International Journal of Primatology, Vol. 15, No. 2, 1994

Day-Journey Length and Daily Diet of Solitary Male Gorillas in Lowland and Highland Habitats

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Received July 16, 1992; accepted December 1, 1992

We compared day-journey length and daily diets of solitary male gorillas in lowland versus highland habitats. Solitary males in tropical forests of Zaire tend to travel longer distances, to visit more types of vegetation, and to consume more kinds of food than a solitary male mountain gorilla in the Virunga Volcanoes did. The number of feeding sites per day is larger and the mean distance between feeding sites is far longer for the former than the latter. These observations may reflect differences in food breadth and availability between highland and lowland habitats. The herbaceous plants that are eaten by mountain gorillas are densely and evenly distributed in the higher montane forest of the Virungas, where gorillas need not cover long distances to search for food. In contrast, herbaceous plants are scarce in primary and ancient secondary forests of lowland habitats, where gorillas travel long distances and eat various fruits and insects. The patchy and unpredictable distribution of foods may extend the distances over which gorillas search for food in the lowland habitat. However, solitary males showed a prominent reduction in day-journey length and changed their choices of food during the nonfruiting season (the long rainy and dry seasons) in the lowland habitats. This strategy may have developed during the Pleistocene and may have enabled them to enlarge their ranges to the higher montane forests, where fruits are sparse throughout the year.

KEY WORDS: day-journey length; dietary breadth; solitary male; eastern lowland gorilla; mountain gorilla.

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0164-0291/94/0400-0207$07.00/0 © 1994 Plenum Publishing Corporation

INTRODUCTION

Interpopulational differences in diet and ranging have been reported for many species of primates [*Macaca fuscata* (Uehara, 1977; Maruhashi, 1980), *Macaca mulatta* (Lindburg, 1977), *Cercocebus albigena* (Waser, 1977), *Papio anubis* (Rowell, 1966), *Papio cynocephalus* (Altmann and Altmann, 1970), *Symphalangus syndactylus* (Chivers, 1977); *Pan troglodytes* (Hladik, 1977), and *Gorilla gorilla* (Schaller, 1963; Goodall, 1977; Tutin *et al.*, 1992)]. Dietary breadth differs widely between populations as a direct result of variations in the availability of foods (Clutton-Brock, 1977), and ranging varies with foraging strategies and the distribution of particular foods (Oates, 1987).

Gorillas—the largest of present-day primates—live in a notable variety of habitats, from the lowland to the highland forests of Equatorial Africa. They are classified into three subspecies: western gorillas (*Gorilla gorilla gorilla*), Grauer's gorillas (*G. g. graueri*), and mountain gorillas (*G. g. beringei*). The former two subspecies inhabit both tropical and montane forests, and the latter inhabits higher montane forests.

Previous field studies have concentrated on mountain gorillas in the Virunga Volcanoes. Mountain gorillas are regarded as terrestrial folivores (Schaller, 1963; Fossey, 1974; Fossey and Harcourt, 1977; Watts, 1984). Their daily travel distances (Elliott, 1976; Fossey and Harcourt, 1977; Yamagiwa, 1986) are relatively short, compared with those of chimpanzees (Wrangham, 1975; Goodall, 1986) and other terrestrial primates [*Presbytes entellus* (Jay, 1965), *Erythrocebus patas* (Hall, 1965), *Theropithecus gelada* (Kawai and Iwamoto, 1979), *Papio hamadryas* (Kummer, 1968), and *Papio anubis* (DeVore and Hall, 1965)], and may reflect the relatively rich habitat for mountain gorillas in the Virunga region.

Grauer's gorillas, which live in the montane forest of Kahuzi, also exhibit folivorous characteristics but daily tend to travel slightly longer distances than mountain gorillas do (Casimir, 1975; Goodall, 1977; Yamagiwa, 1988). Moreover, since they tend to shift their range seasonally, their annual range size is far larger than that of mountain gorillas (Casimir and Butenandt, 1973; Goodall, 1977; Yamagiwa, 1983). The limited availability of fruits and bamboo shoots in different types of vegetation is responsible for this seasonal change.

