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Territory Characteristics among Three Neighboring Chimpanzee Communities in the Taï National Park, Côte d'Ivoire

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We studied territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire, and compared them with other chimpanzee populations. We characterized territories and ranging patterns by analyzing six variables: (1) territory size, (2) overlap zone, (3) territory utilization, (4) core area, (5) territory shift, and (6) travel distance. Data collection covered a period of 10 mo, during which we simultaneously sampled the local positions of mostly large parties, including males in each community, in 30-min intervals. In Taï, chimpanzees used territories in a clumped way, with small central core areas being used preferentially over large peripheral areas. Although overlap zones between study communities mainly represented infrequently visited peripheral areas, overlap zones with all neighboring communities also included intensively used central areas. Territory utilization was not strongly seasonal, with no major shift of activity center or shift of areas used over consecutive months. However, we observed shorter daily travel distances in times of low food availability. Territory sizes of Taï chimpanzees tended to be larger than territories in other chimpanzee communities, presumably because high food availability allows for economical defense of territorial borders and time investment in territorial activities. Therefore we suggest, that use of territory in Taï chimpanzees is strongly influenced by intercommunity relations. To understand differences in territory

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characteristics between various populations, it is of major importance to consider not only the intracommunity but also the intercommunity context.

KEY WORDS: chimpanzee; territory size; territory utilization; food availability; intercommunity relations.

INTRODUCTION

A territory is defined as an area and its resources, such as food, mates or breeding sites that is defended against conspecifics (Noble, 1939; Nice, 1941). It is different from a home range, which is an undefended area where animals perform their daily activities, such as searching for food and rearing their offspring (Burt, 1943). Territories are common not only in primates (Carpenter, 1934; Jolly, 1966; Bates, 1970; Clutton-Brock and Harvey, 1977) but also in birds, fish, insects, reptiles, rodents and ungulates (Breder, 1934; Gordon, 1940; Nice, 1941; Greenberg and Noble, 1942; Owen-Smith, 1977; Baker, 1983). Typically, territories are defended by one individual, often male (Holm, 1973; Howard, 1978; Jones, 1981; Severinghaus *et al.*, 1981). Defense by a group of individuals occurs less often; examples include prairie dogs, lions and chimpanzees (King, 1955; Goodall, 1986; Rayor, 1988; Heinsohn, 1997; Boesch and Boesch-Achermann, 2000). The maintenance of a territory can vary from a few days to several years. Territories that are maintained only for short periods of time are mainly known from birds and ungulates, which establish leks—mating territories—to attract mates (Emlen and Oring, 1977; Clutton-Brock *et al.*, 1989). Mate defense has also been proposed as a major function of territoriality in some primate species by Dunbar (1988) and van Schaik *et al.* (1992). However, the primary function of territoriality has been widely interpreted as resource defense, as the most common benefit of territorial behavior is to secure an increased rate of food intake (Goss-Custard *et al.*, 1972; Jolly, 1985; Kinnaird, 1992).

Questions about the function of territoriality can only be addressed once ranging patterns in a given species are characterized. There has been an ongoing discussion as to whether chimpanzees occupy home ranges in which only frequently used areas—core areas—are defended or if they occupy territories (Lowen and Dunbar, 1994). Because of their fission-fusion social system, chimpanzees may not fit into the classical concept of a territorial species, in which individuals range in stable groups on relatively predictable travel routes and encounter neighboring groups of known composition and size. However, over the last two decades there have been various reports of intercommunity encounters from several study sites that clearly indicate that chimpanzees behave territorially by aggressively defending not only core areas but also patrol wide peripheral parts of their ranges (Kawanaka and Nishida, 1974; Goodall, 1986; Nishida *et al.*, 1985; Boesch and Boesch-Achermann, 2000). Therefore, we prefer to refer to chimpanzees as occupying a territory rather than a home range.

