Ranging and Grouping Patterns of a Western Lowland Gorilla Group at Bai Hokou, Central African Republic

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The ranging and grouping patterns of a gorilla group were studied during 27 months from 1990–1992 at the Bai Hokou study site, Central African Republic. The study group ranged far daily (average = 2.3 km/day) and had a large home range (22.9 km^2), relative to mountain gorillas, and ranging patterns differed between years. During 1990–1992, the bimale study group foraged less cohesively and had more flexible grouping patterns than mountain gorillas. The study group sometimes split into two distinct foraging subgroups, each led by a silverback, and these subgroups occasionally slept apart (mean = 950 m apart). Lowland gorillas rely on many of the same fruit resources as sympatric chimpanzees, and under certain demographic situations gorillas, like sympatric chimpanzees, may adapt their foraging group size to reduce intragroup feeding competition. However, the fiber content of the lowland gorilla diet likely relaxes constraints on foraging party size and facilitates group cohesion relative to chimpanzees. Am. J. Primatol. 43:111–133, 1997.   © 1997 Wiley-Liss, Inc.

Key words: *Gorilla gorilla gorilla;* **socioecology; apes**

INTRODUCTION

Western lowland gorillas (*Gorilla gorilla gorilla*) have proved difficult to study in the wild [Calvert, 1985; Carroll, 1988, 1996; Fay, 1989; Jones & Sabater-Pi, 1971; Mitani, 1992; Nishihara, 1995; Tutin et al., 1992; Williamson, 1988]. Lowland gorillas are shy, occur at low densities in areas of limited visibility, and travel widely. For all these reasons, no western lowland gorilla group is as fully habituated as some groups of mountain gorillas (*Gorilla gorilla beringei*). However, long-term studies at Lopé Gabon, Congo, and the Central African Republic show that western lowland gorillas are more frugivorous and climb trees more frequently than mountain gorillas [Mitani, 1992; Nishihara, 1995; Remis, 1994, 1995; Tutin & Fernandez, 1985; Williamson et al., 1990].

The western lowland gorillas observed during 27 months (August 1990 to November 1992) at the Bai Hokou study site, Central African Republic, like those during other work at Bai Hokou and at Lopé, consumed large quantities of fruit and other foods with discontinuous spatial and temporal distributions [Carroll, 1988, 1996; Goldsmith, 1996c; Remis, 1994; Tutin et al., 1991; Tutin & Fernan-

dez, 1993]. In fact, whenever gorillas are found in habitats where fruit is widely available, it is a large component of their diet [Kuroda et al., 1996; Rogers et al., 1990; Tutin, 1996; Yamagiwa et al., 1996]. Many of the large but unpredictable fruit resources used by both chimpanzees and gorillas in lowland forests exhibit marked seasonal and interannual variation in fruit production [Kano 1992; Nishihara, 1995; Tutin & Fernandez, 1993; Yamagiwa & Mwanza, 1994; Remis, 1994, 1996].

Despite the widespread correlations between body size and folivory [e.g., Clutton-Brock and Harvey, 1977], the western lowland gorilla diet is similar to that of the other frugivorous apes [Remis, 1994, 1996; Rogers et al., 1990]. As available data do not support a body size distinction between western lowland and mountain gorillas [Jungers and Susman, 1984], the extremely folivorous and terrestrial adaptation of mountain gorillas is likely shaped by montane habitat as much as body size [also see Remis, in press].

The large fruit component of the western lowland gorilla diet suggests that these gorillas may be more influenced by intragroup feeding competition than mountain gorillas that (with the exception of bamboo) do not rely heavily on seasonally or spatially discontinuous foods [Schaller, 1963; Stewart & Harcourt, 1987; Watts, 1991a]. Since ranging is shaped by diet [Clutton-Brock & Harvey, 1977; Isbell, 1991; Mace & Harvey, 1983], lowland gorillas should range further and in a less cohesive fashion than mountain gorillas [Chapman et al., 1995; Terborgh and Janson, 1986; Tutin et al., 1992; Van Schaik et al., 1983; Watts 1988, 1991a; Wrangham et al., 1993]. Foraging party sizes have been positively correlated with patch size or fruit abundance among many primate species [Leighton & Leighton, 1982; Strier, 1989; Sugardjito et al., 1987; White & Wrangham, 1988], and the gorillas at Bai Hokou are no exception [Remis, 1995].

Although a growing body of evidence has shown western lowland gorillas to be seasonally frugivorous, very little has been published on their long-term ranging patterns [Goldsmith, 1996a,b,c; Tutin et al., 1992; Tutin, 1996]. The analysis presented here reports on the ranging and grouping patterns of one group of gorillas at Bai Hokou, Central African Republic. It provides data to support predictions that fruit-eating gorillas range farther and in a less cohesive fashion than mountain gorillas. Flexibility in grouping and seasonal and intraannual variation in travel distances and home range sizes of the focal study group are discussed and compared to those of other African ape populations.

