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Ranging Patterns of Chimpanzees in a Montane Forest of Kahuzi, Democratic Republic of Congo

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I studied ranging patterns of a semihabituated unit-group of chimpanzees for 60 mo at Kahuzi. They had a total home range of 12.81 km^2 *and a mean annual home range of 7.55 km*^{2}*. Considering the low density of chimpanzees in the area vis-à-vis chimpanzees in arid areas, their home range is very small. Kahuzi chimpanzees used the home range in a clumped pattern, frequently visiting the core area and only rarely entering peripheral areas. The monthly range changes with fruit availability, increasing during periods of fruit scarcity. There was no consistent seasonal difference in the size of the home range. However, use of different habitat types may vary seasonally. While there was no seasonal effect in the use of primary forest, the chimpanzees showed a statistically consistent seasonal difference in their use of secondary forest, visiting it mainly during the dry season when fig trees were in fruit. Since the primary forest provides them with more food fruits, chimpanzees tended to use more frequently the small patches of primary forest in their home range. Thus, the size and distribution of small fragmented primary forests may be an important factor influencing the ranging pattern of chimpanzees at Kahuzi.*

KEY WORDS: chimpanzees; ranging; fruit seasonality; habitat use.

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INTRODUCTION

Studies of habitat use and ranging patterns facilitate our understanding of the complexities of animal behavior and ecology including feeding strategies (Boinski, 1987).

Theory on primate-ranging behavior predicts that frugivorous species travel farther per day and have larger home ranges than those of folivorous species (Milton and May, 1976; Cluton-Brock and Harvey, 1977) because leaves are generally more abundant and evenly distributed than fruits are. Also, larger groups need to travel farther than smaller groups to exploit a greater supply area because of increased feeding demands (Strier, 1987).

Chimpanzees live in communities (or unit-groups) comprising both females and males in which they exhibit fluid fission-fusion grouping, forming temporary parties of various age/sex compositions (Goodall, 1968; Nishida, 1968). Intercommunity relationships are usually hostile and territorial. Males sometimes kill chimpanzees of other communities (Goodall *et al.*, 1979; Wilson and Wrangham, 2003).

Chimpanzee home range sizes are relatively small in moist forest habitats. Range size estimates are 27 km^2 in the lowland forest of Tai (Boesch and Boesch-Achermann, 1989), 20 km^2 and 23–38 km^2 in the medium-altitude forests of Budongo (Reynolds and Reynolds, 1965) and Kibale (Ghiglieri, 1984), respectively, and 11–34 km^2 in the woodland of Mahale (Nishida and Kawanaka, 1972). By contrast, their home ranges are extremely large in drier habitats: 122–124 km^2 at Kasakati (Izawa, 1970), 150 km^2 at Filabanga (Kano, 1971), 250–560 km^2 at Ugalla and Wansisi (Kano, 1972) and 278–333 km^2 at Mt. Assirik (Baldwin *et al.*, 1982).

Wide variation in the size of unit groups and mean party size also occurs in chimpanzees. The smallest chimpanzee unit-group ($n = 20$) was at Bossou, (Sakura, 1994), whereas the largest unit-group was at Kibale $n > 140$: (Mitani *et al.*, 2002). To compare variation of mean party size between communities of different sizes, Boesch and Boesch-Achermann (2000) proposed to use the relative size of the parties: mean party size divided by the community size. The variation in chimpanzee mean party size across habitats is then explained by the variation in community sizes: the smaller the community, the larger the mean relative party size.

The mean foraging party size of Kahuzi chimpanzee (mean = 4.43; range: 1–13) is 20% of the community size (Basabose, 2004), which is proportionally similar to those reported for other small community at Bossou (Sakura, 1994); Mt. Assirik (Tutin *et al.*, 1983) and Mahale (Nishida, 1968).

The montane forest in Kahuzi-Biega National Park, Democratic Republic of Congo, is the upper elevational limit of chimpanzee distribution;

they range up to 2,600 m above sea level (asl) in the bamboo forest. The estimated chimpanzee population density based on a population census in 1990 is 0.13 individual/km^2 in Kahuzi (Yamagiwa *et al.*, 1992). It is the lowest reported density for chimpanzee populations in forested habitats, but is similar to that reported for populations inhabiting drier areas: 0.33 ind./km^2 at Filabanga, Tanzania (Kano, 1971); 0.08–0.12 at Ugala, Tanzania (Kano, 1972); 0.07 ind./km^2 at Mt. Assirik, Senegal (Baldwin *et al.*, 1982). A vegetation survey revealed low abundance and diversity of chimpanzee fruit foods in the Kahuzi montane forest in contrast to the lowland forest (Yamagiwa *et al.*, 1996a,b).

Spatial and temporal variation in fruit abundance influences the frequency with which chimpanzees use different habitat types at several sites (Nishida and Kawanaka, 1972; Doran, 1997; Basabose and Yamagiwa, 2002).

Kahuzi chimpanzees are selectively frugivorous, changing their diet according to seasonal and annual variations in availability of succulent fruit species. When ripe fruits are scarce, the chimpanzees rely heavily on pith and leaves as fallback foods, but continue to search for fig fruits, their year-round staple food at Kahuzi (Basabose, 2002).

Given that a frugivorous diet may be associated with large home ranges (Milton and May, 1976; Strier, 1987), and given the low density of chimpanzee fruit foods in Kahuzi, the chimpanzees may have relatively large home ranges.

Via 60-mo study I examined factors that have been proposed to explain chimpanzee ranging patterns under different ecological conditions, particularly the effects of season and forest structure.