Although some information on territory characteristics is available from various chimpanzee communities, no detailed comparison of ranging variables between different chimpanzee communities in a specific population and between populations has yet been conducted. This is primarily due to the fact that in most study sites only one, or at most two, communities have been habituated to human observers (Wrangham, 1979; Goodall, 1986; Hasegawa, 1990; Nishida *et al.*, 1990; Chapman and Wrangham, 1993). In the Taï National Park, Côte d'Ivoire, due to the effort of various Ivorian assistants and international students, three communities have been habituated, enabling data collection on ranging patterns of three neighboring communities of wild chimpanzees (*Pan troglodytes verus*).

Our primary is to compare territory characteristics within the Taï population and between different chimpanzee populations across Africa. Specifically, we examine the following 6 variables: (1) territory size, (2) overlap zone, (3) territory utilization, (4) core area, (5) territory shift, and (6) travel distance. We also consider how intercommunity relations may influence territory characteristics in different populations.

Territory size within species can be influenced by several factors. Larger territories can be observed when groups are larger, in habitats with low food availability and in areas where the pressure of neighboring groups is reduced due to low population densities (Clutton-Brock and Harvey, 1977; Suzuki, 1979; Dunbar, 1988). Defense behavior is another important factor affecting territory size. Although defended areas—territories—are generally smaller than undefended ones—home ranges—in carnivores and ungulates, this is not true for primates (Grant *et al.*, 1992). This may be explained by their high mobility. Certain primate species with comparatively large ranges have evolved territorial behavior and are able to defend their ranges (Lowen and Dunbar, 1994). Goodall (1986) and Boesch and Boesch-Achermann (2000) proposed that variation in territory size of chimpanzees is influenced first, by the total size of a community and secondly by the number of adult males within a community.

Similarly, the use of a territory is influenced by ecological and social factors. Most animals do not use the entire territory with an equally distributed intensity (Clutton-Brock *et al.*, 1982; Woollard and Harris, 1990; Newton, 1992). Typically, some areas are preferred over others (Mason, 1968). These intensively used areas or core areas (Kaufman, 1962) are often exclusively used by the territory owners (De Vore and Hall, 1965). Bordering areas between territories mostly represent overlapping zones with neighboring groups (Peres, 1989; Mendes Pontes and Monteiro da Cruz, 1995;

Reichard and Sommer, 1997). Overlapping zones consisting of 30–50% of the territories have been noted at chimpanzee communities in Mahale and Gombe, Tanzania by Kawanaka and Nishida (1974), Nishida (1979) and Goodall (1986).

Both the spatial and the temporal variation in territory use is of interest to determine factors that influence ranging patterns. Typically, the seasonality of ranging patterns in primates and other animals is related to changes in food availability (Newton, 1992; Agetsuma, 1995; Olupot *et al.*, 1997). Primates respond to reduced food availability by either reducing daily travel ranges, thereby feeding on lower-quality food items or increasing daily travel ranges in search for high-quality food items (Dunbar, 1988; Zhang, 1995; Heiduck, 1997). However, intergroup interactions and predation pressure influence ranging temporally (Kawanaka and Nishida, 1974; Kinnaird, 1992; Garber *et al.*, 1993).

METHODS

Study Site and Study Communities

We collected data in the Taï National Park, Côte d'Ivoire, over a period of 10 consecutive mo from June 1996 to March 1997. The Taï National Park comprises evergreen lowland rain forest with an area of 4540 km^2 and remains the largest protected forest fragment in West Africa. The average annual rainfall is approximately 1800 mm and the average temperature is between 24 and 30°C. We differentiated two seasons within the study period: the rainy season from April to November and the dry season from December to March. The study area is located in the western part of the Taï National Park and covers an area of 55 km^2, encompassing the territories of the three study communities. To quantify the location of the chimpanzees, we divided the study area into a grid of 500 × 500-m cells, and X-/Y-coordinates refer to individual cells.