METHODS
Data Collection

Study area. The Bai Hokou study area is located in the Dzanga-Ndoki National Park sector of the Dzanga-Sangha Reserve, Central African Republic, near the Congo border (2°50′ N, 16°28′ E). The area was selectively logged at low intensity for two species of hardwoods prior to 1982 [Carroll, 1996; Slovenia Bois records] (Fig. 1). The habitat is primarily mixed species semideciduous forest, and differences between logged and unlogged forest in density and abundance of tree species are few [Carroll, 1996]. Average rainfall in the region is approximately 1,400 mm per year. Typically fewer than 100 mm of rain falls during the dry season, January through March [Remis, 1994, 1997a]. Abandoned logging roads (unused for more than 10 years) and major elephant trails used by the gorillas and researchers became the framework for a trail system. Additional trails were cut and marked, and compass bearings were taken at 50 m intervals on all trails.
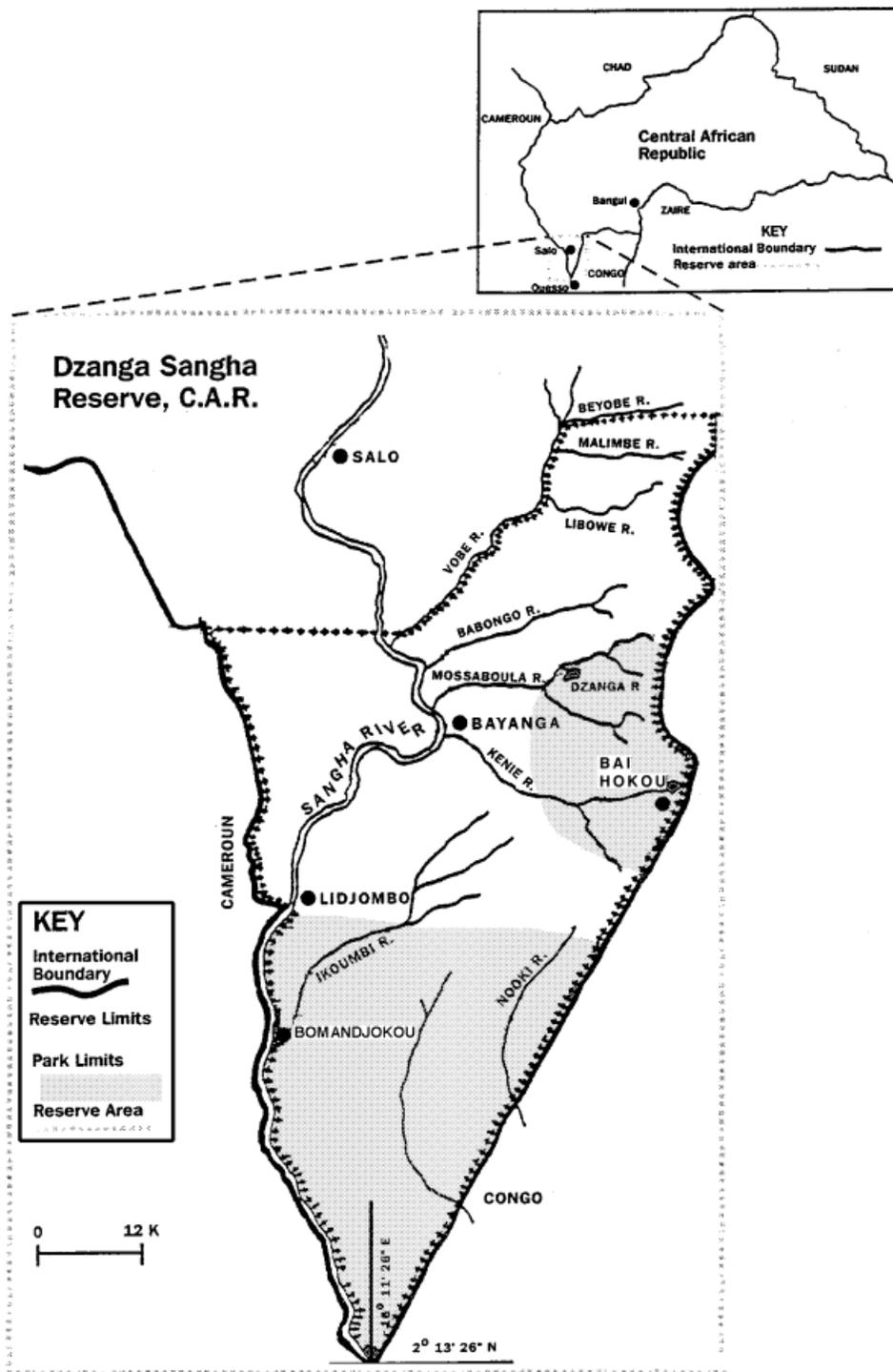
Fig. 1.   Map of the study area within the Dzanga-Sangha Reserve.

Study subjects. The gorillas were always located with the assistance of one or two Aka trackers and sometimes additional teams of trackers and other research assistants. The trackers, particularly E. Wonga and P. Mokedi, were skilled at finding subtle traces of gorilla activity and greatly increased our ability to locate gorillas and their trail. Unlike the large swaths mountain gorillas make through herbaceous vegetation, the tracks and feeding remains of lowland gorillas are rarely continuous [Remis, 1994; Tutin et al., 1992]. Thus, tracking was difficult, especially in the dry season when dry leaf litter covered the ground and gorilla movements left little trace. Whenever possible, observational samples of activity budgets, diet, and positional behavior were taken at 1 min intervals, and information on party size was collected at 10 min intervals on undisturbed (nondisplaying) focal animals [Remis, 1995].

Research focused on Combetti's group (group C). Group C varied in composition over the course of the study from 12–15 weaned, nest-building individuals. There were two mature silverbacks, two blackbacks, four to five adult females, one subadult of unknown sex, three to five juveniles, and two infants in the group. The ranges of at least two groups (group sizes = 6 and 8) overlapped the peripheries of group C's range but not each other's ranges. Only a third group consisting of four individuals was ever found inside the central portion of group C's range.

