.

INTRODUCTION

The behavioral ecology of sympatric nonhuman primates offers important information about their evolution, since aspects of specific diets, foraging strategies, and grouping patterns can be molded by ecological competitors (Terborgh, 1983: New World Monkeys; Gautier-Hion, 1983: Old World Monkeys; Yamagiwa *et al.*, 1996: African apes). Chimpanzees and gorillas are closely related great apes that are marked by similar genetically (Gagneux *et al.*, 1996), morphologically (Shea, 1983), and physiologically (Chivers and Hladik, 1984; Milton, 1984). However, socioecologically, they differ in important ways: gorillas live in cohesive groups (Watts, 1996) while chimpanzees live in fission-fusion communities (Goodall, 1986).

Few researchers have examined the behavioral ecology of sympatric chimpanzees and gorillas, and their studies all involved lowland gorillas. Jones and Sabater-Pi (1971) reported that chimpanzees in Equatorial Guinea were arboreal frugivores, while sympatric gorillas were terrestrial folivores, though they collected no systematic diet data. Tutin and Fernandez, 1985, 1993) and Williamson *et al.* (1990) conducted a more detailed ecological study of chimpanzee/gorilla sympatry in the Lopé Reserve in Gabon. Lopé gorilla diet was much closer to that of chimpanzees than to that of Virunga gorillas (Rogers *et al.*, 1990; Tutin and Fernandez, 1993). At Lopé, *ca.* 60–80% of food in chimpanzee and gorilla diets were eaten by both species (Williamson *et al.*, 1990; Tutin and Fernandez, 1993). Diets diverged most at times of fruit scarcity; gorillas ate more terrestrial herbaceous vegetation (THV), while chimpanzees continued to forage extensively for ripe fruit (Williamson *et al.*, 1990).

Research on sympatric lowland gorillas and chimpanzees in the Nouabalé-Ndoki forest of the Congo and Central African Republic revealed similar patterns of resource use. Ndoki gorilla are more highly frugivorous than any other known population (Kuroda, 1992; Nishihara, 1995); their annual diet consisted of >63% fruit. Dietary overlap with chimpanzees was even greater than at Lopé (Kuroda *et al.*, 1996). Ndoki gorillas made extensive year-round use of swamp forest (Nishihara, 1995) and fed in fig trees in proximity to chimpanzees during times of fruit scarcity (Suzuki and Nishihara, 1992).

Graueri gorillas (*Gorilla gorilla graueri*) and chimpanzees are sympatric in Kahuzi-Biega National Park in eastern Democratic Republic of Congo, (Yamagiwa *et al.*, 1994, 1996). Gorillas occur at higher density than chimpanzees, possibly related to the chimpanzee frugivorous diet. Yamagiwa *et al.* (1996) found that Kahuzi gorillas fed on more species of fruit than chimpanzees did, and the two apes ate many of the same fruit species but at

different times of year. The two species cofed on ≥ 4 important fruit species. The Kahuzi gorilla population is intermediate between western and mountain gorilla populations in degree of frugivory.

Gorillas in Bwindi Impenetrable National Park number *ca.* 300, or *ca.* $1/\text{km}^2$ (McNeilage *et al.*, 1998). Mitochondrial DNA studies showed them to be virtually indistinguishable from their sister population in the Virunga Volcanoes (Garner and Ryder, 1996; Jensen-Seaman and Kidd, 2001) with which they occupied continuous forest until 400-500 years ago (Hamilton *et al.*, 1986; Stanford, 2001a). Very little was known about the Bwindi chimpanzee population before our study.

We report on the diet of Bwindi gorillas and chimpanzees. We also discuss implications of patterns of resource use for strategies of their co-existence.

METHODS

The study area covers *ca.* 25 km^2 of afromontane forest in the Ruhija section of Bwindi Impenetrable National Park in southwestern Uganda (from *ca.* $0^\circ 53'$ to $1^\circ 08'$ South and $29^\circ 35'$ to $29^\circ 50'$ East). The study site is rugged, wet terrain, with an elevational range of 2000–2300 m. The forest is quite heterogeneous, with ≥ 163 tree species (Butynski, 1984). Bwindi comprises a complex floristic composition that includes 8 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 $>50\%$ of gorilla habitat is bamboo forest (Bitariho, 1999), the bamboo zone in Bwindi covers $\leq 2\%$ 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 to 2400 mm (Butynski, 1984), and the climate is characterized by 2 dry seasons lasting from about May to July and from late December to February.

Research on Bwindi chimpanzee-gorilla sympatry began in late 1996 and is ongoing. Until 1999, there were 2 research 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. Our data is from Ruhija between January and December, 2000.

The study populations are the Ruhija chimpanzee community and a sympatric gorilla group, the habituated Kyagurilo research group. Nkurunungi and field assistants have studied the gorilla group since 1997.

They are habituated and individually identified. We collected both direct observational and indirect data. During most of the study period, the group comprised 13 individuals (1 silverback, 1 blackback, 5 adult females, 6 immatures) and was monitored daily by research staff of the Institute of Tropical Forest Conservation. The Ruhija chimpanzee community is not habituated to close approach, but many of its members tolerate approach by observers to ≤ 25 m when feeding in trees. The community comprises ≥ 26 individuals, including ≥ 5 adult males whose identities and dominance ranks are known. Stanford 3 field assistants collected data on the Ruhija community.

Our quantitative diet data is based on fecal analysis augmented by observations, for instance, ingestion of wood by gorillas and of bees and honey by chimpanzees. Because we tracked the gorillas almost daily, sampling their diet via fecal collection was more easily achieved than for chimpanzees, whose fresh dung we collected near feeding and nesting trees in the home range of the Ruhija community. Fecal samples occur near chimpanzee feeding and nesting trees and in and near gorilla nests. Fresh dung of the two species is easily distinguished by size and odor. We washed the samples in 1 mm mesh sieves, after which a local field assistant, who has extensive experience in plant identification, manually searched for fruit, seeds, leaves, flowers of some species, plus nonplant items such as bone, wood and insects. We used a 4-point scale of abundance and distinguished fiber from fruit products. We recorded non-fruit plant remains that could not be identified as fiber. We listed the contents of each sample by abundance on the 4-point scale and by the percent fiber/non-fiber in order to correlate feeding patterns with phenological data. We also noted the presence of other foods, such as insects or vertebrate remains, and stones and wood. Afterward, we sun-dried and stored the samples in plastic bags for further analysis. This method has been used often in field studies of great apes (McGrew *et al.*, 1988; Nishihara, 1995; Remis, 1997); it allows identifications of at least some plants specifically.