The northern and the southern study communities have been habituated to the presence of humans for 15 and 3 years, respectively. We could follow all individuals to within a distance of 5–10 m. The middle community was not fully habituated at the time of the study, consequently we could establish close contacts for only a few minutes several times a day. However, we could regularly achieve all-day follows within hearing distance (mostly <500 m). The middle community had the smallest total size and was presumed to have consisted of 11 individuals during the observation period: 4 adult males, 3 adult females, 4 infants. The north community comprised 35 individuals: 2 adult males, 12 adult females, 1 adolescent male and 1 female, 6 juveniles and 13 infants. The south community included 63 individuals: 6 adult males, 23 adult females, 1 adolescent female, 6 juveniles and 27 infants.

Data Collection

In the two habituated communities (north and south) we conducted continuous focal animal sampling from nest to nest (0630–1830 h) (Altmann, 1974). Generally, we chose focal animals randomly, but some individuals were sampled more frequently due to different ongoing studies in the Taï chimpanzee project during the observation period. We sampled 2 adult males, 1 late adolescent male and 10 females in the north community (days of observation: males: $\bar{x} = 17$, range $= 15–20$; females: $\bar{x} = 16$, range $= 5–26$). In the south community we sampled 5 adult males and 13 females (days of observation: males: $\bar{x} = 14$, range $= 10–21$; females: $\bar{x} = 6$, range $= 3–10$). Individuals of the middle community were not habituated well enough for focal animal sampling. Instead, we mostly followed the largest party that contained males because their vocal and drumming activity enabled us to follow them consistently. Because Taï chimpanzees often range in parties of mixed composition [(adult females and males and immatures: 52% (Boesch, 1996) 33% (Doran, 1997)] observational differences (male follows for north community: 25%, for south community: 46%) are not expected to strongly effect the results. To improve comparability between the data sets of the three communities (sampling the largest party with males within each community) we always attempted (in case of female follows) to choose female focals that associated with the males of their community throughout the day. We sampled the local position (X-/Y-coordinates) of the largest party in each of the three study communities in 30-min intervals.

Operational Definitions and Methods to Determine Territory Characteristics

Territory Size

A territory included all areas where we observed adult females and males of the same community. Methods to determine the size of a territory are numerous and there is little agreement in the results. To enable comparisons of different studies and between methods we calculated territory size by three nonstatistical methods: minimum convex polygon (MCP), restrictive polygon (RP) and grid cell (GC) (in Wildtrak 1.12 by Todd, 1992) and one statistical method: Fourier (in Antelope 1.3 by Bradbury and Vehrencamp, unpubl.). Via the MCP method one determines territory size by joining the outer limits of the local positions by straight lines to create a polygon and calculates the area within the polygon. The RP method excludes outlying local positions that contribute disproportionately to the calculated area. The GC method is a sum of all cells used to determine territory size. With the Fourier method one creates a grid of 32 × 32 cells and calculates the probability with which the original local positions are distributed in this grid. Territory size is then calculated by determining the area that accounts for 95% or 50% of the distribution. Detailed description of the different methods are provided by Anderson (1982) and Harris *et al.* (1990). An advantage of nonstatistical methods is their simplicity and comparability, as they are widely used. Their greatest disadvantage is an overestimation of the area used, since calculations also include areas or lacunas within the territory that have not been used by the animals (Anderson, 1982; Harris *et al.*, 1990; Kool and Croft, 1992). However, including the lacunas might correct for days when we could not follow the chimpanzees. One bias of the grid cell method is that the size of a territory is strongly influenced by the size of the grid cells. We reduced possible misjudgement by calculating large territories with relatively small grid cell sizes. A disadvantage of the polygon-methods is the assumption that territories have the shape of a convex-polygon. This assumption is probably unfounded, especially for heterogeneous habitats (Anderson, 1982). In contrast, the statistical Fourier method has no underlying assumption about the form of a territory and its estimation of territory size is probably more precise, as lacunas within the territory are excluded (Anderson, 1982). A disadvantage of the statistical Fourier method is its large effect on territory size, e.g., when only 50% of the territory is calculated.