MATERIALS AND METHODS

Study Area and Study Animals

The study area (2° 5′ S, 28° 45′ E) is located along the eastern border of the montane forest of Kahuzi-Biega National Park, at an elevation of 2,050–2,350 m asl (Fig. 1(a)). The vegetation consists of bamboo (*Arundinaria alpina*) forest, primary forest, secondary forest and swamps of *Cyperus latifolius* (Fig. 1(b)). Description of the vegetation and analysis of its composition were provided by Casimir (1975), Goodall (1977) and Yumoto *et al.* (1994).

I measured sizes of the different vegetation types within the study area by digitizing a vegetation map in geographic information system software (Arc/View). The study site covers 33.11 km^2, with 21.23 km^2 (64.1%) of

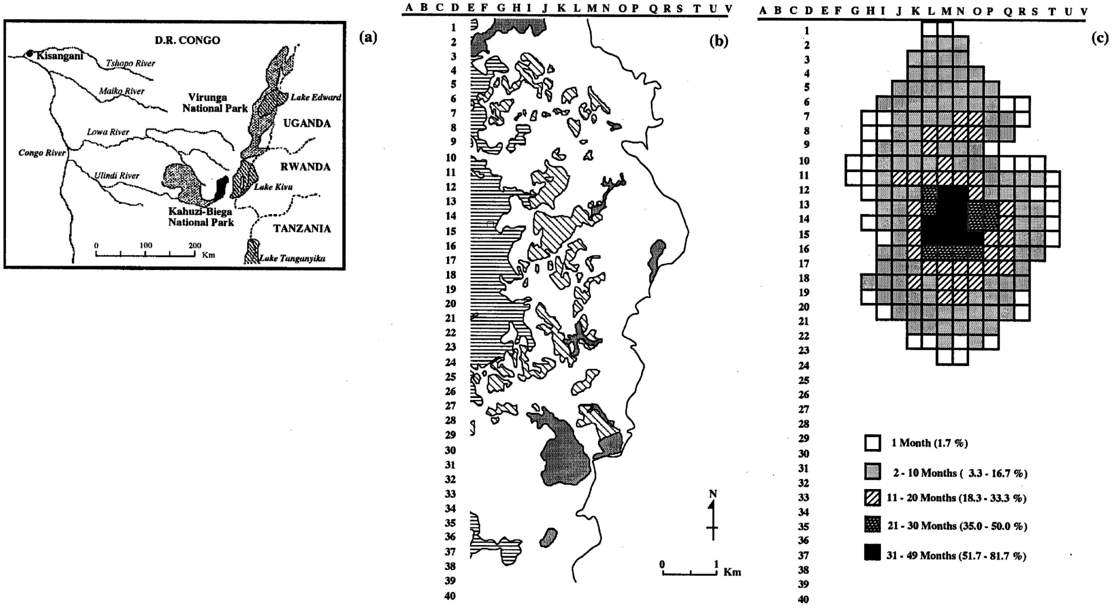

Fig. 1. (a) Location of Kahuzi Biega National Park in eastern Democratic Republic of Congo: Black area is the montane forest of the Park (600 km^2). (b) Vegetation of the study site: Dotted area, *Cyperus* swamp; horizontal lined area, bamboo forests; hatched area, primary forests; white area left of the Park boundary, secondary forests. The study area covers 33.11 km^2 between E and the eastern border of the Park. (c) Total home range of chimpanzees for the 60-mo study period. The chimpanzees used a core area (black quadrats) very frequently and only rarely entered peripheral regions. Boundary areas of the community home range comprise by dried bamboo forest in the western side, large swamps in northern and southern areas and by cultivated fields in the eastern part of the study area. Their home range extends beyond the eastern border of the park.

secondary forest; 5.8 km^2 (17.6%) of bamboo forest; 4.46 km^2 (13.5%) of primary forest and 1.59 km^2 (4.8%) of *Cyperus* swamp.

The climate is characterized by a clear dry season (June-August) and a distinct rainy season from September to May. Climatic data during the study period shows a mean annual rainfall of 1,586 mm ($N = 7$; Range: 1409–1809 mm). The monthly mean temperature is 20.1°C ($r = 13.2$–26.4°C) and varied little throughout the study period.

From nest counts, Yamagiwa *et al.* (1992) found 3 chimpanzee unit-groups ranging in the montane area of Kahuzi-Biega National Park including my study unit-group (Kaboko). They contained 13, 20 (Kaboko) and 27 individuals, respectively. They were located in different regions and their home ranges did not overlap.

Since 1991, we have routinely followed Kaboko unit-group in attempts to habituate the members to human observers without provisioning. Based on individual identification in 1994, I counted 22 chimpanzees (Basabose and Yamagiwa, 1997). One infant was born in 1999, giving a total of 23 recognized individuals that included 4 adult males; 4 adolescent males; 5 adult females; 2 adolescent females; 6 juveniles and 2 infants.

The chimpanzees have been semihabituated and tolerate our presence when we stay at a distance of 20–50 m.

At Kahuzi, chimpanzees live sympatrically with eastern lowland gorillas (*Gorilla beringei graueri*) and 6 other primate species (*Papio anubis, Colobus angolensis; Cercopithecus mitis, Cercopithecus hamlyni; Cercopithecus l'hoesti* and *Galago demidovi*). Additionally, 35 other large mammals inhabit the montane forest of Kahuzi (Mankoto *et al.*, 1994).

Estimation of Home Range Size

I conducted the study on 729 days over 60 mo, with an average of 12 observation days per mo (range: 5–24).