Group C gradually became semihabituated [following Fossey, 1983; Tutin & Fernandez, 1991], and, if resting or feeding in a tree or at a comfortable distance (30 or more meters depending on visibility), the study group tolerated the presence of human observers. If gorillas expressed fear (e.g., diarrhetic dung on the trail, screaming), we ceased our efforts to follow them or to record their ranging.

Seasonal variation in diet and food availability. Whenever possible, observational data were collected using focal animal samples on nondisplaying, nonfleeing individuals.

Data on party size were collected at 10 min intervals, and activity, height, positional behavior, and plant part and species eaten were recorded at 1 min intervals. Additional information on diet was obtained from feeding trail remains and macroscopic fecal analysis [Remis, 1994, 1995, 1996]. During the dry season months, January through March, gorillas primarily ate herbaceous piths, barks, leaves, and fibrous fruits. In the wet seasons, gorillas ate large quantities of fleshy fruits, and consumption of fibrous foods was often quite low. Fruit availability differed seasonally and between years during the study. Few fleshy fruits were available during the dry seasons.

In 1991, relatively few trees bore fruit, and even fewer produced ripe fruit [see Remis, in review]. In order to estimate the relative availability of tree foods in the forest, marked and identified trees on five cut transects (4 km each) were monitored monthly to determine the presence of young leaves, flowers, and unripe and ripe fruits (n = 973 trees). No efforts were made to quantify fruit production [Carroll, 1996; Remis, 1994, 1996, in review].

Nest sites. For the purposes of this study, nest counts at nest sites were used to aid group identification, in conjunction with observations and trail evidence [see below; Tutin, 1996]. At nest sites, feces were collected for analyses of diet. Maps of nest sites and individual nests were drawn to facilitate counts and to study overall nesting patterns. Nest counts of a given group varied, as, on rare occasions, individuals would make more than one nest. Moreover, although nests were typically clustered, occasionally juveniles made peripheral nests that could be difficult to locate. However, most incorrect counts were off by one or two individuals, and these could often be attributed to a group of known size and composition [Remis, 1994; also Tutin et al., 1995; Tutin, 1996]. During this study,

group C (n = 12–15 individuals) was the only group known in its range that contained more than ten individuals. Thus, nest sites that contained 11–16 nests could be attributed to group C.

Gorillas at Bai Hokou often nested on bare ground, without using vegetation (44% of all gorilla night nests found during the study period, n = 1,231 nests at 163 group nest sites) [Remis, 1993]. At 85% of nest sites, one or more nests were constructed from vegetation. To ensure the accuracy of nest counts, only nest sites less than 4 days old were used for the analyses which follow [Remis, 1993; Tutin & Fernandez, 1984; Tutin et al., 1995]. Individual night nests without vegetative construction could be detected by the presence of night and morning dung, hair, and an impression on the ground. These were included in total nest counts.

Ranging patterns. Paths taken by the researchers, gorilla trails, nest sites, direct contacts with gorillas, and major food trees were mapped daily based on estimated distances from marked trails and known landmarks. A pedometer was used in conjunction with counting paces to estimate distances from landmarks and opportunistically, between nests with a site and between nests and first feeding sites and to estimate group spread. A 250 by 250 m grid was superimposed onto the map of the study area, and single daily entrances of the gorillas and the researchers into particular quadrats were recorded [Casimir & Butenandt, 1973; Fossey, 1974; Goodall, 1977; Watts, 1991a; Tutin et al., 1992; Tutin, 1996]. The large grid was chosen for comparability with previous mountain gorilla studies [e.g., Fossey, 1974] because of the wide-ranging habits of the gorillas and the coarseness of our trail system.

Minimum home range was calculated by mapping all contacts, nest sites, and trails which met the criteria for belonging to group C and calculating the smallest area enclosing all 250 by 250 m quadrats entered [also see Tutin et al., 1992]. A single foray made by the group far outside the periphery of its range was excluded from the analyses. The smaller quadrats comprising the study area were grouped into 2.5 km regions (blocks).

Entrances into blocks were calculated by summing daily entrances into the smaller quadrats within the region. In order to distinguish shifts in home range by the gorillas from shifts in areas searched by the researchers, we compared our entries (scored once daily) into the large blocks of the study area with the frequency of daily gorilla sightings and signs in those same blocks. Complete day journey lengths for group C were collected opportunistically by tracking between consecutive nest sites. Complete day journey lengths and estimates of minimum day journey lengths were obtained from summing numbers of quadrats entered by the gorillas on complete or partial trails.

Criteria for Data Inclusion

Because the gorillas were not fully habituated and never observed for an entire day, estimates of their ranging are based on a combination of direct contacts with gorillas, trails, and nest sites. On some of the occasions when we failed to locate the gorillas or their trails, they were likely to be outside their known range. As a result, the data presented here are likely to be underestimates of their range.

For the following analyses, data on the movements, nest sites, and contacts of group C were selected from the total data set using the following criteria: 1) visual contact with a well-known individual, usually one of the two group silverbacks, or 2) a visual or auditory contact, trail, or nest site directly associated with a positive identification of a known individual.

During the study period we became more familiar with the gorilla groups in the area and acquired additional teams of trackers. Thus, in this analysis, we were able to include data collected after the first 10 months of the study that adhered to the following additional criteria: 1) a visual or auditory contact or trail directly associated with a nest site of 11–15 individuals within the known range of group C and 2) trail fragments or nest sites with fewer than 11–16 individuals in the vicinity of the last confirmed observation of group C and directly associated with other nest sites which when combined totaled 11–15 and indicated that group C had temporarily split into subgroups (see below). To avoid confusing the group of 4 with a subgroup of group C, nest sites of four were not included in these latter criteria unless within a string of trails and consecutive nests of group C. By these methods, 66% of the 163 nest sites found and 57% of the 143 contacts with groups could be attributed to group C.