Recent studies of western and Grauer's gorillas that live in lowland forests have indicated that they regularly consume fruits and insects, such as ants and termites (Sabater Pi, 1977; Tutin and Fernandez, 1983, 1985; Carroll, 1986; Nishihara and Kuroda, 1991; Yamagiwa *et al.*, 1991, 1992). However, terrestrial herbaceous vegetation, such as Zingiberaceae and Marantaceae, may be an important buffer for gorillas against seasonal shortages of fruits in their lowland habitats (Tutin and Fernandez, 1985; Rogers and Williamson, 1987; Yamagiwa *et al.*, 1992).

These studies suggest that gorillas exhibit flexible ecological characteristics in their various habitats. The factors that influence ranging and foraging patterns of gorillas are explained by a complex of climatic vegetational factors, nutritional needs, the presence or absence of other gorilla groups or individuals or both, local culture, and human disturbances creating secondary forest (Schaller, 1983; Jones and Sabater Pi, 1971; Fossey, 1974; Casimir, 1975; Fossey and Harcourt, 1977; Goodall, 1977; Vedder, 1984; Watts, 1984; Tutin and Fernandez, 1985; Yamagiwa, 1983, 1986; Williamson *et al.*, 1990; Rogers *et al.*, 1992; Yamagiwa *et al.*, 1992). Goodall (1977) suggested that different patterns of food distribution were the most important factors which influence gorillas' movements. Mountain gorillas increased their rate of travel and their foraging area in response to temporal changes in food availability (Vedder, 1984), and western gorillas may have an ability to form mental maps of their home ranges and to judge the timing of fruit production (Williamson *et al.*, 1988).

However, ranging and diets of groups do not represent individual foraging patterns. The intensity and patterning of interference competition for food within social groups are influenced in several ways by group size and composition in the Virunga region (Watts, 1985), and the mean length of day journey by gorilla groups increases with increasing group size in the Kahuzi region (Yamagiwa, 1988). Their ranging patterns are also affected by interunit encounters between conspecifics (Fossey, 1974; Yamagiwa, 1987). These intra- and intergroup interactions prevent us from discussing the environmental factors that influence individual movements of gorillas in the different habitats of Equatorial Africa.

As a further step in the comparison among subspecies of gorillas, we discuss the activity of solitary male gorillas in highland and lowland habitats. We describe their daily travel distance, the types of vegetation visited, and the foods consumed by them and relate their foraging patterns to the availability of food in different seasons and habitats.

STUDY AREAS AND METHODS

The survey was conducted in the Virunga and the Itebero regions, north and west of Kivu Lake in Central Africa (Schaller, 1963). Both study areas are mountainous, and they constitute the highland (Virunga) and lowland (Itebero) parts of the escarpment along the African Rift Valley. The gorillas that inhabit the Virunga and the Itebero regions are classified as mountain gorillas (*Gorilla gorilla beringei*) and eastern lowland or Grauer's gorillas (*Gorilla gorilla graueri*), respectively (Napier and Napier, 1985; Tuttle, 1986).

The Virunga region is encompassed by Rwanda, Zaire, and Uganda and has been protected as their national parks. The parks cover an area of 450 km^2 at an altitude of 1800 to 4507 m. The study area lies within the Parc des Volcans of Rwanda and the Parc des Virungas of Zaire. Fossey (1974) reported that the main vegetational zonation of the study area could be divided into a moist montane forest belt (1800–2300 m), a bamboo (*Arundinaria alpina*) zone (2300–3000 m), a Hagenia (*Hagenia abyssinica*)–Hypericum (*Hypericum revolutum*) woodland zone (2300–3200 m), a subalpine zone (3000–3700 m), and an alpine zone (> 3600 m). The subject usually ranged on the herbaceous slopes of Mt. Visoke (3717 m) at an altitude of 2800–3700 m. Hypericum trees are commonly found in this area, with thick herbaceous ground foliage, such as nettles (*Laportea alatipes*), thistles (*Carduus nyassanus*), and giant celery (*Peucedanum linderi*).