We established phenology transects in the Ruhija study site in 1998. We tagged and monitored 176 trees > 10 cm dbh of 11 species (*Ficus sp.* (N = 9), *Chrysophyllum gorungosanum* (N = 22), *Olea capense* (N = 15), *Mystrocydon aethiopica* (N = 3), *Podocarpus milijianus* (N = 23), *Maesa lanceolata* (N = 19), *Xymalos monospora* (N = 10), *Myrianthus holstii* (N = 12), *Teclea nobilis* (N = 15), *Olinia usambarensis* (N = 23), *Syzigium guineense* (N = 25)), which are food species of chimpanzees or gorillas or both, on 2 separate transects that sampled the elevational gradient in the site. The transects are located along existing trails. Nkurunungi and field assistants monitored the 176 trees monthly, scoring fruit abundance via a 0–4 scale (Figure 1; Nkurunungi, 2003).

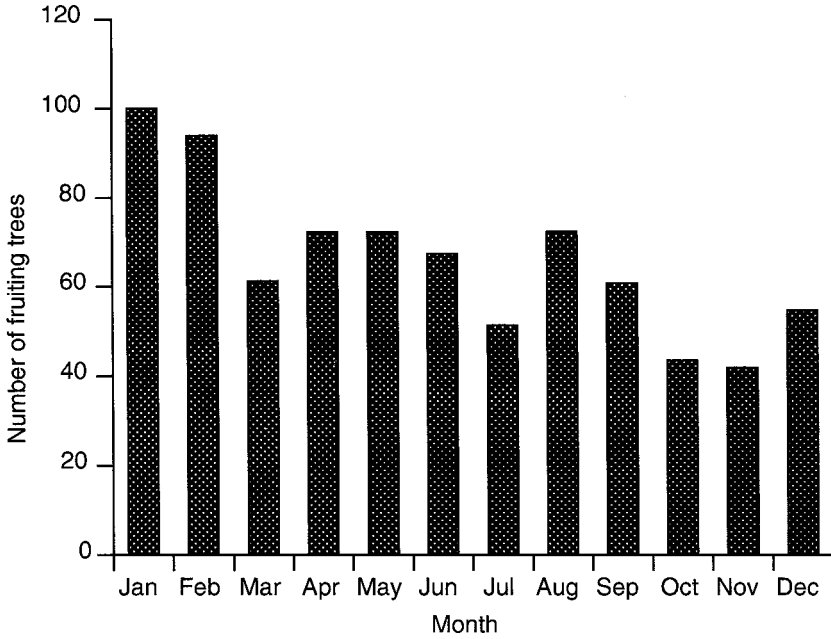


Fig. 1. Monthly variation in number of fruiting trees in phenology transects, January 1999–December 2000. N = 176.

RESULTS

We collected and analyzed 451 fecal samples during 2000; 264 from gorillas and 187 from chimpanzees (Table I). Gorillas fecal samples are from all months of the study period (monthly mean = 63.9, s.d. ± 20, range = 28–87, N = 767). Chimpanzee fecal samples are also from all months (monthly mean = 15.9, s.d. ± 9.1, range = 8–30). There is no statistically significant bias in the monthly variation in fecal sample size for either species (gorillas, Kruskal-Wallis one-way test, df = 11, U = 11.89, p > .05; chimpanzee; df = 11, U = 41.05, p > .1). The number of food species per dung sample show no significant positive correlation with the number of fecal samples collected

Table I. Fecal samples collected by month in 2000

Species	J	F	M	A	M	J	J	A	S	O	N	D
Chimpanzee	16	15	16	13	16	11	16	18	16	14	15	21
Gorilla	24	16	20	20	21	28	15	24	31	39	16	10

Note. N = 187 (chimpanzees), N = 264 (gorillas).

per month for either species (Spearman rank correlation; $N = 12$, $r_s = .222$, $p > .05$).

Chimpanzees ate 60 different plant parts of ≥ 32 species, representing 26 plant families. Gorillas ate 133 different plant parts of ≥ 96 species, representing 58 plant families (Table 1). In addition, chimpanzees ingested ≥ 2 vertebrate and 3 invertebrate species, and gorillas ingested stones and the dead wood of rotting logs.

Plant foods. Fruit is the most common class of food in the chimpanzee diet, with 30 species eaten. Based on the overall percentage of nonfiber versus fiber remains in Ruhija fecal samples, 64.6% of their diet was fruit. An additional 27.1% was fiber, including both leaves and pith of plants. Remains of ≥ 1 fruit species were in 184 of 187 (98.4%) Ruhija fecal samples. The mean number of different fruit species per fecal sample is 2.05 (range of monthly variation = 1–6 species per sample).

Ruhija chimpanzees ate a wide variety of fruit types, from tiny-seeded figs to composite fruits of *Myrianthus holstii* with large seeds. Some fruits, such as *Syzigium guineense*, are pulpy sweet fruits when ripe. Others, like *Chrysophyllum gorungosanum*, are latex-filled and appeared to pass largely intact through the gut. Figs were the most common fruits in chimpanzee samples, appearing in more than twice as many as the next most common fruit: *Drypetes gerrardii* (29% vs. 14%). Fig seeds were the most abundant seeds in 69% of chimpanzee fecal samples. Because of confusion over specific identification of figs among both botanists and local field assistants, who refer to multiple species and different fig sexes by the same name, we lumped all figs as *Ficus sp.* in our analysis. They include *Ficus natalensis*, *F. exasperata*, *F. sur* (formerly *F. capensis*) and *F. vallis-choudae*. Chimpanzees often ate figs while standing bipedally on tree limbs (Stanford, 2002).

Diet and Food Availability

Phenological data showed that important food species of both chimpanzees and gorillas fruited every month during the study period (Figure 1). The percentage of transect trees bearing ripe fruit varied between 23 and 57% per mo. Monthly percentage of individual trees with leaf flush varied between 10% and 38%.