The home range is based on data from recognized individuals. During the study period, only individuals belonging to Kaboko unit-group ranged in the study area. To investigate the home range of chimpanzees, I used a grid with 250 × 250-m quadrats (6.25 ha). Different quadrat sizes have been used in apes ranging pattern studies: 200 × 200-m quadrats (Chapman and Wrangham, 1993: chimpanzees); 250 × 250-m quadrats (Remis, 1997: gorillas) or 500 × 500-m quadrats (Hashimoto *et al.*, 1998: bonobos; Herbinger *et al.*, 2001: chimpanzees). I located chimpanzees by following their fresh trails in the forest, localizing calls and searching where calls were heard, and by visiting fruit trees that chimpanzees frequently visited. I mostly followed larger parties that contained adult males and females, whose vocalizations enabled me to locate them consistently. I also followed lone individuals and mother-offspring parties when encountered.

I drew the daily routes followed by the chimpanzee parties ($n = 4.5$; range: 1–11 chimpanzees/party) on 1: 25,000 scale map. The study area is divided into two sectors by the Lwiro River, which crosses the site from west to east. Two teams of 3 persons each walked simultaneously through each sector, searching for chimpanzee signs. We usually used radios to communicate between teams to avoid recounting or missing a party. A team searched for chimpanzee signs and endeavored to cover all quadrats of the entire sector. Each team alternately visited the 2 sectors at least once per mo. A team monitored a sector for half a month before shifting to another sector. I measured monthly home range size by counting the number of quadrats entered per day and the cumulative number of different quadrats entered per mo. This was accomplished by superimposing a grid of 250 × 250-m quadrats over the daily ranging sketch maps on which location sightings of chimpanzees were plotted. The total home range size is the sum of the 0.0625-km^2 quadrats that the chimpanzees used, plus others through which they must have travelled. I used the same method to define the type of habitat entered. Whenever more than one type of vegetation was covered by the quadrat, I considered all the forest types covered as having been visited. I considered each quadrat entered by chimpanzees as part of the Kaboko unit-group's home range. For habitat use comparison, I considered only observations of chimpanzees that lasted $\geq$1 h, which includes 607 different sightings made over 339 days in both sectors. Additionally, when a habitat type was visited x times a day for $\geq$1 h, I counted x different location sightings for that habitat.

I defined the core area as the quadrats that the chimpanzees used for 51.7–81.7% of all observation mo (31–49 mo).

Ranging Patterns

I analyzed ranging patterns by plotting the number of different quadrats and the cumulative number of quadrats entered for 58 pairs of sequential mo. To evaluate how much the ranging area shifted from one mo to the next, I examined differences in quadrat use between sequential pairs of mo and computed C values (Strier, 1987). I computed C values as the ratio of b/a, where in b is the number of new quadrats entered on the second mo of a pair and a, the total number of quadrats entered on the second mo. If no quadrat was entered on the second mo, C equals zero; if only new quadrats were entered on the second mo, C equals 1. A low C value implies a more concentrated pattern of range use, whereas a high C

value indicates a wide ranging pattern resulting from new quadrats being visited the following mo. I assumed that Kahuzi chimpanzees use relatively small parts of their home range per mo and shift from one area to another between mo. To investigate my assumption, I performed a C-value test on a few randomly selected pairs of mo. The assumption was confirmed; then I used the method for the entire study period. Using a month-by-month comparison captures what Kahuzi chimpanzees actually do. Because of the variation in observation days each mo, I could not calculate the C-value using day ranges.

Sampling of Chimpanzee Diet

I sampled the diet of chimpanzees via fecal analysis. Over the 60-mo study period, we collected 5,967 chimpanzee fresh ($\leq$1 day old) fecal samples, with a mean of 101 samples per mo (range: 18–427). We sluiced each dung sample in 1-mm mesh sieves and dried them in sunlight. We divided the contents of each sample into fruits (including seeds and fruit skins), foliage (including fiber and digested fragments of leaves), bark, fragments of insects, animal matter and other matter. We estimated volume percentage of each of the contents via 5% intervals. We identified large seeds ($>$2 mm) to species whenever possible. We estimated small seeds macroscopically as rare, common, or abundant with respect to the total mass of the fecal sample. I identified the seeds to specific level via seed samples identified by Yumoto (1994) at the National Botanical Garden in Belgium and kept at our herbarium.

Fruit Availability Index

To estimate the density of woody species and to assess the fruit availability in different types of vegetation within the study area, I conducted a vegetation survey using the line transect method. The transect was 5,000 m long and 20 m wide and passed through most vegetation types within the chimpanzee range. Phenological data presented here are from 2 sets: Set 1 from August 1994 to July 1996 and Set 2 from February 1998 to December 2000. In Set 1, we recorded, a total of 2033 trees and shrubs $>$10 cm in DBH consisting of 48 species from 28 families and 2 unidentified species in the transect. Among them, Kahuzi chimpanzees ate fruits of 29 species from 17 families represented by 1228 trees and shrubs. We recorded presence of fruits of these plant species twice a mo; a monthly datum is the average of the 2 records.

We calculated the density and basal area $[(1/2\text{DBH})^2 \times \pi]$ of each species. The habitat comparison is only available for Set 1.

I calculated the monthly fruit availability index (F_m) using the following formula:

$$F_m = \sum P_{km} \times B_k;$$

where P_{km} denotes the proportion of trees or shrubs in fruits for species k in month m and B_k denotes the total basal area per ha for species k. Basal area is a good estimation of canopy volume (Strier, 1989). I compared monthly fluctuation of the fruit availability index to the chimpanzee ranging pattern.

In the data analysis, I used nonparametric tests; 2-tailed probabilities ≤ 0.05 are significant.