The Itebero region is located at an altitude of 600–1300 m, and it has been protected since 1980 as an extension of Kahuzi-Biega National Park. The study area is covered with tropical forests, which include primary forest, secondary forest, ancient secondary forest, abandoned cultivated fields, and swamps. High stands of trees, such as *Gilbertiodendron dewevrei*, *Staudtia gabonensis*, *Michelsonia microphylla*, and *Cynometra alexandri*, are frequent, with scarce ground vegetation in the primary forest. *Musanga cecropioides* and herbaceous plants, such as Zingiberaceae or Marantaceae, grow at gaps in the forest, beside ravines and along rivers. Secondary forests are characterized by *Musanga cecropioides* and *Macaranga spinosa*, with thick herbaceous plants. Several small cultivated fields, surrounded by secondary forest, were abandoned by the local people before 1985. Palm trees (*Elaeis guineensis*) frequently grow in these areas. Ancient secondary forests were produced as a result of deforestation by a mineral company in the colonial era and subsequent successional reforestation. *Ficus sur*, *Uapaca guineensis*, and *Celtis brieyi* are common in this forest. *Halopegia azurea* is one of the dominant herbaceous plants, and *Uapaca corbisieri* is occasional in swamps. By reference to the annual rainfall records of the Meteorological Station at Mt. Bukulumiza, which is located between the Virunga and the Itebero regions, a year in the study areas can be divided into four seasons: the short dry season, January–March; the long rainy season, March–June; the long dry season, June–September; and the short rainy season, September–December.

Yamagiwa studied a well-habituated, solitary male mountain gorilla in the Virunga region. Solitary male mountain gorillas either have voluntarily left or have been expelled from their natal groups and travel alone for a long period after emigrating from them until they lure females away from neighboring groups to establish their own groups (Fossey, 1974; Caro, 1976; Harcourt *et al.*, 1976; *Yamagiwa*, 1986). Yamagiwa collected data during a 9-month field study from October 1981 to January 1982 and from July to December 1982. He tracked the solitary male's fresh trails (up to 2 days old), recording his field signs, and tried to make contact with him in the daytime. During contact with the subject, Yamagiwa carefully followed him, using focal sampling methods, to collect data on his behavior and to record his feeding activity. In the Itebero region, each of us studied at least three unhabituated, solitary male Grauer's gorillas. We collected data during a 7-month field study from October 1989 to February 1990 and from May to July 1991. Since fruits were scant in the latter period (the long rainy and dry seasons), the former period is referred to as the fruiting season and the latter as the nonfruiting season. Itebero gorillas did not tolerate the presence of humans because of the previous high incidence of hunting. We tried to follow 1-day-old trails, recording field signs, in order to avoid direct contact with them. We also collected feces for an analysis of their feeding habits.

We measured the length of each day journey between consecutive night beds by pacing (≈ 70-cm paces) in both regions. A feeding site is defined as a place where several feeding signs occur within 10 m of one another. A field sign separated by > 10 m from other signs is a separate feeding site. We recorded types of vegetation zones in which solitary males ranged, plant species used for food by them, numbers of feeding sites visited per day, and distances between consecutive feeding sites and compared them between the study areas. All the statistical tests are one-tailed.

RESULTS

Travel Distance

During the 9-month study period in the Virunga region, the solitary male mountain gorilla was usually on the herbaceous slopes of Mt. Visoke. The mean length of his day journey is 378 m ($N = 69$; range, 28–1671 m). It falls within the range of day-journey lengths reported for gorillas in the Virunga region (Table I). Mountain gorillas usually travel about 0.5 km per day. Fossey and Harcourt (1977) also reported that the median lengths of the day journeys per month for two groups were 295 and 360 m during an 8-month period. Grauer's gorillas in the montane forest of Kahuzi tended to travel slightly longer distances than mountain gorillas do, and gorillas inhabiting tropical forests traveled farther than gorillas in montane

Table I. Day-Journey Length for Groups and Solitary Male Gorillas in Different Habitats