Statistical methods are only applicable to independent data samples. This means that the local positions of the chimpanzees have to be far enough apart in time or in distance that it is not possible to tell from one position where the next one is going to be. We used the Moran's index (Antelope 1.3) to determine the distance, from which successive local positions no longer showed dependence. With this index one calculates a correlation for the frequency with which grid cells are used, weighted by the distance that two cells have to each other. The correlation is high when two cells a certain distance apart are used with a similar frequency. A correlogram depicts the variation in the spatial autocorrelation with respect to the distance between cells (Fig. 1). The middle community used cells with a different frequency (showed no correlation) when they were 2.6 km apart from each other (indicated by the arrow under the first open circle, Fig. 1). This distance was 2.9 km and 3.2 km, for the north and the south communities, respectively. As this distance was on average covered once a day by the north and south communities, we used only one local position per day for independent data samples.

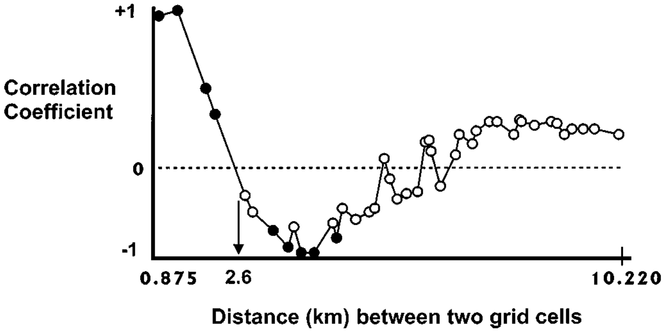

Fig. 1. Correlogram for the middle community. Black dots indicate a significant correlation between the frequency of use of two cells separated by a given distance. Open circles indicate no correlation.

Although the daily travel distance for the middle community did not reach 2.6 km, we still used one local position per day for statistical analyses because we could not follow this community over the entire day and therefore we certainly underestimated their day range. To avoid day time influences, we shifted back the time at which we would choose one local position for each consecutive day (0630 h for day 1; 0700 h for day 2; 0730 h for day 3).

Territory Utilization

We calculated two indices of dispersion (Table I) to describe the pattern of territory use (uniform, random, or clumped) for the three study communities (Antelope 1.3). The index of clumping (David and Moore, 1954) is a modification of the index of dispersion (ID), which is widely used in ecological studies (Ludwig and Reynolds, 1988). Both indices are strongly influenced by the sample size. This is not the case for the modification of the index of clumping by Green (1966). Therefore this index is suitable for comparisons between samples of different size. The indices that we employ

Table I. Properties of two indices of dispersion. Modified from Ludwig and Reynolds (1988)

Dispersion type index	Formula	Maximum uniformity	Randomness	Maximum clumping
		Value of index		
Index of clumping	$s^2/\bar{x} - 1$	-1	0	$n - 1$
Green's index	$(s^2/\bar{x}) - 1/(n-1)$	$-1/(n-1)$	0	1

Key: $\bar{x}$ = mean number of local positions/grid cell, s^2 = variance in the number of local positions/grid cell, n = total number of local positions.

only describe the degree of clumping. They do not test for randomness. To test if the territory utilization follows a random pattern, we compared it to a Poisson-distribution (Ludwig and Reynolds, 1988).

Core Area

When determining core areas within a territory, most studies concerning territory utilization include 50% of the local position (Dixon and Chapman, 1980; Anderson, 1982; Harris *et al.*, 1990). However, in chimpanzee studies core areas mostly included 75% of the positions (Wrangham, 1979; Chapman and Wrangham, 1993). To enable comparisons of different studies and between methods, we calculated core areas by the nonstatistical MCP-method, using 50% and 75% of the locations and by the statistical Fourier method (50%). Furthermore, we determined which area of the 75% and 50% MCP was exclusively used by the territory owners, and not by neighboring communities.