Group C was considered to be traveling or foraging as a single unit if individuals moved together or along parallel paths (maintaining vocal contact, usually within 300 m when estimated) and by nightfall all members nested at one nest site (all nests within 1 hectare [see Remis, 1993]). Subgroups were difficult to detect in dense forest but were defined as spatial subsets of group C that moved as a single unit independently from (at least 500 m apart and apparently often out of auditory range) the rest of group C and slept separately [Robinson & Janson, 1987]. Foraging parties, on the other hand, fed together within a tree or cluster of trees but also maintained vocal contact with the rest of the group. These parties coordinated travel with the rest of the group and rejoined a larger unit for sleeping. Foraging parties could be comprised of lone individuals or groups of females up to 500 m from males and were more temporary, fluid, and less predictable in size and composition than subgroups of group C [Elsacker et al., 1995].

If only one silverback was observed in a small subset of group C and auditory, nest, and trail evidence gave no sign of other individuals within a carefully searched area of at least 500 m^2 (trackers often returned the next day to confirm the absence of trail sign), group C was considered likely to be moving in distinct subgroups. However, because of the difficulty of measuring group spread and confirming the presence or absence of partially habituated individuals [Chapman et al., 1993], subgrouping was only considered confirmed when 1) clear trail and/or contact evidence of group C connected two small nest sites (>500 m apart), for a particular day, 2) consecutive nest sites confirmed to belong to group C varied by three or more individuals, or 3) isolated small nest sites were associated with contacts with members of group C. Foraging party sizes or the frequency with which the group foraged as several foraging parties could not be quantified during this study.

RESULTS
Minimum Home Range Estimates

From 1990–1992, group C entered 336 quadrats (n = 778 entrances) which yielded a minimum home range of 22.9 km^2. The estimated home range for the group was smaller during a single year than for the whole study period and differed between years. In 1991, we recorded the gorillas in a total of 186 quadrats (n = 317). Estimated minimum home range during this time was 13.7 km^2. In 1992, we recorded the gorillas in 250 quadrats (n = 454), yielding an annual home range estimate of 18.1 km^2. Fifty-nine percent of these quadrats had not been entered previously. During the 3 month dry season, the gorillas used a much smaller range than in the wet seasons (1992 dry range = 4.6 km^2; 1991 wet

season range = 13.1 km^2; 1992 wet season range = 15.1 km^2). The 108 nest sites attributable to group C account for only 13% (n = 810) of nights during the study period. Although large, the estimated home range size of the group was still increasing at the end of the study (Fig. 2).

Our success in finding the gorillas appeared to increase over the study. However, the monthly success rate (number of days gorillas were sampled/number of days searched for gorillas) was only weakly and nonsignificantly correlated with the time period of the study (Pearson correlation coefficient: r = .3134, P = .104) and not likely related to season (r = .0571, P = .773). In addition, the monthly home range index for the gorillas (number of quadrats used per month/number of days sampled) was not strongly or significantly correlated with the monthly success rate (r = .2552, P = .19). Thus, the findings regarding home range were not likely related to any unevenness of sampling or monthly differences in our ability to track the gorillas. The monthly home range index varied by season and showed that gorillas ranged over larger areas during the wet months of 1992 than during dry months of 1991 or 1992 or during the poor fruit wet season of 1991 (two-tailed, independent two-way t-tests: wet '92 vs. wet '91, P = .02; wet '92 vs. dry '92, P = .02; wet '92 vs. dry '91, P = .005; wet '91 vs. dry '91, not significant; wet '91 vs. dry '92, not significant).

Intensity of Range Use

The gorillas traveled widely throughout their home range, although a few areas within group C's home range were used more intensively. While entries into blocks were too few to positively identify these areas as core areas [e.g., Samuel et al., 1985], four of the nine blocks making up their total range accounted for 80% of all quadrat entrances (scored once daily), and just one block (block e) accounted for 30% (Fig. 3). Intensity of use varied seasonally and throughout the study (Fig. 4).

Our knowledge of the home range of group C increased with our ability to locate the group and with the number of trackers. We were successful in predicting where the gorillas would be, as demonstrated by the high correlation between our entry into the nine blocks composing the study area and that of the gorillas (Fig. 5) (Spearman rank r = .89). If the gorillas ranged regularly, the proportion of encounters with the group in each block should be similar to the proportion of time we spent searching in each block. Nevertheless, sometimes we found the gorillas more or less frequently than would be expected based on the time we spent searching in that block (Fig. 5).

In order to distinguish between real shifts in group C's ranging and our own increases in areas searched and success in finding the gorillas, we measured the discrepancy between our observations and our expected rates of encounter based on time spent searching in an area. By this analysis, the variations in our success in contacting the gorillas represent real shifts in their ranging patterns rather than ours. Figure 6 shows the positive and negative differences (rather than the actual visits) between the frequency of gorilla sightings (observed) and the frequency of our presence (expected) in each block of the study area. By this measure, positive values were "super successes" and indicate that the gorillas and their traces were found in those blocks more than we had expected based on previous encounters.

Over the course of the study we ventured further and began to search eastern sectors of the study area more frequently. Although there were no apparent differences in ease of observation or tracking between areas, in 1992 we found

August 1990-October 1992

total no. quads entered

total numbers of quads entered

1990

1992

Fig. 2. Cumulative increase in home range of group C, 1990–1992.