Study site	Habitat	Sample	Day-journey length (m)		Reference
			N	Mean (range)	
G. g. beringei Virunga	Montane forest	7 groups	114	472 (92–1830)	Schaller (1963)
		1 group	41	522 (83–1342)	Elliott (1976)
		4 groups	160	575 (48–2143)	Yamagiwa (1986)
			33	473 (112–1160)	
			32	683 (182–2484)	
			29	1034 (345–2868)	
		2 solitary males	91	385 (SD = 385)	Caro (1976)
			35	460 (SD = 530)	
		1 solitary male	69	378 (28–1671)	This study
G. g. graueri Kahuzi	Montane forest	1 group	209	1057 (140–3400)	Goodall (1977)
		2 groups	53	1333 (210–5642)	Yamagiwa (1988)
			22	789 (51–2619)	
Itebero	Tropical forest	3 solitary males	8	1531 (142–3439)	This study
G. g. gorilla Lope	Tropical forest	3 groups	12	1238 (700–1650)	Tutin *et al.* (1992)
			10	1368 (550–2600)	
			5	1190 (800–1700)	

forests do. Casimir (1975) estimated that the Kahuzi gorillas traveled between 600 and 1100 m per day ($N = 36$), and Yamagiwa *et al.* (1992) recorded 2155 and 2735 m for groups of gorillas in the tropical forest of Itebero. Jones and Sabater Pi (1971) reported that the day-journey length of western gorillas in Equatorial Guinea ranged from 700 to 1600 m. However, the differences in the day journey-length by gorillas among different habitats are not consistent and are unclear in some cases, probably because social factors from inter- and intragroup interactions may affect their daily travels in various ways.

We calculated the mean length of day journeys by the solitary male mountain gorilla from data on his journeys both when he encountered other social units and when he did not. Social factors may influence his journey in the former case. When he encountered groups of gorillas that occasionally entered his range, he followed them and left the slopes. During or after such encounters, he traveled much longer distances than usual (Yamagiwa, 1986). Fossey (1974) also reported that a solitary male shifted his monthly range dramatically after interunit encounters.

The mean length of his day journey is affected by social factors; namely, on the day of and for 3 days after such encounters, it is 671 m ($N = 7$; range, 117–1518 m). This is significantly greater than the mean day-journey length (110 m; $N = 12$; range, 42–259 m) when he was not affected by social factors (Mann–Whitney U test, $U = 5.5$; $P < 0.01$). For the other journeys, we cannot establish that he was outside the auditory range (2 km) of other social units. When his journey was not socially affected, he traveled with continuous feeding on herbaceous ground foliage, such as nettles or thistles, and nested near the feeding sites. In two cases, he moved < 50 m in the daytime and nested beside the previous night's bed. The mean number of feeding sites per day is 3.3, and the mean distance between consecutive feeding sites is 22 m (Table II).

In the Itebero region, we often were unable to follow trails of gorillas in their entirety, because of the scant undergrowth of the primary and ancient secondary forests. From October 1989 to February 1990, we found three solitary males within the study area (ca. 220 km^2), but we were able to measure the complete length of a day's journey only five times for solitary males. From May to June 1991, we found two solitary males and were successful on three occasions. In all cases, the subjects were not within visual (500-m) or auditory (2-km) range of other solitary males or groups. Therefore, we regard their day journeys to have been unaffected by social factors from the other units during these measurements. The mean length of a day's journey calculated from data on them is 1531 m ($N = 8$; range, 142–3439 m), which is significantly greater than that of the solitary Virunga mountain gorilla ($Z = 3.47$, $P < 0.01$). It is 14 times longer than that of

Table II. Daily Distance Traveled and Feeding Sites by Solitary Males When They Were Not Within Auditory Range of Other Gorillas

Study area	No. of day samples	Travel distance (m) [mean (range)]	No. of feeding sites [mean (range)]	Distance (m) between consecutive feeding sites	
				N	Mean (range)
Virunga	12	110 (42–259)	3.3 (1–7)	27	22 (13–40)
Itebero	8	1531 (142–3439)	17.5 (5–31)	133	83 (11–1278)
FS[a]	5	2126 (799–3439)	19.8 (14–31)	95	107 (11–1278)
NFS[a]	3	539 (142–793)	13.7 (5–20)	38	24 (11–107)

[a] FS, Fruiting season; NFS, nonfruiting season.

the solitary mountain gorilla when he was outside the auditory range of other social units. We observed many more feeding sites per day in the Itebero region than in the Virunga region ($U = 2.5$, $P < 0.01$). Field signs showed that the solitary Itebero males did not eat much at each feeding site. They traveled longer distances between consecutive feeding sites than the solitary mountain gorilla did ($Z = 2.50$, $P < 0.01$).