The number of fruit species in chimpanzee samples per month varied seasonally (Figure 2), as did the monthly fiber score (Figure 3). Monthly fiber scores for gorillas also varied seasonally, and the relative amount of fruit they consumed, based on fruit-fiber abundance estimates, is positively correlated with the mean number of trees that were in fruit in the phenology transects (see Figs. 1 and 2; Spearman rank correlation $N = 12$, $r_s = .702$,

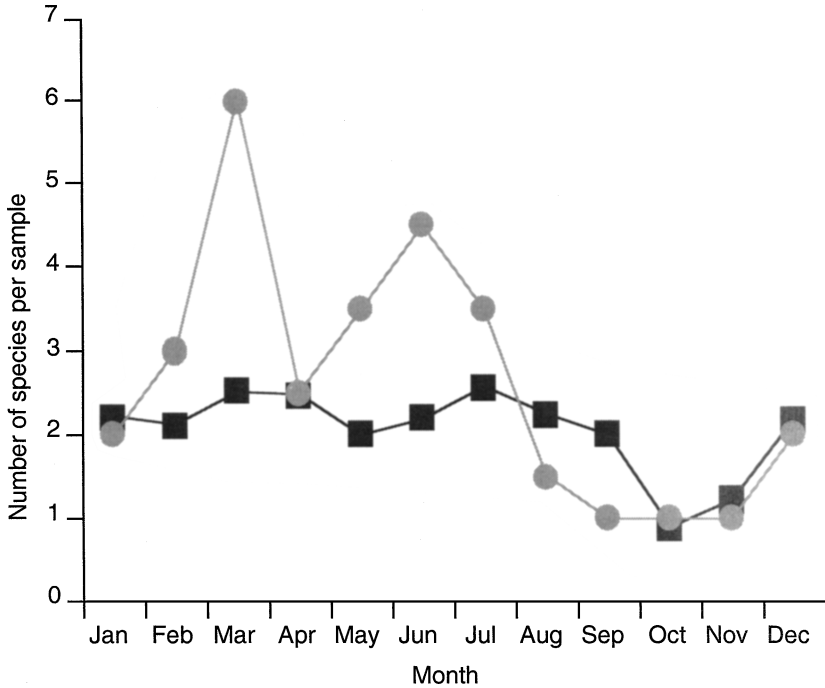


Fig. 2. Mean number of fruit species in fecal samples of chimpanzees and gorillas in each month, January–December 2000. Squares = chimpanzees; circles = gorillas.

$p < .01$). There is no positive correlation between available fruit and fruit consumed by chimpanzees ($N = 12, r_s = .189, p > .10$). Some trees of *Ficus sp.* and *Myrianthus holstii* were in fruit in all months of the year, and they were the 2 most important chimpanzee plant foods. Other important food species, such as *Chrysophyllum sp.*, are highly seasonal and exert a strong influence on ranging patterns (Nkurunungi and Stanford, unpublished data). At least one fruit species *Podocarpus milijianus* did not fruit during the study period, built it fruited heavily the following year for the first time in 4 years.

The nonfruit part of the plant diet is more difficult to identify. Chimpanzees ate substantial quantities of terrestrial herbaceous vegetation (THV), but we lumped it as fiber along with leafy material in our analysis. Gorillas ate more plant species than chimpanzees did (Table II), which result may be due partly to the fact that Nkurunungis detailed analysis of Ruhija vegetation ecology allowed field assistants to identify many herbaceous species generically or specifically.

The gorilla diet was 24.6% fruit, based on the overall percentage of food remains by estimated volume on the 4-point abundance scale. An additional

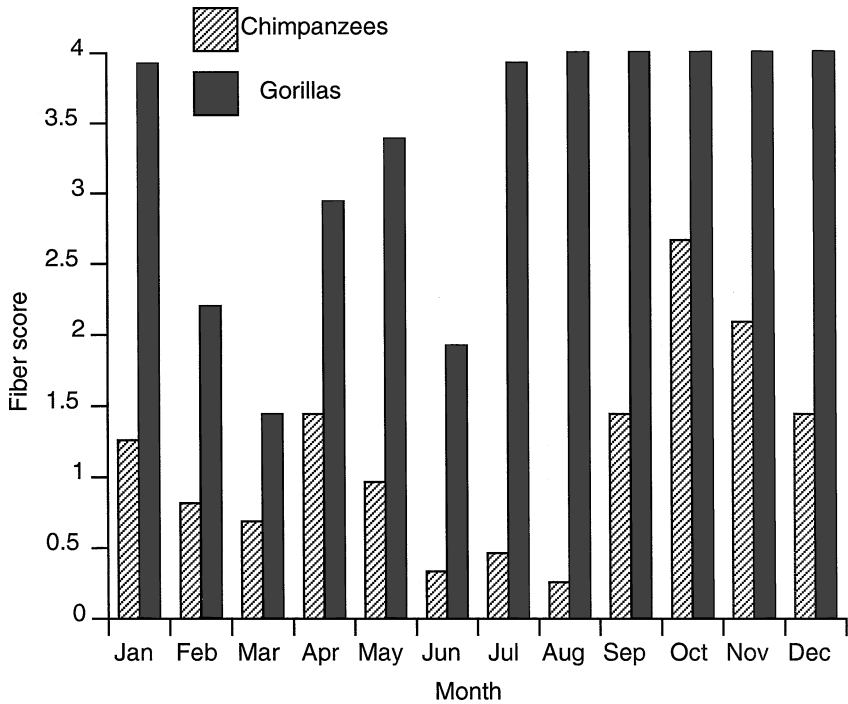


Fig. 3. Monthly variation in fiber score of chimpanzee and gorilla fecal samples, January–December 2000.

75.4% (based on the 4-point abundance scale) contained fiber, including both leaves and herbaceous plants, and 21% contained wood particles. Remains of ≥ 1 fruit species were in 47.2% of 264 samples. The mean number of different fruit species per gorilla fecal sample is 2.2 (0–6 species per month).

Non-plant foods. In addition to plant foods, 3% of chimpanzee samples contained apian remains, 4.3% contained mammalian bones or skin (duiker antelope, probably *Cephalophus nigrifrons*, and monkeys, probably *Cercopithecus mitis mitis* or *C. lhoesti* or both) and 1.8% contained remnants of driver ants (*Dorylus sp.*). Chimpanzees ate honey and bee larvae of ≥ 2 species: *Apis mellifera* and *Meliponula brocandei*. They used different tools to extract the honey of each species (Stanford *et al.*, 2000).

Bwindi gorillas consumed ≥ 2 nonplant items, frequently small stones (≤ 0.5 cm diameter). Whether they ingested them incidentally while eating plant foods or soil or sought them actively is unknown. Gorillas foraged for wood from rotting logs, traces of which occurred in 19.4% of all samples.