RESULTS

Home Range and Types of Habitats Used

The total home range of the focal unit-group (Fig. 1(c)) for 60 mo is 12.8 km^2, with a mean annual home range size of 7.6 km^2 (range: 7.1–8.3 km^2). Table I displays the mean size of the daily ranging area used by chimpanzees monthly. Chimpanzees did not shift their activity area during the 60 mo, and it remained relatively small throughout the study. The core area is 0.69 km^2 (11 quadrats). Moreover, analysis of the cumulative number of quadrats visited showed that only the first 5 mo (6.4%) of the study were enough for the chimpanzees to cover more than half of their total home range (Fig. 2). A plot of the cumulative monthly home range size of the community to observation time reached an asymptote after only 17 mo, explaining the small total home range. Moreover, mean annual home range overlap (79.5%) was high.

Although chimpanzees used all the vegetation types within their home range, the proportion of utilization differed among habitat types. Chimpanzees used secondary forest for 67.8% of the time, primary forest for 10.5%, swamp forest for 6.6% and bamboo forest for 5.9% (Table II). The bamboo forest was dominated by dry and dead bamboo shoots during the study period, and the chimpanzees rarely visited it.

Comparison between the proportion of different habitat types within the study area and their use by chimpanzees shows a clear preference for primary forest. The secondary forest was 5 times larger than the primary forest. They spent more time than expected in the primary forest ($\chi^2 = 625.01$; $df = 1$; $p < 0.0001$), whereas they used the secondary and

Table I. Mean number of quadrats visited by chimpanzees per day in each month and by season

															Difference between seasons	
Year	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Rainy season Sept–May	Dry season June–August	Mann-Whitney *z*	Probability *p*
1994	—	—	—	—	—	—	—	—	1.77	2.62	3.80	2.40	2.56	—	—	—
# days of observation	—	—	—	—	—	—	—	—	*13*	*16*	*10*	*20*	*59*	—	—	—
1995	3.69	2.27	1.93	2.09	3.35	3.19	2.92	2.73	2.08	2.43	1.90	3.25	2.43	2.97	−0.83	ns
# days of observation	*13*	*11*	*14*	*11*	*17*	*16*	*12*	*11*	*24*	*14*	*10*	*8*	*122*	*39*	—	—
1996	3.71	3.37	2.86	3.14	1.94	2.90	3.86	4.31	3.23	3.60	—	—	3.00	3.70	−1.25	ns
# days of observation	*7*	*8*	*14*	*14*	*16*	*10*	*14*	*13*	*13*	*10*	—	—	*82*	*37*	—	—
1998	—	—	2.67	3.90	2.00	1.92	1.78	2.57	2.56	3.00	2.20	2.75	2.72	2.09	−1.71	ns
# days of observation	—	—	*9*	*10*	*12*	*13*	*18*	*7*	*9*	*7*	*10*	*8*	*65*	*38*	—	—
1999	2.20	2.75	2.20	2.00	2.69	3.67	1.93	2.14	1.80	2.82	2.64	2.42	2.46	2.25	−0.37	ns
# days of observation	*5*	*12*	*13*	*6*	*15*	*7*	*15*	*11*	*11*	*12*	*17*	*21*	*112*	*33*	—	—
2000	245	2.21	2.57	1.77	1.53	1.35	2.00	3.00	2.27	2.33	2.86	2.00	2.22	2.12	−0.37	ns
# days of observation	*11*	*14*	*14*	*13*	*15*	*17*	*15*	*5*	*11*	*6*	*7*	*14*	*105*	*37*	—	—

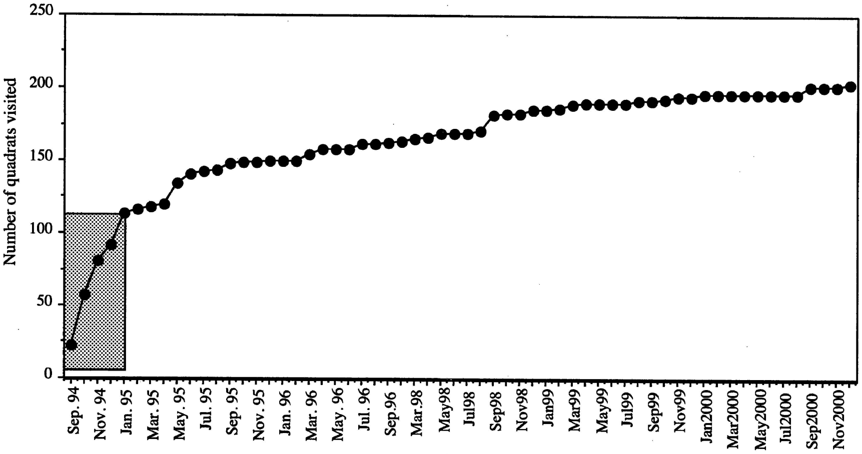

Fig. 2. Cumulative number of quadrats visited per month. The box in the figure shows the number of quadrats visited by chimpanzees for the first 5 mo of the study.

bamboo forests less often than expected ($\chi^2 = 34.95$; $df = 1$; $p < 0.0001$ and $\chi^2 = 12.26$; $df = 1$; $p < 0.001$, respectively). However, the *Cyperus* swamp was used by chimpanzees in direct proportion to its representation in their home range (Table II).