However, during the nonfruiting season, they traveled relatively short distances: the mean length of their day journeys is 539 m, which is significantly shorter than the length (2116 m) during the fruiting season ($U = 0$, $0.01 < P < 0.05$). Although the mean numbers of feeding sites per day are not different between the two seasons ($U = 5$, $P > 5$), the mean distance between consecutive feeding sites in the nonfruiting season is shorter than that for the fruiting season ($Z = 4.78$, $P < 0.01$). These facts suggest that solitary gorillas did not travel long distances to search for food during the nonfruiting season compared with the fruiting season.

The mean length of a day journey during the nonfruiting season is greater and the mean number of feeding sites per day is larger than those of the solitary mountain gorilla ($U = 2$, $P < 0.01$, and $U = 2.5$, $0.01 < P < 0.05$, respectively). However, the mean distance between consecutive feeding sites during the nonfruiting season is not significantly different from that of the solitary mountain gorilla ($Z = 1.06$, $P > 0.05$). This suggests that solitary gorillas in the Itebero region tend to decrease travel distances between feeding sites during the nonfruiting season, but they still need more feeding sites than the solitary mountain gorillas does.

In summary, when outside the auditory range of other social units, solitary Itebero gorillas traveled longer distances daily than a solitary Virunga gorilla did. They also fed at more sites per day than the mountain gorilla did. However, they tended to decrease travel distances between consecutive feeding sites during the nonfruiting season. This suggests that the availability and choice of food for male Itebero gorillas may change seasonally and may affect their daily travel distances.

Foraging Patterns

The solitary male Virunga gorilla usually ranged in a herbaceous zone, where he fed on fibrous plants. Yamagiwa recorded seven plant species as his food during 12 days when he observed all his feeding activity during the daytime (Table III). Eight of nine food items show no seasonal changes in availability (Fossey and Harcourt, 1977). He ate the other item (flowers of *Vernonia adolf-fredericii*) only in small amounts. The mean num-

Table III. Number of Plant Species Used as Food by Solitary Male Gorillas

Study area	No. of day samples	No. of plant species in each food item					Total No. of plant species
		Fruit/seed	Leaf	Stem/pith	Bark	Flower	
Virunga	12	0	4	4	1	1	7
Itebero	8	13	20	10	0	0	39
FS[a]	5	12	13	9	0	0	30
NFS[a]	3	5	12	4	0	0	19

[a] FS, fruiting season; NFS, nonfruiting season.

ber of food plant species on which the Virunga male fed per day is 3.6 ($N = 12$; range; 3–6). He ate no fruits or insects during this time.

In the Itebero region, the solitary males visited all vegetation zones during the study period. During the fruiting season, they ranged in two or three vegetation zones per day when their entire trails could be followed. During the nonfruiting season, they ranged in one or two vegetation zones per day. We recorded 39 species of plants as their food during the course of 8 days: 30 species in the fruiting season and 19 species in the nonfruiting season. The mean number of plant species eaten per day is 12.6 ($N = 5$; range, 10–17) in the fruiting season and 13.3 ($N = 3$; range, 10–18) in the nonfruiting season. Fecal analysis and field signs indicated that they also consumed ants and termites on ≥7 days and ≥1 day respectively, during an 8-day period.

The major differences in the foraging patterns between the fruiting and the nonfruiting seasons involve (1) the species and parts of plants eaten, (2) the types of vegetation visited, and (3) the distances traveled without feeding. The gorillas used more kinds of tree (14 vs 4 species) and herb (8 vs 4 species) as food and fed on more kinds of fruits and seeds (12 vs 5 species) in the fruiting season than in the nonfruiting season. In the latter season, leaves (12 species) constituted a major part of their food. They fed on the leaves of several vines (6 species), which the gorillas apparently did not consume in the fruiting season.

During the fruiting season, the Itebero gorillas visited primary, ancient secondary, and secondary forests (Table IV). They traveled significantly shorter distances between consecutive feeding sites in the secondary forest than in the primary and ancient secondary forests (Mann–Whitney U test, $Z > 1.76, P < 0.01$ or $0.01 < P < 0.05$). In contrast, they ranged extensively in the primary forest during the nonfruiting season. The mean distance between consecutive feeding sites in the primary forest is very small and is not significantly different from that in the secondary forest during the fruiting season ($Z = 1.40$, $P > 0.05$). The diversity of fruits in the primary forest decreased during the nonfruiting season. Gorillas might have changed their selectivity for food items—from fruits to leaves—in the primary forest. This may have caused the reduction of their travel distances in the nonfruiting season.