NORTH

.6% g	12% h	21% i
2% d	33% e	21% f
CAMP a	6% b	4% c

Fig. 3. Intensity of home range use by group C, 1990–1992. The figure and those which follow represent a map of group C's range superimposed by a grid. Each cell depicts one 2.5 km² region/block. The letters represent the names of each block. The camp was located in block a and included for reference only. Percentages in each block represent the proportion of time group C was recorded in each region of its 22.9 km² home range from 1990–1992 (778 entrances (scored once daily) into smaller quadrats within each block were summed).

the group in the north, northeast, and south more than expected (and in formerly used central areas less than expected) based solely on our increased time spent searching in those regions.

Despite the likelihood that, on occasion, group C was present but undetected within the study area, this analysis allows us to detect seasonal shifts in its range. We had frequent contacts with group C in the northern section of its range during the wet seasons and rarely contacted it there during the dry season. In the wet seasons, the gorillas were encountered less frequently in the wetter central and southern regions (adjacent to the stream system) than they had been during the previous dry seasons (Fig. 6).

Daily Ranging

Complete day journey estimates. Complete day journey data were obtained only during the wet seasons of 1991 and 1992, when gorillas entered 9.4 quadrats on average, giving a mean distance of 2.3 km per day (n = 8; range 1–3.25 km per day). This figure is likely to be an underestimate of the average and range of distances traveled during the rainy season because trails of gorillas moving long distances between fruiting resources were often lost without reaching the nest sites. Individuals circuiting repeatedly between two *Gambeya*

1991 Wet Season n=282
NORTH

--	12%	14%
g	h	i
3	44%	15%
d	e	f
CAMP	7%	5%
a	b	c

1991 Dry Season n=24
NORTH

--	--	--
g	h	i
--	79%	--
d	e	f
CAMP	21%	--
a	b	c

1992 Wet Season n=361
NORTH

2%	17%	30%
g	h	i
1%	22%	27%
d	e	f
CAMP	.5%	.5%
a	b	c

1992 Dry Season n=93
NORTH

--	--	5%
g	h	i
--	14%	29%
d	e	f
CAMP	20%	16%
a	b	c

Fig. 4. Seasonal intensity of range use. Percentages displayed in each block represent the proportion of the entrances by group C during each season of the study period. For this analysis numbers of entrances into smaller quadrats (scored once daily) within each block were summed. The study groups made differential use of the regions (as represented by blocks) of their home range seasonally and annually. In 1992, blocks i and f replaced block e as the regions of most intense use. RxC contingency tables, G tests of independence (corrected by the Williams Correction Factor). Tests are performed on raw data and are two-tailed. Differences between seasons and years are significant $P < 0.001$. Total data set = G(w) = 223.9. Wet vs. dry season; 1991, G(w) = 28.26. Wet vs. dry season; 1992, G(w) = 123.0. Wet 1991 vs. wet 1992 season, G(w) = 92.5. Dry 1991 vs. dry 1992 season, G(w) = 44.6.

lacourtia trees probably traveled over 8 km in 1 day, although the group's nest site was never located and only 19 quadrats were entered. In addition, the quadrat method used to determine range in this study is likely to underestimate distance travelled by as much as 20–25% [Goldsmith, 1996a,b,c; Tutin, 1996].

Estimates of minimum day journey length. When partial trails of group C were followed, the group was recorded in 6.1 quadrats per day on average (range = 1–19; n = 119 paths followed). Although these data are not accurate reflections of total day journey, they yield a mean minimum day journey length of 1.5 km per day (range = .25–4.75 km). Mean minimum day journey length during the wet seasons was 1.6 km (1991 range = .25–4.25 km, n = 45; 1992 range = .25–4.75 km, n = 55). Mean minimum day journey length during the 1992 dry season was 1.2 km per day (range = .25–3 km, n = 19). As dry season

NORTH

1% (3%) g	9% (8%) h	11% (7%) i
4% (8%) d	41% (35%) e	15% (13%) f
CAMP (a)	14% (20%) b	5% (6%) c

Fig. 5. Regional use of range of group C, 1990–1992: Observed vs. expected. Percentage of gorillas' entrances into large regional blocks by group C (observed) (n = 237) compared with those of the researcher (expected) (in parentheses, n = 1,112). Spearman rank test r = .89, $P < 0.001$. In this figure and in fig. 6, the gorillas and researchers were scored as entering blocks once daily.

data are few, differences between seasons do not reach statistical significance (t = 1.7, df = 18, $P < .08$) (but see Discussion).

GROUP DYNAMICS: FLEXIBILITY OF GROUPING

Distance between foraging individuals was difficult to quantify but varied widely (estimated to be 15–500 m). During 89 visual contacts with group C, on average only 2.5 animals were observed (range = 1–12, S.D. = 2). Despite the difficulty of observing individuals on the ground, the presence of an individual in a tree could usually be detected. During focal animal sampling (n = 138; 10 min interval samples), the average number of group members feeding together in a party within a tree was three (party size range = 1–12, S.D. = 2). Within 29 feeding trees, the average party size was 3.5 (range = 1–12), although there were usually several individuals detected on the ground below and the total subgroup or group size was typically larger.

It was rare to observe more than six gorillas feeding together within a single tree (less than ten occasions). Even if on the ground, silverbacks were not likely to be overlooked because of their frequent vocalizations, chest beats, and characteristic odors [Fossey, 1972; Harcourt et al., 1993; Schaller, 1963; Tutin & Fernandez, 1991]. The absence of one of the two group silverbacks during an extended observation was considered an indication that the group was likely foraging in a dispersed manner, either as several foraging parties or two subgroups.