The monthly percentage of habitat use shows that they visited the secondary forest more frequently during the dry season than in the rainy season (Mann-Whitney test, $z = -2.288$; $p < 0.05$; $n_1 = 15$ mo of dry season and $n_2 = 45$ mo of rainy season), whereas there is no seasonal difference in the use of primary forest (Table III). The phenological survey showed that ripe chimpanzee fruit foods were more abundant in the primary forest than in the secondary forest for almost all the study period (Fig. 3), but

Table II. Habitat differences in chimpanzees visits compared to expected values based on the area of vegetation types within their home range (607 chimpanzees sightings,[a] each of which lasted $\geq$1 h)

Habitat types	Proportion (%) size within home range	# Observed sightings	# Expected sightings[b]	χ^2	p
Secondary forest	67.82	292	412	34.95	$p < 0.0001$
Primary forest	10.55	264	64	625.01	$p < 0.0001$
Bamboo forest	5.93	15	36	12.26	$p < 0.001$
Cyperus swamp	6.60	36	40	0.40	ns

[a] No sighting lasted one hour has been made outside the park's boundary in the cultivated area.
[b] Expected sightings were calculated from the total study area (33.11 sq. km) covering 21.23 sq. km of secondary forest; 4.46 sq. km of primary forest; 5.83 sq. km of bamboo forest and 1.59 sq. km of *Cyperus* swamps.

Table III. Seasonal changes in the use of different habitat types (proportion of quadrats used)

Habitat	% use rainy season ($N = 201$ quadrats)	% use dry season ($N = 140$ quadrats)	Seasonal difference Mann-Whitney z	 Probability p
Primary forest	38.74	33.09	−0.896	ns
Secondary forest	77.48	85.87	−2.288	$p < 0.05$
Cyperus swamp	3.58	4.88	−0.854	ns
Bamboo forest	0.50	0.00	−0.608	ns
Cultivated area	0.40	0.00	−0.898	ns

ripe fig fruits were more abundant in the secondary forest (Fig. 4(a)). There is a significant positive correlation between the fruit availability index of *Ficus spp.* and the number of new quadrats visited by chimpanzees in the secondary forest (Fig. 4(b)). Ficus trees occur at low density (0.7 tree/ha) in the study area (Basabose and Yamagiwa, 2002), so chimpanzees might have to range widely in the secondary forest to forage for ficus fruits. However, they stayed close to the primary forest, which provides them with a variety of other edible fruit species.

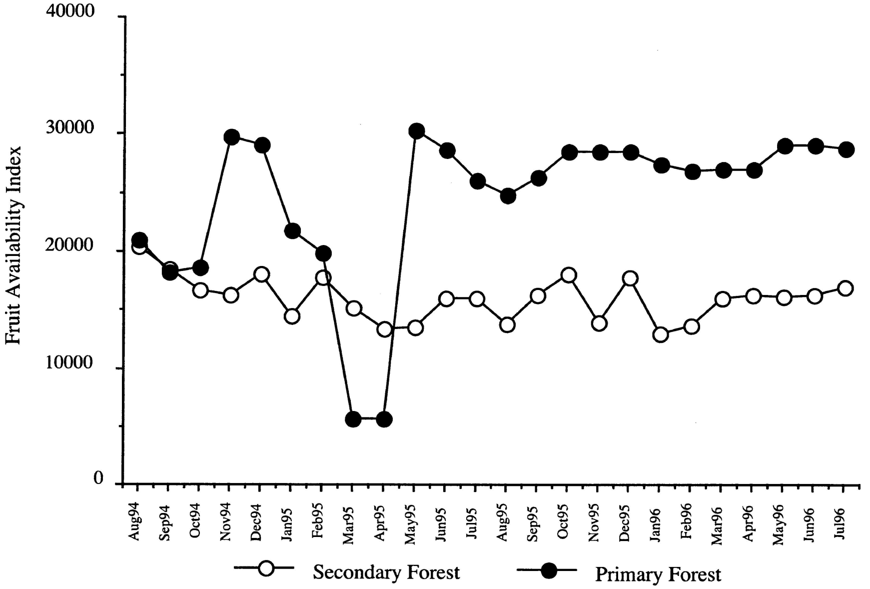

Fig. 3. Habitat difference in availability of chimpanzees food fruits.

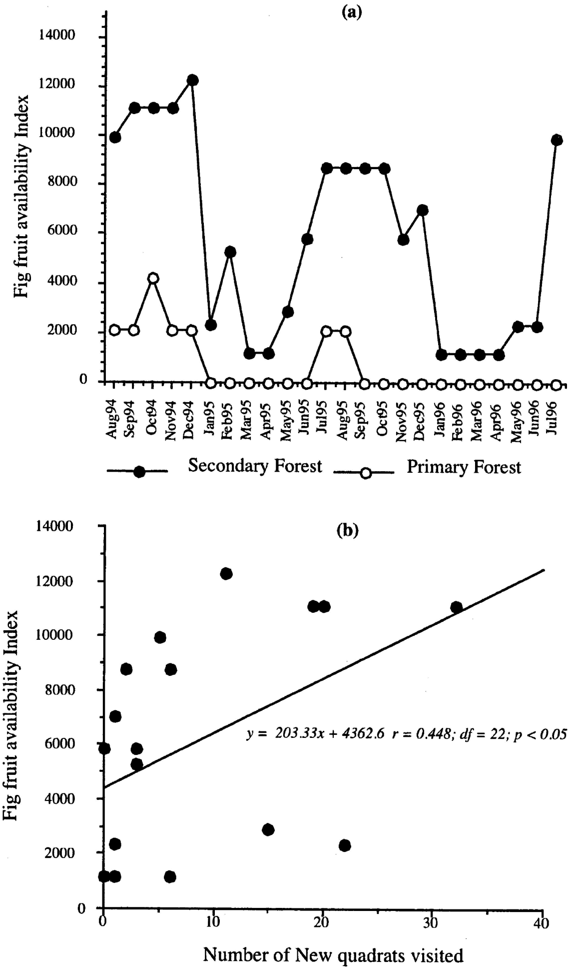

Fig. 4. Habitat changes in fruit availability index of *Ficus* spp. (a) and its correlation with the number of new quadrats visited in the secondary forest (b).