Among plant species of which fruits were eaten by gorillas in the fruiting season, *Anonidium mannii* and *Dacryodes edulis* are found mostly in primary forest, *Uapaca guineensis* and *Alchornea floribunda* in primary or ancient secondary forest, *Musanga cecropioides* and *Ficus* spp. in secondary forest, and *Cissus dinklagei, Aframomum laurentii,* and *Haumania liebrechtsiana* in all vegetation zones. This distribution of fruits may stimulate gorillas to travel long distances, as they seek fruits in various types of vege-

Table IV. Distances (m) Between Consecutive Feeding Sites in Each Type[a] of Vegetation in the Itebero Region

	P–P		As–As		S–S		P–As		P–S		As–S		P–Sw	
Season[b]	*N*	Mean (range)	*N*	Mean (range)	*N*	Mean (range)	*N*	Mean (range)	*N*	Mean (range)	*N*	Mean (range)	*N*	Mean (range)
FS	19	165 (16–1113)	16	174 (11–896)	33	26 (11–61)	7	245 (12–1278)	7	74 (11–153)	13	87 (12–252)		
NFS	36	25 (11–107)											2	19 (13–25)

[a] Trials were measured in primary forest (P–P), in ancient secondary forest (As–As), in secondary forest (S–S), and across different types of vegetation (P–As, P–S, and As–S). Trials were measured only twice across primary forest and swamps (P–Sw).

[b] FS, fruiting season; NFS, nonfruiting season.

tation during this season. In contrast, only a few kinds (three trees and two herbs) of fruit were eaten in gaps in the forest or beside ravines in the primary forest during the nonfruiting season.

DISCUSSION

The activity time budgets and activity cycles of solitary male mountain gorillas are similar to those of groups (Caro, 1976; Yamagiwa, 1986). However, their daily travel distances and ranging patterns are strongly affected by the presence of neighboring groups (Fossey, 1974; Yamagiwa, 1986). We found that the mean day-journey length of a solitary male mountain gorilla was notably less when he traveled outside the auditory range of other gorillas.

When day journeys were unaffected by social factors, the solitary Virunga gorilla tended to travel shorter distances than the solitary Itebero gorillas did. The number of feeding sites per day is smaller and the mean distance between consecutive feeding sites is much shorter for the one versus the others.

These observations may reflect differences in dietary breadth and distribution of particular food between highland and lowland habitats. Gorillas exhibit a lower dietary breadth in the highland than in the lowland habitats. Fossey (1983) listed only 49 species of plants that were used for food by mountain gorillas. Goodall (1977) noted at least 104 species for Grauer's gorillas in the montane forest of Kahuzi, and Williamson *et al.* (1990) listed 134 species for western gorillas in Gabon. Mountain gorillas are regarded as specialized, terrestrial folivores (Fossey, 1974; Fossey and Harcourt, 1977; Watts, 1984), while gorillas in both western and eastern lowland habitats tend to eat many kinds of fruits and to feed regularly on insects, such as termites and ants (Sabater Pi, 1977; Tutin and Fernandez, 1983, 1985; Carroll, 1986; Nishihara and Kuroda, 1991; Yamagiwa *et al.*, 1991, 1992). We have shown that solitary males also exhibit far greater dietary breadth in lowland (39 species) than in highland (7 species) habitats.

Herbaceous plants eaten by mountain gorillas are densely and evenly distributed and are predictably available. The fruits of trees consumed by Grauer's gorillas are highly dispersed among different types of vegetation. Most ants that are consumed by Grauer's gorillas are available in primary or ancient secondary forest, in which herbaceous plants are sparse (Yamagiwa *et al.*, 1991). Although solitary Iteboro males decreased daily travel distances during the nonfruiting season, they traveled longer distances than the Virunga male did. Rogers and Williamson (1987) compared the density and distribution of herbaceous foods of gorillas between highland (Virunga) and lowland (Gabon) regions and reported that the biomass, in terms of units of food per square meter, is lower in the lowland region. Gorillas may need to use more kinds of food in lowland habitats than in highland habitats. This tendency may result in higher dietary breadths and larger numbers of feeding sites per day for solitary Itebero males versus solitary Virunga males.