WET SEASON 1990–WET SEASON 1992:

NORTH

-1 g	+13 h	+12 i
-22 d	**-43** e	+14 f
CAMP a	+14 b	+1 c

WET SEASON 1991 (differences between dry and wet seasons 1991):

NORTH

0 g	+3 h	+3 i
+8 d	**-14** e	+2 f
CAMP a	**-6** b	+3 c

WET SEASON 1992 (differences between dry and wet seasons 1992):

NORTH

-2 g	**+18** h	**+10** I
-2 d	-1 e	**+5** f
CAMP a	-7 b	-4 c

Fig. 6. Shifts in range by group C: Seasonal and yearly differences in success rates of locating gorillas. Seasonal and yearly differences between gorilla entrances (observed) and observer presence (expected) in regions of the study area. This figure shows our success and failure rates as measured by the discrepancy between gorilla sighting and researcher presence in each block (rather than actual occurrences).

Group C sometimes split into two subgroups which traveled separately and occasionally slept apart. Each subgroup always contained a silverback. Females were seen in single-sex foraging parties with a tree, but no female was ever seen traveling independently of other individuals or in a subgroup without a silverback within a few hundred meters (similar to mountain gorillas [Harcourt, 1978; Steward & Harcourt, 1987]).

Typically, group C had 13 weaned members. If at least 11 nests of the individuals in group C were found at a nest site, the group was considered to be sleeping as a single unit. However, of the 108 nest sites at Bai Hokou confirmed to be associated with group C, 58% contained fewer than 11 nests (range = 4–16, mean = 9.3, median = 9, S.D. = 3.3). On seven of eight occasions when group C trails were followed from morning to evening nests, at least one of the nest sites contained fewer than 11 individuals. While Tutin et al. [1995] report that only 30% of nest sites at Lopé accurately reflected group size over a 4 year period, 74–90% of nest counts were within one or two nests of group size. Thus, the variability in nest site counts at Bai Hokou differed considerably from that at Lopé [Remis, 1993, 1994], and at least some of the nest counts that differed from total group size by more than two nests resulted from animals sleeping in subgroups. Inspection of nest sites did not reveal any detectable stability of subgroup composition. Subgroups rarely persisted for more than a couple of days, although on one occasion the group did not sleep as a single unit for at least 4 days.

It was unusual to be able to locate and follow the trail of more than one subgroup to its nest site, especially if the subgroup nest sites were widely separated. However, on four occasions we confirmed that the subgroups had slept, on average, 950 m apart (range = 800–1000 m).

On at least 34 occasions (19% of all days on which group C's movements were recorded, n = 182) the group split, slept apart, and came back together. Sixty-five percent of the confirmed subgrouping of group C occurred during the wet season of 1991, when availability of fruit was unusually low; only 19% of individual trees on phenology trails produced ripe fruit in 1991, as compared with 47% in 1990 and 36% in 1992 [Remis, 1994, 1996, in review].

DISCUSSION

African apes are highly variable in their ranging and foraging habits, from the mountain gorilla on one hand to the chimpanzee and bonobo on the other. Mountain gorillas have short day journeys, a small range, densely distributed foods, a herbivorous diet, and cohesive grouping patterns [Fossey, 1974; Fossey & Harcourt, 1977; McNeilage, 1995; Watts, 1990]. Chimpanzees and bonobos have long day journeys, large ranges, variable party sizes, and a heavy reliance on fruit [Boesch & Boesch, 1984; Goodall, 1986; Kano & Mulavwa, 1984; Nishida, 1979; Thompson-Handler, 1990; Wrangham, 1986]. The lowland gorilla, as predicted, is intermediate between these two extremes [also see Casimir & Butenandt, 1973; Goodall, 1977; Mwanza et al., 1992; Remis, 1994; Tutin et al., 1992; Williamson et al., 1990; Yamagiwa et al., 1994; Yamagiwa & Mwanza, 1994].

In many respects, lowland gorillas remain enigmatic, and their study has necessitated some degree of opportunism in data collection. However, similarities between studies lend support to the conclusions drawn in this study. The gorillas at Bai Hokou, like those at Lopé and Kahuzi-Biega, Zaire, had large annual and total home ranges relative to those of mountain gorillas (Table I). Moreover, the methods used to calculate home range in many of these studies may underestimate range size relative to the minimum convex polygon method used by McNeilage [1995] for mountain gorillas.

TABLE I. Ape Frugivory and Ranging Patterns: Gorillas

Species	Study[a]	Study length (months)	Number of fruits in diet	Daily travel (km) mean[b]	Annual home range (km²)[c]	Number of groups
Gorilla gorilla beringei						
	Schaller, 1963	16	3		20	1
	Fossey, 1974	60	—	(.25–1)	8	
	Fossey and Harcourt, 1977 (10–17)	84	—	.35–.45 (.1–2.5)	4–8.1	5
	Vedder, 1984 (12–14)	18	1	(.25–2.5)	8.6	1
	Yamagiwa, 1986 (1)	9	—	.43 (.3–1.7)	—	1
	Yamagiwa, 1987	11	—	.63 (.98–2.9)	9.7	
	Watts, 1991a (2, 7, 9, 12, 17)	55	3 [Watts, 1984]	(.4–.8)	—	5
	McNeilage, 1995 (10, 13)	39		.55–.76	11.6, 4.7	2
Gorilla gorilla graueri	Casimir and Butenandt, 1973 (20)	15	2 [Casimir, 1975]	.9 (.6–1.1)	30	1
Kahuzi	Goodall, 1977 (20)	6	3	1 km (.1–3.4)	16–34	1
	Yamagiwa et al., 1992	12		1.2 (.5–2.6)	—	2
Itebero	Yamagiwa et al., 1992	5	48 [Yamagiwa et al., 1994]	2.1 (.8–3.4)	—	1
	(1) (group)			2.2, 2.7		2
	Yamagiwa et al., 1996 (5, 12, 17, 20)	48?		.81		4
Gorilla gorilla gorilla	Jones and Sabater-Pi, 1971	17	52 [Sabater-Pi, 1977]	—	5.6	2
	Tutin, 1996 (11)	108	100 [Tutin et al., 1997]	1.14 (.43–2.8)	6.8	4
	Tutin et al., 1992	78			8.1 (21.7)	1
	(8)			1.2 (.7–1.7)	5.2	1
	(4)			1.2 (.8–1.7)	3.9	1
	This study (13)	27	77	2.3 (1–3.3)	18.1 (22.9)	1