Ranging Pattern and Fruit Availability

Figure 5 shows the monthly distribution of fruit production in the study site. We observed an overall monthly mean of only 18.6% trees and 14.8% of species in fruit over 60 mo. March–August was a high fruiting period, with a peak in the dry season (June–July) and September–February was a low fruiting period.

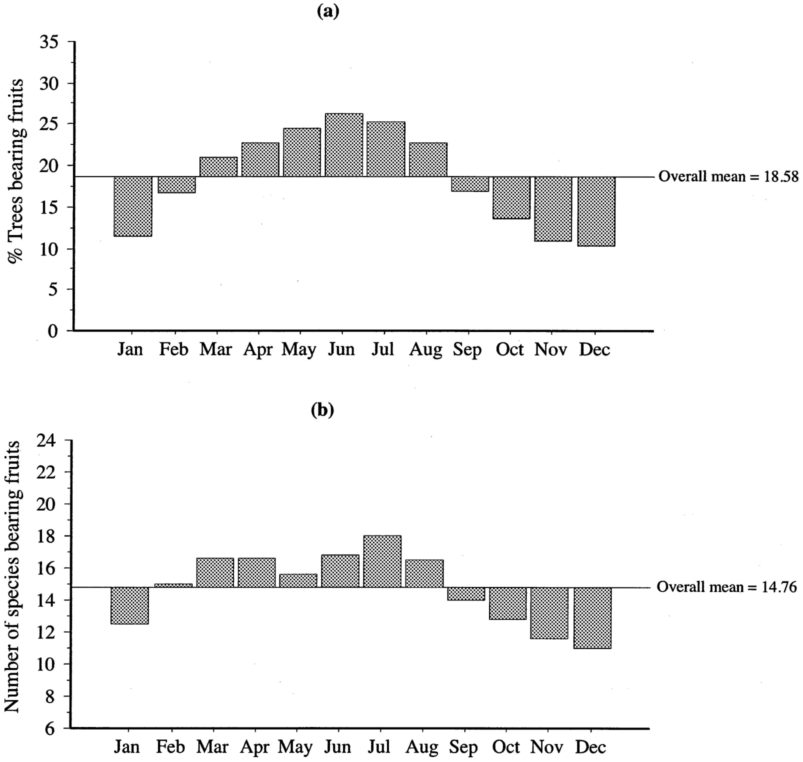

Fig. 5. Monthly distribution of the% of trees bearing ripe fruits (a) and the number of species bearing ripe fruits (b): divergence from the overall monthly mean.

Figure 6 presents the frequency distribution (a) and divergence from the overall monthly mean (b) of the C-value. Overall, C-values are lower during high fruiting mo than low fruiting ones (Mann-Whitney test, $z = -2.014$; $p < 0.05$; $n_1 = 30$ mo; $n_2 = 30$ mo), except for May. Though the percentage of trees bearing fruits is relatively high during then, the number of species bearing ripe fruits is low in comparison to other high fruiting mo (Fig. 5(b)).

The results suggest that Kahuzi chimpanzees were more likely to visit new quadrats during period of fruit scarcity. However, despite shifting to new quadrats when fruit availability decreased, chimpanzees did not use larger areas per mo than while fruit availability was high (Mann-Whitney U-test, $z = -0.688$; $p = 0.4913$). There is significant negative correlation between the C-values and both the percentage of trees and the number of species bearing ripe fruits (Fig. 7(a) and (b); Spearman Rank

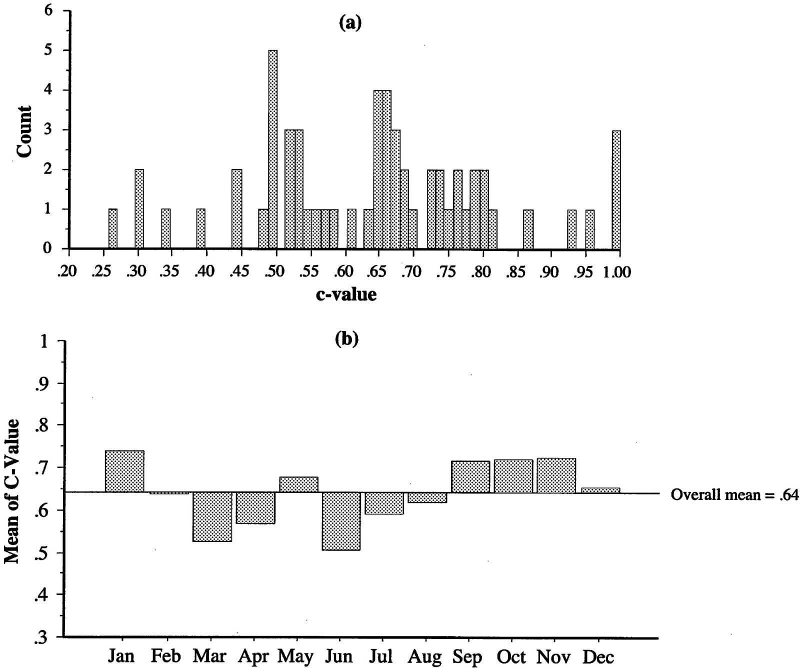

Fig. 6. Frequency distribution (a) and divergence from the overall monthly mean (b) of the C-value.

test; $r = -0.51$; $p < 0.0001$; $df = 52$ and $r = -0.57$; $p < 0.0001$; $df = 52$, respectively). There is a similar significant negative correlation between the C-value and the monthly mean percentage of fruits in chimpanzee feces (Fig. 7(c); Spearman Rank test; $r = -0.31$; $p < 0.05$), while there is a significant positive correlation with the monthly mean percentage of foliage in chimpanzee feces (Fig. 7(d); $r = 0.32$; $p < 0.05$). The results suggest that Kahuzi chimpanzees tend to enlarge their range area when fruit is scarce, visiting remote areas but not farther from their core area, toward which they return shortly.