Table II. Species of plants eaten by Bwindi chimpanzees and gorillas

Species/family	Eaten	by ?	Pulp	Seed	Leaf	Flower	Pith
<i>Acalypha agrogyna</i> (Tiliaceae)	G						x
<i>Adenia</i> sp. (Passifloraceae)	G				x		
<i>Allophylus macrobotrys</i> (Sapindaceae)	G	x			x		
<i>Allophyllus</i> sp. (Sapindaceae)	G	x					
<i>Alchornea hirtella</i> (Euphorbiaceae)	G/C	x			x		
<i>Arundinaria alpina</i> (Poaceae)	G	x			x		x
<i>Basella alba</i> (Basellaceae)	G				x		
<i>Brillantsia</i> sp. (Acanthaceae)	G				x	x	
<i>Carapa grandiflora</i> (Meliaceae)	C	x			x		
<i>Cardus</i> sp. (Compositae)	G/C				x	x	
<i>Carpodinus glabra</i> (Apocynaceae)	G				x		
<i>Cassipourea</i> sp. (Rubiaceae)	G/C				x	wood	
<i>Chrysophyllum gorungosanum</i> (Sapotaceae)	G/C	x	x				
<i>Chrysophyllum albidum</i> (Sapotaceae)	G/C	x	x				
<i>Cissus</i> sp. (Vitaceae)	G				x		
<i>Clematis</i> sp. (Ranunculaceae)	G/C				x		
<i>Clerodendron</i> sp. (Verbenaceae)	G				x		
<i>Clutia abyssinica</i> (Euphorbiaceae)	G	x					
<i>Coccinia bateri</i> (Cucurbitaceae)	G				x		
<i>Coccinia mildbraedi</i> (Cucurbitaceae)	G	x			x		
<i>Crassocephalum manni</i> (Compositae)	G					x	
<i>Crassocephalum rubens</i> (Compositae)	G				x		x
<i>Cyantheae maniana</i> (Cyanthaceae)	G						x
<i>Cyperus</i> sp. (Cyperaceae)	G					x	
<i>Desmodium repandum</i> (Fabaceae)	G					x	wood
<i>Desmodium</i> sp. (Fabaceae)	G					x	x
<i>Diciliptera</i> sp. (Acanthaceae)	G				x		
<i>Dombeya goetzenii</i> (Sterculiaceae)	G				x		
<i>Drynaria volkensii</i> (Polypodiaceae)	G						x
<i>Drypetes gerrardii</i> (Euphorbiaceae)	G/C	x					
<i>Englerina</i> sp. (Loranthaceae)	G		x		x		
<i>Faurea saligna</i> (Protaceae)	G						wood
<i>Ficus</i> sp. (Moraceae)	G/C	x	x		x		bark
<i>Ficalhoa laurifolia</i> (Theaceae)	G						wood
<i>Fleurya ovalifolia</i> (Urticaceae)	G				x		
<i>Galiniera coffeioides</i> (Rubiaceae)	G	x					
<i>Galium</i> sp. (Rubiaceae)	G				x		x
<i>Ganoderma australe</i> (Polyporaceae)	G				fungus		
<i>Geranium</i> sp. (Geraniaceae)	G				x		x
<i>Govania longispicata</i> (Rhaminaceae)	G				x		
<i>Gynura</i> sp. (Asteraceae)	G				x		
<i>Helichrysum</i> sp. (Compositae)	G				x		
<i>Ipomea</i> sp. (Convolvulaceae)	G				x	x	bark
<i>Jasminium eminii</i> (Oleaceae)	G/C				x		
<i>Justicia</i> sp. (Acanthaceae)	G				x		
<i>Kosteletzkya grantii</i> (Malvaceae)	G				x	x	
<i>Landolphia buchani</i> (Apocynaceae)	G				x		
<i>Langenaria</i> sp. (Cucurbitaceae)	G				x		
<i>Laportea</i> sp. (Urticaceae)	G				x		
<i>Loranthus</i> sp. (Loranthaceae)	G				x	x	
<i>Maesa lanceolata</i> (Myrsinaceae)	G/C	x	x				
<i>Maytenus acuminata</i> (Rhizophoraceae)	G						wood

Table II. (Continued)

Species/family	Eaten	by ?	Pulp	Seed	Leaf	Flower	Pith
<i>Mimulopsis</i> sp. (Acanthaceae)	G/C				x		
<i>Mormodica calantha</i> (Cucurbitaceae)	G/C	x			x		
<i>Mormodica foetida</i> (Cucurbitaceae)	G/C	x			x		
<i>Myrianthus holstii</i> (Moraceae)	G/C	x		x		bark	
<i>Myrica salicifolia</i> (Myricaceae)	G					wood	
<i>Mystroxyton aethiopica</i> (Celastraceae)	G/C	x		x		wood	
<i>Olea capense</i> (Oleaceae)	G/C	x		x	x	wood	
<i>Olinia usambarensis</i> (Olinaceae)	G/C	x		x		wood	
<i>Parinari holstii</i> (Chrysobalanaceae)	G/C	x		x			
<i>Piper capense</i> (Piperaceae)	G						x
<i>Pleirpoca linearifolia</i> (Asclepidaceae)	G				x		
<i>Podocarpus milinjanus</i> (Podocarpaceae)	G/C	x					
<i>Prena angolensis</i> (Verbenaceae)	G					wood	
<i>Prunus africana</i> (Rosaceae)	G/C				x		
<i>Psychotria mahonii</i> (Rubiaceae)	G					wood	
<i>Pycnostachys elliotii</i> (Labiatae)	G				x		
<i>Rapanea rhodrodites</i> (Celastraceae)	G				x	wood	
<i>Rawsonia lucida</i> (Flaucourtaceae)	G/C	x					
<i>Rubia cordifolia</i> (Leguminosae)	G/C				x		x
<i>Rubus</i> sp. (Rosaceae)	G/C	x			x		
<i>Rumex bequertii</i> (Polygonaceae)	G				x		x
<i>Rumex</i> sp. (Polygonaceae)	G				x		
<i>Rhytidia beninensis</i> (Rubiaceae)	G				x		
<i>Rhytidia</i> sp. (Rubiaceae)	G	x			x		
<i>Rhytidia ruenzoriensis</i> (Rubiaceae)	G/C	x					
<i>Salacia elegans</i> (Celastraceae)	G	x			x		
<i>Sapium ellipticum</i> (Euphorbiaceae)	G/C	x				wood	
<i>Schefflera barteri</i> (Araliaceae)	G				x		
<i>Sellaginera</i> sp. (Sellaginaceae)	G				x		
<i>Senecio</i> sp. (Asteraceae)	G				x		
<i>Smilax anceps</i> (Smilacaceae)	G	x			x		
<i>Solanum welwitschii</i> (Solanaceae)	G			x			
<i>Strombosia</i> sp. (Olacaceae)	C	x		x			
<i>Symphonia globulifera</i> (Guttiferaceae)	G/C	x		x			
<i>Syzigium cordatum</i> (Myrtaceae)	G/C	x					
<i>Syzigium guineense</i> (Myrtaceae)	G/C	x		x		wood	
<i>Teclea nobilis</i> (Rutaceae)	G/C	x		x			
<i>Tetrorchidium</i> sp. (Euphorbiaceae)	G				x		
<i>Triumphetta rhomboidea</i> (Tiliaceae)	G				x		
<i>Triumphetta</i> sp. (Tiliaceae)	G/C				x		
<i>Urera</i> sp. (Urticaceae)	G				x	bark	
<i>Vernonia calongensis</i> (Compositae)	G				x	bark	
<i>Vernonia kirungae</i> (Compositae)	G						x
<i>Vernonia pteropoda</i> (Compositae)	G					bark	
<i>Vernonia</i> sp. (Compositae)	G/C						x
<i>Xymalos monspora</i> (Apocynaceae)	G/C	x		x	x		