[a]Group size given in parentheses.
[b]Range given in parentheses.
[c]Total given in parentheses.

Home range among African apes is related to the degree of frugivory, as approximated by the numbers of fruit species eaten (Tables I, II) [Remis, in review]. Spatial dispersion of foods, a better measure for this comparison, was not quantified in this study or many others. Mountain gorillas eat few fruits and range short distances. Most shifts in home range among mountain gorillas have been attributed to mating tactics rather than food availability [Watts, 1994]. Lowland gorillas, like chimpanzees and bonobos, are seasonally frugivorous. They experience yearly and seasonal shifts in foraging patterns and home range that have been related to food availability [Kano, 1992; Mwanza et al., 1992; Remis, 1994; Tutin et al., 1992; Tutin and Fernandez, 1993; Yamagiwa et al., 1994]. Therefore, it is not surprising that lowland gorilla groups range further than mountain gorillas and most draw from a larger total food supply area.

Lowland gorillas have longer day journey lengths than do mountain gorillas (Table I), although day journey length may vary with group size [Elliott, 1976; Fossey and Harcourt, 1977; Watts, 1991a; Tutin et al., 1992; but see Goldsmith, 1996a,c; Tutin, 1996] and some studies (including this one) sample only one or two groups.

When gorillas were concentrating on widely scattered fruits, their day journey lengths appeared longer than during dry seasons when they were feeding on herbs, leaves, and bark [Remis, 1994]. The gorillas appeared to restrict their movement to smaller core areas during the dry season. The monthly home range index analysis indicated that gorillas ranged farther during the fruit-rich wet season of 1992 than during the fruit-poor wet season of 1991 or the dry seasons. Moreover, distances between consecutive dry season feeding sites were short, and the gorillas did not typically travel more than 20 m from nest to first feeding site. It is therefore likely that the short trail fragments in the dry season are a true reflection of shorter day journey lengths at that time. Similarly, Tutin [1996] reports longer day journeys during fruit months, with decreases during fruit poor months.

Very large groups (>18 gorillas) have not been reported for western lowland gorillas. The Bai Hokou study group is large compared to other lowland gorilla groups but similar in size to those of mountain gorillas (Table III and references there) [but see Tutin et al., 1992]. Group C had two silverbacks, like the majority of other large groups known in the Dzanga-Sangha region [Goldsmith, 1996c; Remis, unpublished data]. Among mountain gorillas, 40% of groups contain more than one silverback [Schaller, 1963; Weber and Vedder, 1983], and the demographic records for Karisoke show the mean number of silverbacks per group to be 1.7 [Robbins, 1995]. Moreover, differences in behavior and mating patterns between single and multimale mountain gorilla groups have been reported [Robbins, 1995; Sicotte, 1993].

During this study, 1990–1992, the Bai Hokou group formed subgroups which foraged and slept separately on more than 34 occasions. Goldsmith [1996b,c] documented 29 cases of subgrouping by group C and other multimale groups at Bai Hokou using consecutive nest sites on 93 complete morning to evening trails between 1993 and 1995. Schaller [1963] and Watts [1991b, 1992] have reported more restricted episodes of subgrouping by day and night for bimale mountain gorilla groups. Subgrouping has also been suggested but not confirmed for western lowland gorillas in the Congo [Doran, personal communication; Mitani, 1992; Mitani et al., 1993].

In contrast, Tutin [1996] has reported only two instances of subgrouping by Lopé gorillas during the day (and never at night). The gorilla groups at Lopé have been described as cohesive and similar in structure to those of most moun-

TABLE II. Ape Frugivory and Ranging Patterns: Chimpanzees and Orangutans

Species	Study (group)	Study length (months)	Fruits in diet	Daily travel mean (km)[a]	Annual home range (km^2)
Pan troglodytes shweinfurtheii	Pierce, 1978	13		2.4	
	Gombe (Kasekela)				15.0
	(Kahema)				3.9
	Wrangham, 1975	12	68	3.9	
	Gombe			(M = 4.9, F = 3.0)	
	Nishida, 1979	35	100		10.4
	Mahale		[Nishida & Uehara, 1983]		13.4
	Ghiglieri, 1984, Kibale	17			23.1–37.9
	Goodall, 1986	300			
	Gombe community				10.4–33
	Males				9–12
	Females				5.8–7
	Estrus females				8.3–11
Pan troglodytes verus	Tutin et al., 1983	47	34 [McGrew et al., 1988]		278–333
	Mt. Assirik				
	Boesch and Boesch, 1984,				
	Tai	48			27
Pan paniscus	Kano and Mulavwa, 1984,	28	67	2.4 (.4–6)	58
	Wamba				
	Thompson-Handler, 1990	17	62 [Badrian & Malenky, 1984]		23.4 (12–13)
	Lomako community n=81,				
	(individual units)				
Pongo pygmaeus pygmaeus	Galdikas, 1988,	48	169	(F) .71	(F) 5.6
	Tanjung Puting			(M) .85	(M) ?