DISCUSSION

Community Size and Home Range

Although it is difficult to make direct comparisons of chimpanzee home range sizes across study sites because of different methods used and length of study periods, some aspects of ranging patterns in relation to

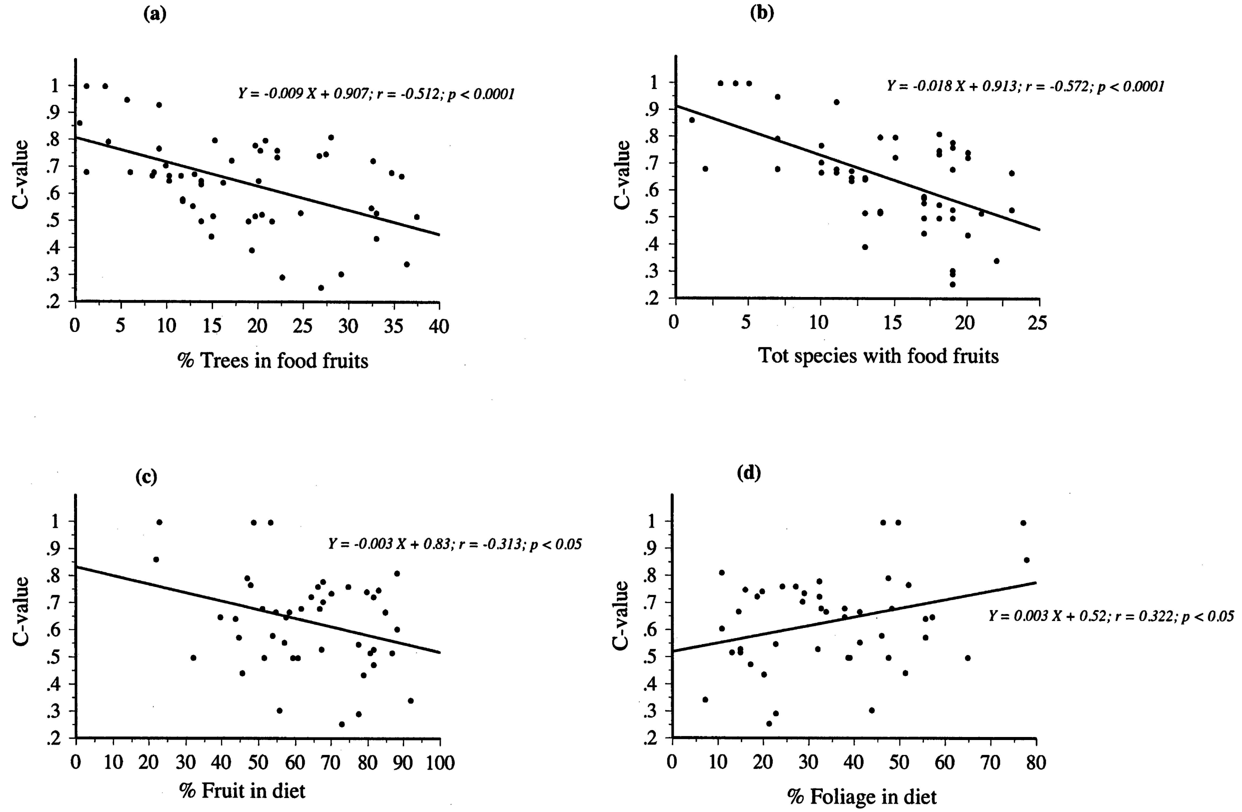

Fig. 7. Relationships between the C-value and the proportion of trees (a) and species (b) bearing ripe fruits; proportion of fruit (c) and foliage (d) in the chimpanzee diet.

forest structure and the availability of important foods make a rough comparison possible. Chimpanzees occupy a wide range of habitats, from low to high elevation rain forests, to more seasonal forests, to woodland, to gallery forest and woodland mixed with savanna areas (Reynolds and Reynolds, 1965; Nishida, 1979; Goodall, 1968; Kawanaka, 1984).

Kahuzi Chimpanzee population density is as low as those for the driest habitats, but the estimate of their home range size is similar to values for forest populations. Although home range size might have been similar, estimated community size for Kahuzi is 25–50% of the values for forest communities (Table IV). The relatively small home range (12.8 km^2) reported in this study may partially be due to the small community size in comparison to other forest communities, except for the semi-isolated population of Bossou. This is consistent with findings of Herbinger (2001), who reported that range area tends to increase with community size.

Home range size in primates indicates resource availability, with low abundance and high dispersal of food resources combining to produce larger ranges (Dunbar, 1988). The small home range and high local population density of Sonso chimpanzees, which is 3.2–6.8 individuals/km^2, is linked to the high productivity of chimpanzee foods in Sonso habitat (Newton-Fisher, 2003). In contrast, Kahuzi montane forest has low productivity of chimpanzee fruit foods, but chimpanzees use a small range area.