Note. All bark/dead wood feeding records are for gorillas only; all other plant parts are shared by both species where indicated.

Dietary Overlap Between Bwindi Chimpanzees and Gorillas

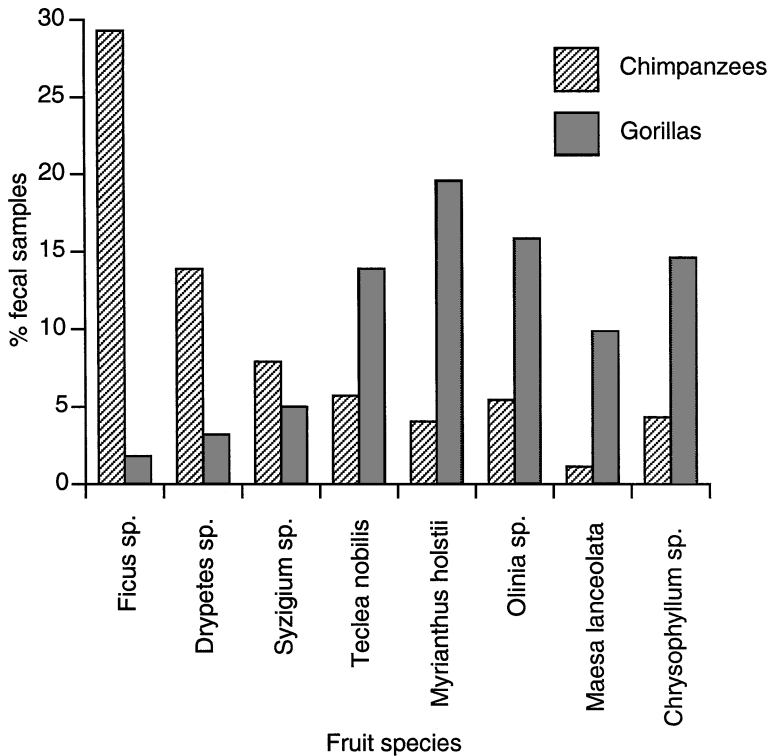
Overall gorillas used significantly more fruit species than chimpanzees did (Figure 2). During both dry seasons (February–March and May–July), gorillas included significantly more fruit species in their diet than chimpanzees did (Mann-Whitney U-test, $U = 5,433$, $p < .01$). During the rest of the year, gorilla and chimpanzee diets included statistically similar numbers of plant food species (Mann-Whitney U-test, $U = 875.5$, $p > .05$) and closely resembled each other for much of the annual cycle. All chimpanzee fecal samples contained ≥ 1 fruit species in every month of the year except October and December. All gorilla fecal samples also contained ≥ 1 fruit species, except from August to December, when fruit in the diet dropped markedly to $< 10\%$ of samples with evidence of frugivory.

Gorillas and chimpanzees often fed on the same plant species in a given month. There is a positive correlation between the presence of fruit remains of the same fruit species in their dung. (Spearman rank correlation, $N = 12$, $r_s = .805$, $p > .01$). When chimpanzees fed on their most important plant food, fruits of *Ficus sp.*, gorillas were significantly more likely to be feeding on the same plants ($r^2 = .565$, $p < .01$).

The amount of fiber ingested also varied seasonally (Figure 3); fiber abundance scores in both gorilla and chimpanzee dung showed a significant negative correlation with fruit abundance score (gorillas; Spearman rank correlation, $N = 12$, $r_s = .607$, $p < .05$; chimpanzees; $N = 12$, $r_s = .769$, $p < .001$). Chimpanzees ingested substantial amounts of fiber only during September to January. From June to August, chimpanzees ate almost no fiber. Gorillas consumed large quantities of fibrous foods in all months, even when their diet was more frugivorous. Fiber consumption scores for gorillas show a significant negative correlation with the mean number of fruiting trees in the phenology transects (Spearman rank correlation, $N = 12$, $r_s = .539$, $p > .05$).

Fruit availability peaked significantly in January and February (Kruskal Wallis test, $df = 11$, $U = 121.5$, $p > .05$, but except for a marked increase in frugivory in February by gorillas, neither species seemed to respond quickly to the increased supply of fruit in their habitat. Interannual variation in fruit supply appeared to exert a major influence on feeding patterns, as well as ranging patterns, by both chimpanzees and gorillas, though the variation was difficult to quantify.

An examination of specific tree species on which chimpanzees and gorillas fed reveals the divergence in their diets in the same habitat (Figure 4). The most important food species in the chimpanzee diet is *Ficus sp.*, seeds of which were present in 29% of their fecal samples. Conversely only *ca.* 2% of gorilla fecal samples contained *Ficus sp.* Chimpanzees also fed heavily on



Percentage of fecal samples containing major fruit species in diets of both chimpanzees and gorillas. N = 353 (chimpanzees), 543 (gorillas).