[a]Range given in parentheses.
M = males, F = females.

TABLE III. Average Group Sizes of Gorillas

Species	Average group size[a]
Gorilla gorilla gorilla	
Fay, 1989 (n = 135 sites) (Census, South Dzanga-Sangha, CAR)	4.1 (1–13)
	5.2, solitaries excluded
Carroll, 1988 (n = 261 sites) (Census, North Dzanga-Sangha, CAR)	5.1 (1–52)
Remis, 1993 (n = 163 sites) (Bai Hokou, Dzanga-Sangha, CAR)	8, solitaries excluded (2–16)
Remis, unpublished (n = 24 sites) (Census, Bai Hokou, CAR)	3.6 (1–13)
Fay and Agnagna, 1992 (n = 51 sites) (Census, North Congo)	3.8 (not available)
	5.0, solitaries excluded
Mitani et al., 1993 (n = 7 groups) (Ndoki, Congo)	4.7
	7.3, solitaries excluded
Mitani, 1992 (Ndoki, Congo) (n = 232 sites)	2.2 (1–10)
	1.6
Tutin and Fernandez, 1984 (n = 136 sites) (Census, Gabon)	4, median = 3.7 (1–19)
Jones and Sabater-Pi, 1971 (n = 13 groups) (Rio Muni)	6.4–7.1, median = 5 (2–12)
Tutin et al., 1992 (n = 8 groups) (Lopé, Gabon)	Median = 10, (4–16)
Gorilla gorilla beringei[a]	
Schaller, 1963 (10)	16.9 (2–16)
Harcourt et al., 1981 (31)	7.9, median = 9.2 (2–21)
Weber and Vedder, 1983 (28)	8.8 (3–21)
Aveling and Harcourt, 1983 (28)	8.5 (not available)
Aveling and Aveling, 1987 (29)	10.4 protected
	7.1 unprotected (not available)
Gorilla gorilla graueri[a] Kahuzi, Zaire	
Yamagiwa et al., 1993 (25)	10.8 (2–24)
Murnyak, 1981 (14)	15.6, median (2–37)

[a]Number of groups given in parentheses.

tain gorillas [Tutin et al., 1992]. The best studied groups at Lopé contain only one male. The degree of dispersal observed at Bai Hokou may be restricted to groups containing multiple silverbacks and may be related to habitat differences between study sites. Differences between populations and habitats of western lowland gorillas warrant further study. Comparative studies of group composition and dynamics will be aided by pending genetic analyses of the Bai Hokou and Lopé populations [Wickings, 1993, personal communication; Tutin, 1996].

Flexible or "fission–fusion" grouping patterns have been viewed as a response to feeding competition [Kinzey & Cunningham, 1994; Sugardjito et al., 1987; Symington, 1990; White and Wrangham, 1988] and/or predation pressure [Boesch, 1991; Kano, 1992; Sakura, 1994; Tutin et al., 1983]. The clumped distribution of many foods at Bai Hokou [Carroll, 1996; Goldsmith, 1996c] may generate greater levels of intragroup feeding competition than are faced by mountain gorillas [Vedder, 1984; Watts, 1985, 1990, 1991a], and large groups may benefit from increasing group spread or reducing foraging group size. Although a high intake of terrestrial foods by gorillas may help reduce competition [Malenky et al., 1994; Wrangham, 1986], foraging party size was correlated with patch size at Bai Hokou, and the foraging budgets of individuals were affected by the presence of conspecifics [Remis 1994, 1995].

Subgrouping by gorillas at Bai Hokou appears restricted to groups containing at least two silverbacks [Goldsmith, personal communication; Remis, unpublished]. The behavior described for group C may represent a temporary response possible for any gorilla group under certain demographic, historic, or social conditions or a rare response to poor fruiting conditions. Subgrouping by group C is unlikely to have been part of a gradual fission process, as the study group was still intact and occasionally subgrouping in December 1995 [Remis, personal observation]. Under any of these scenarios, however, feeding competition may be important.

Although feeding competition may favor subgrouping of large gorilla groups, gorillas are vulnerable to predation [Fay et al., 1995; Nishihara, personal communication; Schaller, 1963; Tutin & Benirschke, 1991], and females may aggregate for protection against predators or outsider males or for social reasons. The grouping pattern described here for group C is different from the behavior of other species in which fission–fusion is a ubiquitous feature of society. In contrast to chimpanzees, gorilla females maintain close associations with males while foraging and do not sleep without a male nearby. This suggests that their spatial dispersion is constrained by factors in addition to the distribution of food. For gorillas, proximity to a male rather than absolute group size may provide the best protection from predators [Schaller, 1963; Steward & Harcourt, 1987] or outsider males [Watts, 1989; Wrangham, 1986] and may strongly influence overall grouping patterns.

CONCLUSIONS

1. The study group had larger daily ranges compared to mountain gorillas and a larger annual home range relative to both mountain gorillas and most other lowland gorillas described to date.

2. Ranging patterns differed seasonally and between years.

3. Group C had more flexible grouping patterns than mountain gorillas.

4. While the fiber content of the lowland gorilla diet may relax constraints on foraging party size and facilitate group cohesion relative to chimpanzees, large multimale groups of lowland gorillas may adopt flexible grouping strategies.

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