The travel distances between consecutive feeding sites may be affected by the distribution of one or more particular foods. We found that solitary Itebero males traveled longer distances between consecutive feeding sites during the fruiting season than the nonfruiting season and that the distances in the latter season are similar to those of the solitary Virunga gorilla. This reduction may have been caused by their choice of food in response to a decrease in fruiting trees. Although the solitary gorillas used the same number of feeding sites and plant species for food per day in both seasons, they consumed more kinds of fruit and fewer kinds of leaves during the fruiting season than in the nonfruiting season. The patchy distribution of fruits may act to extend their travel distances to forage for food between feeding sites during the fruiting season.

Although Grauer's gorillas in the montane forest of Kahuzi are regarded as folivores, they seasonally eat large amounts of fruits (*Myrianthus holstii* and *Syzygium guinense*) and climb expertly to harvest them (Casimir, 1975; Goodall, 1977; Goodall and Groves, 1977). Goodall (1977) noted a difference in the day-journey length of a Kahuzi gorilla group between the long rainy season (April–June) and the long dry season (June–September) and suggested that the elongation of the day-journey length and the enlargement of the monthly range in the latter season are correlated with the appearance of the fruits. Williamson (1988) also recorded the longer distances of daily travel when western gorillas visited gallery forests in search of *Uapaca* fruits and shorter distances when large amounts of terrestrial herbaceous vegetation were ingested by them in Gabon. The gorillas' preference for fruits and the seasonal variation in availability of fruits may be the major factors that influence the day-journey length of both Grauer's and western gorillas.

When the availability of food declines, nonmigratory animals might be expected either to increase the time spent searching for food or to reduce selectivity, minimizing the expenditure of energy at the expense of food quality (Schoener, 1971; Clutton-Brock, 1977). Primate species relying heavily on fruits or insects tend to adopt the former strategy, and species that rely heavily on foliage adopt the latter strategy (Oates, 1987). Our results suggest that gorillas may adopt the latter strategy; accordingly, gorillas may share folivorous characteristics in general across habitats, though they, like chimpanzees, occasionally exhibit frugivorous characteristics in lowland habitats (Tutin and Fernandez, 1985; Yamagiwa *et al.*, 1992). When and where high-quality foods (fruits) are scarce, gorillas tend to reduce their day-journey lengths and to change their food selectivity. Their folivorous characteristics appear and support their activities during the nonfruiting season in lowland habitats and during the entire year in highland habitats. It is possible that these behavioral tendencies developed under the influences of worldwide changes in climate during the Tertiary and Quaternary periods. Unlike other African primates, gorillas did not disperse into arid areas (Hamilton, 1988) and they may have remained in the moist forests during these periods. Their present distribution, which overlaps almost completely with the refuge forests of Equatorial Africa in the Pleistocene, supports this interpretation.

ACKNOWLEDGMENTS

Our study was financed by the Monbusho (Ministry of Education, Science and Culture, Japan) International Scientific Research Program in cooperation with the CRSN (Centre de Recherches en Sciences Naturelles) in Zaire. We thank the IZCN (Institut Zairois pour Conservation de la Nature) and ORTPN (Office Rwandais du Tourisme et des Parcs Nationaux) for granting permission to carry out research in their National Parks; the Karisoke Research Centre for permission to study the gorilla monitored by its staff; the late Dr. D. Fossey for her constructive advice during the study; Drs. A. H. Harcourt, K. J. Stewart, N. Zana, B. Baluku, and M. M. Mankoto and M. O. Mankoto, M. Mashagiro, M. E. Linzombi, K. K. B. Kimvuni, and M. M. A. Wathaut for their administrative help and hospitality; Dr. T. Maruhashi and Dr. T. Yumoto for their continued support and guidance; and K. Ndumbo and N. Bosilana for their technical help. We are also greatly indebted to all guides, guards, and field assistants of Kahuzi-Biega National Park and Karisoke Research Centre for their technical help and hospitality throughout the fieldwork.

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