Fig. 4. Percentage of fecal samples containing important fruit species in chimpanzee and gorilla diets January–December 2000. N = 264 (gorillas), 187 (chimpanzees).

the fruits of *Drypetes gerrardii*, an understory tree that is one of the most abundant trees in the study site. *Drypetes gerrardii* is also the favored nesting tree of the chimpanzees; they chose it for night nests significantly more frequently than its availability would predict (Stanford, 2001b).

The most important gorilla fruit species was *Myrianthus holstii*, an abundant riparian species that bears very large (≤ 0.5 kg) fruits. It was present in 20% of gorilla fecal samples. Although other species of *Myrianthus* that also bear large fruits are highly sought by chimpanzee at other study sites, e.g. Gombe (Goodall, 1986), they appeared in only 4% of Ruhija chimpanzee fecal samples containing seeds of *Myrianthus holstii*. Other key gorilla fruits are

Olinia usambarensis, *Maesa lanceolata*, and *Chrysophyllum gorungosanum*. None of them occurred in $\geq 5\%$ of chimpanzee fecal samples in 2000, though in 1997 *C. gorungosanum* fruited heavily and its seeds were in nearly all fecal samples of both chimpanzees and gorillas.

We cannot systematically address whether Bwindi gorillas and chimpanzees engage in contest competition over food. One of two interspecific encounters that we observed at feeding sites was aggressive:

In April, 2002, a party of 9 chimpanzees of the Ruhija community were feeding in the crown of a large *Chrysophyllum gorungosanum*, when the research gorilla group arrived and began feeding on fallen fruits on the ground. Thirty min later an adult female gorilla and the silverback climbed partway up the tree to ≤ 5 m of the chimpanzees. Two male chimpanzees responded to their approach by descending toward the gorillas and engaging in prolonged displays in the tree crown that appeared to be directed at the gorillas. This interaction continued intermittently for *ca.* 1 h, until the approach of a second group of field assistants caused them to flee. Immediately, the gorillas climbed into the tree crown and began to feed on the fruits.

In May 2001, an unhabituated gorilla group entered a large *Ficus sp.* in which ≥ 15 members of the Ruhija chimpanzee community were feeding. During a 15-min encounter, the gorillas, including a silverback, approached, sat, and fed ≤ 3 m of several adult male chimpanzees. No interaction occurred, and little obvious notice was paid by the chimpanzees to the gorillas as they approached and fed.

DISCUSSION

We found little evidence that feeding competition occurs between Bwindi chimpanzees and gorillas. In other studies, chimpanzee and gorilla diets have tended to converge during times of fruit abundance, and diverged during fruit scarcity (Tutin, 1996; Tutin and Fernandez, 1993). The two species sometimes share tree crowns, most often during times of fruit scarcity as well (Suzuki and Nishihara, 1992; Yamagiwa *et al.*, 1996). However, the aggressive interspecific encounter event in April, 2002, is clear, albeit anecdotal, evidence that contest competition occurs between them. Whether this was a rare event, or simply a rarely observed frequent one, is unknown. Future field observation should be able to address the occurrence and the importance of dietary overlap and the interspecific encounters that it causes.

Mountain gorillas in the Virunga Volcanoes are almost exclusively folivorous, choosing THV foods that tend to be widely, evenly distributed and

available throughout the year (Vedder, 1984; Watts, 1984). It appears that Virungas gorillas can satisfy their dietary requirements with minimal travel effort. However, in Bwindi, gorillas have access to ripe fruit that is seasonally abundant. Although they feed heavily on THV, Bwindi gorillas eat ripe fruit whenever it is available (Nkurunungi, 2003).

Watts (1991) and Yamagiwa *et al.* (1996) pointed 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. Conversely, chimpanzees 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 them to avoid feeding competition for fruit when sympatric. It is important to note that in spite of the greater reliance on fruit by Bwindi gorillas relative to their counterpart population in the Virungas, Bwindi gorilla mean daily path length is only *ca.* 100 m longer than that of the Virunga gorillas (Nkurunungi, 2002). This is a paradoxical finding given that elsewhere gorilla daily path length is positively correlated with the amount of fruit consumed (Remis, 1997; Goldsmith, 1999; Stanford, 2001a; Nkurunungi, 2003), and suggests that other factors, such as terrain, may affect daily path length.

An indication that chimpanzees and gorillas across Africa may be ecologically separated due to greater dependence of chimpanzees on fruit can be seen by comparing the effect of increasing elevation on the level of fruit consumption for each species in study sites of varying elevations (Figure 5). For gorillas, there is a statistically significant negative correlation between elevation and frugivory ($r^2 = .72, p < .01$). Gorillas living at the highest recorded elevations—the Virungas—eat almost no fruit, while lowland populations spend $\leq 50\%$ of their time eating fruit. However, no relationship between elevation and frugivory exists, for chimpanzee populations. Instead, chimpanzees eat mainly fruit at all study sites and apparently do not live in habitats that are fruit-poor.

Gorillas rely on THV as a lean season staple, or fallback food (Malenky *et al.*, 1994; Doran and McNeilage 1998), while chimpanzees apparently do not. However, at least one study (Wrangham *et al.*, 1991) showed that chimpanzee feeding on THV is negatively correlated with frugivory, suggesting that THV is a fallback food among chimpanzees also. We have no evidence of this for Bwindi chimpanzees, though our analyses of chimpanzee diet were limited by the lack of identification of herbaceous plant material. We have no nutritional information on the most important plant species. There