Overlap Zone and Territory Shift

To investigate the use of overlapping zones between neighboring communities, and temporal changes in territory use within a community, we applied the static interaction method (Doncaster, 1990) in Wildtrak 1.12. Static interaction analysis investigates spatial overlap of two territories—calculated by the grid cell method—and correspondence in the utilization pattern of two territories: to what extent the same areas are used at the same time and with the same frequency. We compared territories from two communities during the same time span and from one community during different time spans. We analyzed correspondence in territory utilization by applying a Spearman-rank-correlation-coefficient. Correspondence is high (coefficient close to +1), when a large percentage of two territories were used with the same frequency at the same time. A negative coefficient (close to −1) indicates low correspondence. Static interaction analyses can only be applied to independent samples.

To investigate whether the study communities used the same areas of their territories between two successive months, we calculated the degree of overlap for monthly territories. To test whether the overlap was equally distributed throughout the observation period, we applied a configuration frequency analyses (CFA) (Bortz *et al.*, 1990). Moreover, we examined temporal change in territory use by considering shifts of the activity center between the rainy and the dry seasons and successive months. We calculated the activity center of a given territory as the mean arithmetic center of the X- and Y-coordinates (Wildtrak 1.12). Shifts are described as percentage of the territory diameter: we calculated territory size with the MCP method.

We noted encounters between neighboring communities each time we heard or saw another community. Direct encounters involved visual or physical contact, whereas indirect encounters included only aural contact.

Daily Travel Distance

We calculated daily travel distances as the sum of all the straight line distances between the 30-min samples of the local positions of either the focal animal (north and south communities) or the party followed (middle community) (Wildtrak 1.12 by Todd, 1992). This measurement represents only the minimum travel distance per day and therefore underestimates the actual distance traveled by the chimpanzees. For the north and south communities we considered only daily travel distances that were based on an observation period of ≥300 min. Over 80% of the data for the two habituated communities included follows of >500 min. For the middle community we chose the minimum observation period to be 150 min, as it was more difficult to obtain continuous follows for them. Over 60% of the data considered includes follows of ≥300 min.

RESULTS

Territory Size

Territory sizes varied among the three study communities, with the south community consistently occupying the largest territory (all methods considered), followed by the north community (on average 73% of the size of the

Table II. Territory sizes (in km^2) of the three study communities, calculated with 4 different methods (RP = restrictive polygon-, MCP = minimum convex polygon-, GC = grid cell-method, Fourier = Fourier method; June 96–March 97)

Community	n dep.	RP 100%	GC 100%	MCP 100%	MCP 95%	n indep.	Fourier 95%
North	4470	14.8	18.3	16.8	10.5	215	7.5
Middle	1345	9.6	13.0	12.1	9.0	182	3.1
South	3212	20.6	23.3	26.5	13.5	170	9.5

Key: n dep. = dependent local positions, n indep. = independent local positions (one per day).

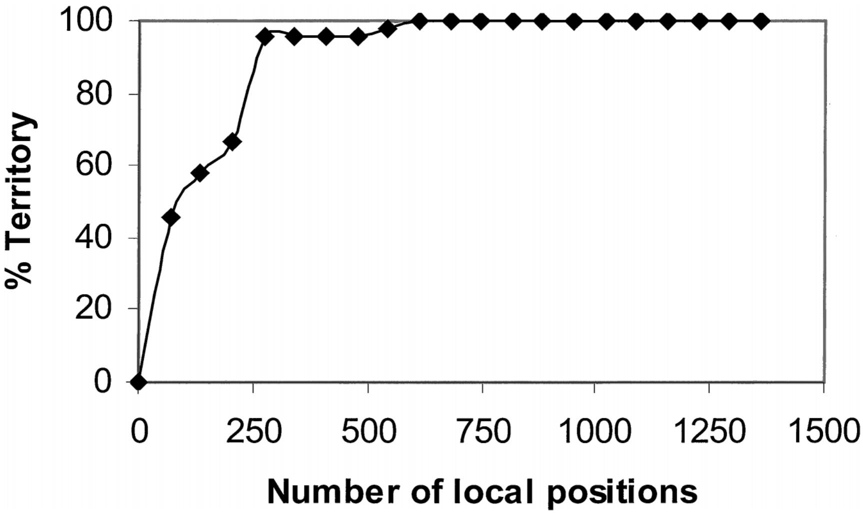

Fig. 2. Cumulative curve of territory size over time of data collection (June 96–March 97) for the middle community, calculated with the minimum convex polygon method: 544 local positions equal 5 month of data collection.