Density estimation at Kahuzi is misleading because much of the habitat is unsuitable for chimpanzees: dry bamboo forest and wet swamp areas. The unsuitable habitats did not contribute to expansion of their home range. By contrast, the low diversity and small amount of fruit in dry savanna habitats may result in the expansion of chimpanzee home range and decrease their density.

Accordingly the small community size and the large unusable habitat are both factors that may limit chimpanzees to range widely in the montane forest of Kahuzi.

Interunit-Group Effect

Chimpanzees sometimes engage in potentially lethal aggression between unit-groups. Male chimpanzees occasionally form parties that move to and along the periphery of their territory, searching for signs of chimpanzees from other communities. The number of males in a unit-group plays a decisive role in the attack of a neighboring unit-group (Goodall *et al.*, 1979; Nishida *et al.*, 1985).

Herbinger *et al.* (2001) found that in Taï Forest, a small community of chimpanzees tended to avoid encounter with a larger community. Boesch

Table IV. Density and home range sizes of chimpanzee communities in different habitat types

Locality	Habitat type	Density Ind./sq.km	Home range sq.km	Unit-group size Nbr Ind,	Source
Bossou (Guinea)	LF	3.67	6	22	Sugiyama, 1999; Yamakoshi, 1998
Taï (Côte d'Ivoire)	LF	2.92	27	79	Boesch and Boesch-Achermann, 1989
Budongo (Uganda)	MAF	4.00	20	80	Reynolds and Reynolds, 1965
Kibale (Uganda)	MAF	2.75	14.9	41	Chapman and Wrangham, 1993
Mahale (Tanzania)	WF	2.56	19.5	50	Turner, 1999
Filabanga (Tanzania)	S	0.33	150	50	Kano, 1971
Mt. Assirik (Senegal)	S	0.07	333	23	Baldwin *et al.*, 1982
Kahuzi-Biega (DR Congo)	MF	1.80[a]	12.8	23	This study

Note. Habitat type: LF: Lowland forest; MAF: Middle-altitude forest; WF: Woodland forest; S: Savanna; MF: Montane forest.

[a] Estimated density of Kaboko unit-group within its home range; Yamagiwa *et al.*, 1992 estimated 0.13 individuals per km^2 for all the 3 communities in all the 600 km^2 of the montane forest.

and Boesch-Achermann (2000) described interunit-group aggression in Taï chimpanzees. They found that when adult males declined in number, the remaining males became more cautious and switched from searching for neighbors to avoiding encounters. It seems that Kahuzi chimpanzees form small communities with few adult males and avoid each other, being separated by unusable areas that mostly contained bamboo forests or swamps. The limited number of adult males per unit-group at Kahuzi may account for this avoidance strategy.

Poaching Effect

Hunting has become the main threat to gorillas and elephants in Kahuzi-Biega National Park. However, unlike the sympatric gorillas, there is no evidence that the chimpanzee population is suffering from hunting pressure at Kahuzi. The presence of fresh nest sites in areas where gorilla slaughter has occurred suggests different avoidance strategies between the 2 species. We need more quantitative data on signs of human activities within chimpanzee home ranges to assess how much the ranging patterns of Kahuzi chimpanzees are affected by human pressure.

Habitat Preference and Fruit Availability

Baldwin *et al.* (1982) hypothesized that forest-dwelling chimpanzee populations might have smaller home ranges than those of chimpanzees in dryer habitats because the distribution of their food is dense. Like savanna populations, the density of Kahuzi chimpanzees is low, presumably because fruit availability is low. However, contrary to savanna dwelling chimpanzees, Kahuzi chimpanzees do not enlarge their home range, but instead seem to adapt the ranging patterns to the seasonality of fruit foods. They lengthen their day journeys during period of fruit scarcity by visiting more remote areas farther from the core area, while keeping close to primary forest. This ranging pattern seems to be a particularity from which they differ from conspecifics in dryer areas where chimpanzees have to range widely in search for sparser fruits (Baldwin *et al.*, 1982).

Availability of particular fruit in small patches of primary forests for a relatively long period (Fig. 3) may stimulate them to adhere to small fragmented primary forests and prevent them from ranging widely. A previous study on nesting site choice also showed that the primary forest was the most frequently chosen habitat by Kahuzi chimpanzees for nest building (Basabose and Yamagiwa, 2002), as in other habitats (Anderson *et al.*, 1983; Tutin and Fernandez, 1984).

Distribution and abundance of resources have been reported as environmental factors influencing range use of other primates (Altmann and Altmann, 1970; Clutton-Brock, 1977; Rasmussen, 1980; Strier, 1987; Kaplin, 2001). Similarly, Turner (2000) found that food distribution might be the key element determining how chimpanzees in the semi-evergreen gallery forest of Kasoje at Mahale (Tanzania) utilize their home range. The lowland semi-evergreen gallery forest with an abundance of fruit trees is critical for chimpanzee survival at Kasoje (Turner, 2000; Nishida, 1990). In the Kalinzu forest, Uganda, chimpanzee density is high in the patchy secondary forests within a primary forest (Hashimoto, 1995).

Kahuzi chimpanzees use some strategies enabling them to survive in the marginal habitat of montane forest characterized by low availability of fruits. They limit their home range around patchy primary forests producing a relatively big amount of their food fruits throughout the year. The patchy primary forests offer them more palatable fruits than any other habitat type within their home range and may therefore contribute to the stability in their ranging patterns. Kahuzi chimpanzees used their home range in a clumped pattern, visiting very frequently the core area and only rarely entered the peripheral areas. The small home range of chimpanzees in the study area may be due to the small community size, the avoidance of antagonistic relationship between neighboring unit- groups and the small fragmentary nature of primary forests.

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