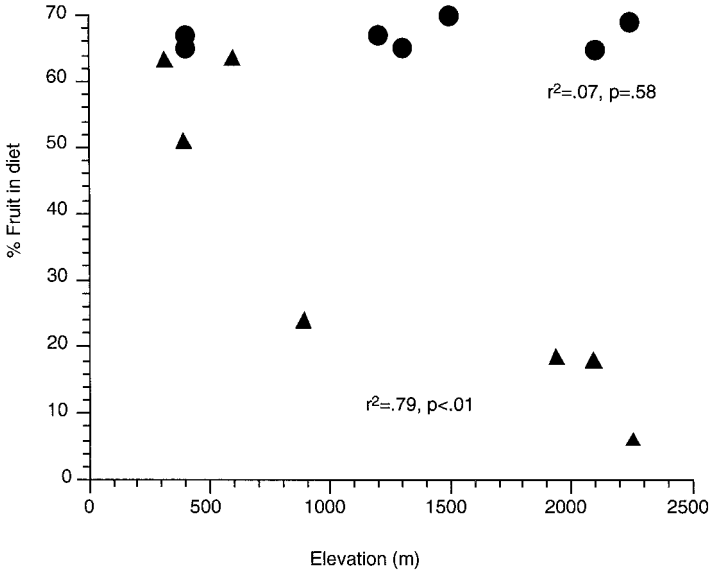


Fig. 5. Relationship between site elevation and importance of fruit in the diet (as percentage feeding time). Triangles = gorillas (Virungas, Watts 1996; Bwindi, this paper; Kahuzi-Biega, Yamagiwa *et al.*, 1996; Lopé, Tutin and Fernandez, 1993; Bai Houkou, Goldsmith, 1999; Ndoki, Kuroda *et al.*, 1996; Itebero, Mwanza *et al.*, 1988. Circles = chimpanzees (Gombe, Goodall, 1986; Kibale-Kanyawara, Wrangham *et al.*, 1993; Bwindi, this paper; Kahuzi-Biega, Yamagiwa *et al.*, 1996; Mahale, Nishida, 1990; Lopé, Tutin and Fernandez, 1993; Ndoki, Kuroda *et al.*, 1996).

has been a debate over whether gorillas seek fatty fruits (Calvert, 1985) or avoid them (Rogers *et al.*, 1990), and whether chimpanzees use figs as a preferred fruit source (Janzen, 1979) or a fallback food (Wrangham and Conklin, 1993). The debate over the value of figs rests on the relative nutritional versus harvesting-efficiency benefits of a diet that includes large quantities of figs. We cannot resolve these issues with the current data set, but as a demonstrably important aspect of ecological difference between gorillas and chimpanzees, it is a future goal of the project.

Although meat is a part of the diet of many other chimpanzee populations (Stanford, 1998), the population density of both monkeys and duiker in Ruhija is low (McNeilage *et al.*, 1998), and red colobus (*Colobus badius*), the main prey of chimpanzees elsewhere, are absent at Bwindi. Whether prey were captured alive or scavenged is not known. Montane chimpanzees in Kahuzi-Biega National Park, Democratic Republic of Congo, hunt for *Cercopithecus mitis* and duiker antelope (Basabose and Yamagiwa, 1997).

ACKNOWLEDGMENTS

We gratefully acknowledge the support of the Uganda Wildlife Authority, the Ugandan National Council for Science and Technology, and the Institute of Tropical Conservation and its staff. In particular, we thank Dr. Gilbert Isabirye-Basuta, Dr. Hannington Oryema-Origa, Dr. Eric Edroma, Caleb Mgambaneza, Mitchell Keiver, Dr. Richard Malenky, Chief Warden Keith Masana, Evarist Mbonigaba, Dr. Alastair McNeilage, Chief Warden Christopher Oreyema, Dr. Martha Robbins, Dr. Nancy Thompson-Handler, and Gervase Tumwebaze. For help in analyzing the data, we thank Terrelita Price, and for comments on the manuscript we are grateful to Dr. Nyuta Yamashita and two anonymous reviewers. We express our gratitude for the funding support of The Fulbright Foundation (C.I.E.S.), The L.S.B. Leakey Foundation, The National Geographic Society, The Wenner-Gren Foundation for Anthropological Research, and the Faculty Development Fund of the University of Southern California.

REFERENCES

- Basabose, K., and Yamagiwa, J. (1997). Predation on mammals by chimpanzees in the montane forest of Kahuzi, Zaïre. *Primates* 38(1): 45–55.
- Basabose, A. K., and Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: Influence of sympatric gorillas. *Int. J. Primatol.* 23(2): 263–282.
- Bitariho, R. (1999). *The abundance, distribution and use of montane bamboo in Bwindi Impenetrable and Mgahinga Gorilla National Parks, S.W. Uganda*. MSc dissertation, Makerere University, Kampala, Uganda.
- Butynski, T. M. (1984). Ecological survey of the Impenetrable (Bwindi) Forest, Uganda, and recommendations for its conservation and management. Report to the Government of Uganda.
- Calvert, J. J. (1985). Food selection by western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia* 65: 236–246.
- Chivers, D. J., and Hladik, C. M. (1984). Diet and morphology in primates. In Chivers, D. J., Wood, B. A., and Bilsborough, A. (eds.), *Food Acquisition and Processing in Nonhuman Primates*, Plenum Press, New York, pp. 213–230.
- Doran, D. M., and McNeilage, A. (1998). Gorilla ecology and behavior. *Evol. Anthropol.* 6: 120–131.
- Gagneux, P., Wills, C., Gerloff, U., Tautz, D., Morin, P. A., Boesch, C., Fruth, B., Hohmann, G., Ryder O. A., and Woodruff, D. S. (1996). Mitochondrial sequences show diverse evolutionary histories of African hominoids. *Proc. Nat. Acad. Sci.* 96: 5077–5082.
- Garner, K. J., and Ryder, O. A. (1996) Mitochondrial DNA diversity in gorillas. *Molec. Phylogenetics Evol.* 6: 39–48.
- Gautier-Hlon, A., Quris, R., and Gautier, J. P. (1983). “Monospecific vs. polyspecific life: A comparative study a foraging and antipredatory tactics in a community of *Cercopithecus* monkeys.” *Behavioral Ecology and Sociobiology*, 12: 325–335.
- Goldsmith, M. L. (1999). Ranging behavior of a lowland gorilla (*Gorilla g. gorilla*) group at Bai Hokou, Central African Republic. *Int. J. Primatol.* 20: 1–23.

- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*, Harvard University Press, Cambridge, MA.
- Hamilton, A. C., Taylor, D., and Vogel, J. C. (1986). Early forest clearance and environmental degradation in south-west Uganda. *Nature* 320: 164–167.
- Howard, P. (1991). *Nature Conservation in Uganda's Tropical Forest Reserves*, I.U.C.N., Glan, Switzerland.
- Janzen, D. H. (1979). How to be a fig. *Annual Review of Ecology and Systematics* 10: 13–51.
- Jensen-Seaman, M., and Kidd, K. K. (2001). Mitochondrial variation and biogeography of eastern gorillas. *Molec. Ecol.* 10: 2240–2247.
- Jones, C., and Sabater-Pi, J. (1971). Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumembach) in Rio Muni, West Africa. *Bibliotheca Primatol.* 13: 1–95.
- Kuroda, S. (1992). Ecological interspecies relationships between gorillas and chimpanzees in the Ndoki-Nouabale Reserve, northern Congo. In Itoigawa, N., Sugiyama, Y., Sackett, G. P., and Thompson, R. K. R. (eds.), *Topics in Primatology, Vol. 2: Behavior, Ecology, and Conservation*, Tokyo University Press, Tokyo, pp. 385–394.
- Kuroda, S., Nishihara, T., Suzuki, S., and Oko, R. (1996). Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*, Cambridge University Press, Cambridge, pp. 71–81.
- Malenky, R. K., Kuroda, S., Vineberg, E., and Wrangham, R. W. (1994). The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. In Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, pp. 59–76.
- McGrew, W. C., Baldwin, P. J., and Tutin, C. E. G. (1988). Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Asserik, Senegal: I. Composition. *Am. J. Primatol.* 16: 213–223.
- McNeillage, A., Plumtre, A. J., Brock-Doyle, A., and Vedder, A. (1998). *Bwindi Impenetrable National Park, Uganda: Gorilla and large mammal census, 1997*. Wildlife Conservation Society Working Papers, New York.
- Milton, K. (1984). The role of food-processing factors in primate food choice. In Rodman, P. S., and Cant, J. G. H. (eds.), *Adaptations for Foraging in Non-Human Primates*. Columbia University Press, New York, pp. 249–279.
- Mwanza, N., Maruhashi, T., Yumoto, T., and Yamagiwa, J. (1988). Conservation of eastern lowland gorillas in the Masisi region, Zaire. *Primate Conservation*, 9: 111–114.
- Nishihara, T. (1992). A preliminary report on the feeding habits of western lowland gorilla (*Gorilla gorilla gorilla*) in the Ndoki Forest of northern Congo. In Itoigawa, N., Sugiyama, Y., Sackett, G. P., Thompson, and R. K. R. (eds.), *Topics in Primatology, Vol. 2: Behavior, Ecology, and Conservation*, Tokyo University Press, Tokyo, pp. 225–240.
- Nishihara, T. (1995). Feeding ecology of western lowland gorilla in the Nouabale-Ndoki National Park, Congo. *Primates* 36: 151–168.
- Nkurunungi, J. B. (2002). *Feeding and ranging ecology of gorillas (Gorilla gorilla beringei) in Bwindi Impenetrable National Park*, PhD dissertation, Makerere University, Kampala, Uganda.
- Nkurunungi, J. B., and Stanford, C. B. (2003). Using GPS technology to study ranging patterns of sympatric mountain gorillas and chimpanzees in Bwindi Impenetrable National Park, Uganda. In Paterson, J., Reynolds, V., and Notman, H. (eds.), *Primates of Western Uganda*.
- Nkurunungi, J. B. (2003). Feeding and ranging behavior of mountain gorillas (*Gorilla g. beringei*) in Bwindi Impenetrable National Park, Uganda. Ph.D. dissertation, Makerere University, Uganda.
- Remis, M. J. (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *Am. J. Primatol.* 43: 87–109.
- Rogers, M. E., Maisels, F., Williamson, E. A., Fernandez, M., and C. E. G. Tutin, C. E. G. (1990). Gorilla diet in the Lopé Reserve, Gabon: A nutritional analysis. *Oecologia* 84: 326–339.
- Schaller, G. B. (1963). *The Mountain Gorilla*, University of Chicago Press, Chicago.
- Shea, B. T. (1983). Size and diet in the evolution of African ape craniodental form. *Folia Primatologica* 40: 32–68.

- Stanford, C. B. (2001a). The subspecies concept in primatology: The case of mountain gorillas. *Primates* 42: 309–318.
- Stanford, C. B. (2001b). The behavioral ecology of chimpanzees in Bwindi Impenetrable National Park, Uganda: Preliminary data. Paper presented at *XVII Congress of the International Primatological Society*, Adelaide, Australia.
- Stanford, C. B. (2002). Arboreal bipedalism in Bwindi chimpanzees. *Am. J. Phys. Anthropol.* 119: 87–91.
- Stanford, C. B., Gambaneza, C., Nkurunungi, J. B., and Goldsmith, M. (2000). Chimpanzees in Bwindi-Impenetrable National Park, Uganda, use different tools to obtain different types of honey. *Primates* 41: 335–339.
- Stanford, C. B. (1998). *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Cambridge, Mass: Harvard University Press.
- Suzuki, S., and Nishihara, T. (1992). Feeding strategies of sympatric gorillas and chimpanzees in the Ndoki-Nouabalé forest, with special reference to co-feeding behavior by both species. Abstracts of the XIVth Congress of the International Primatological Society, Strasbourg, France.
- Terborgh, J. (1983). *Five New World Primates*. Princeton, New Jersey: Princeton University Press.
- Tutin, C. E. G. (1996). Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In *Great Ape Societies* (edited by W. C. McGrew, L. F. Marchant, and T. Nishida), pp. 58–70. Cambridge: Cambridge University Press.
- Tutin, C. E. G., and Fernandez, M. (1985). Foods consumed by sympatric populations of *Gorilla g. beringei* and *Pan t. troglodytes* in Gabon: Some preliminary data. *Int. J. Primatol.* 6: 27–43.
- Tutin, C. E. G., and Fernandez, M. (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *Am. J. Primatol.* 30: 195–211.
- Vedder, A. (1984). Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *Am. J. Primatol.* 7: 73–88.
- Watts, D. P. (1984). Composition and variability of mountain gorilla diets in the central Virungas. *Am. J. Primatol.* 7: 323–356.
- Watts, D. P. (1991). Strategies of habitat use by mountain gorillas. *Folia Primatol.* 56: 1–16.
- Watts, D. P. (1996). Comparative socioecology of gorillas. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*, Cambridge University Press, Cambridge, pp. 16–28.
- Williamson, E. A., Tutin, C. E. G., Rogers, M. E., and Fernandez, M. (1990). Composition of the diet of lowland gorillas in Gabon. *Am. J. Primatol.* 21: 265–277.
- Wrangham, R. W., Conklin, N. L., Etot, G., Hunt, K. D., Hauser, M. D. and Clark, A. P. (1993). The value of figs to chimpanzees. *Int. J. Primatol.* 14: 243–256.
- Wrangham, R. W., Conklin, N. L., Chapman, C. A., and Hunt, K. D. (1991). The significance of fibrous foods for Kibale Forest chimpanzees. *Phil. Trans. Royal Soc. Lond., Series B* 334: 171–178.
- Yamagiwa, J., Mwanza, N., Yumoto, T., and 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., and Mwanza, N. (1996). Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaïre. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*, Cambridge University Press, Cambridge, pp. 82–98.