south territory) and the middle community (46% of the size of the south territory) (Table II, Fig. 3). Territory sizes calculated with nonstatistical methods (RP, MCP, GC) differed by about 25%. Territory sizes determined with the statistical Fourier method resulted in territories half the size compared to those calculated with the nonstatistical methods. Similarly, when independent local positions (one per day) were used to calculate territory size with nonstatistical methods (territory sizes reduced to an average of about 70% of their former size), the smallest territories were always determined by the statistical Fourier method.

Regardless of the method applied, all cumulative curves examining the increase of the territory occupied over time by a given community, reached an asymptote after approximately 4–5 mo of data collection (Fig. 2).

When we calculated territory sizes (MCP method) for individual females and males with a comparable number of local positions in the north community, females occupied on average 93% of the males territories [individuals with >340 local positions included; females: 10.5 km^2 ($n = 6$), males: 11.3 km^2 ($n = 3$), Mann-Whitney-U: $U_1 = 27.5$, $U_2 = 17.5$, $p > 0.05$]. In the south community, male territories were larger than female territories, but this is most likely affected by the small number of local positions for individual females [females: 6.6 km^2 ($n = 7$, range of number of local positions =

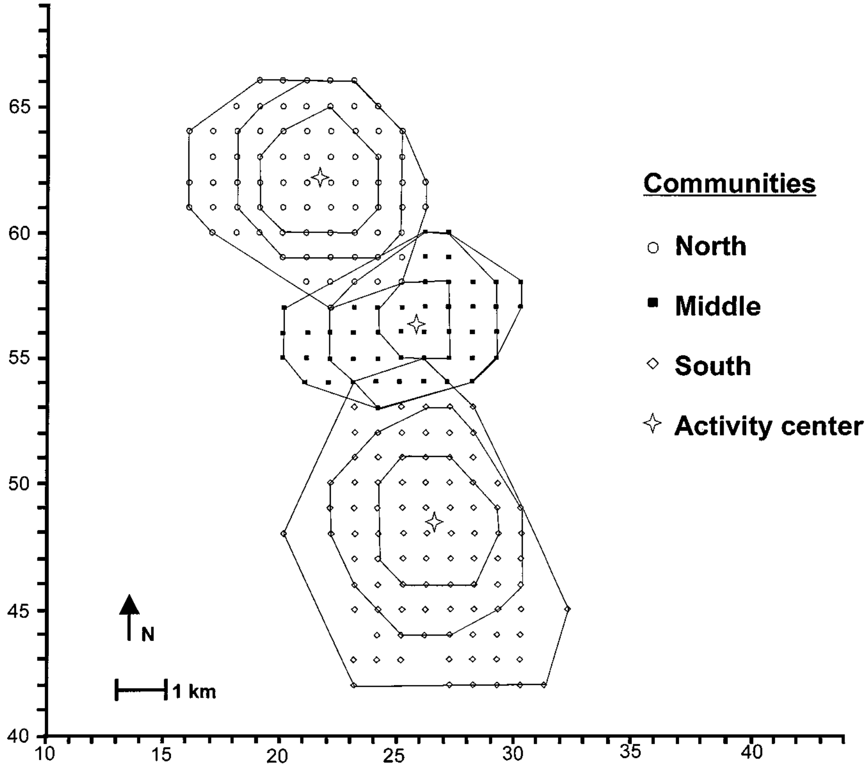

Fig. 3. Territories of the three study communities (June 96–March 97), calculated by the minimum convex polygon method. The three concentric lines indicate for each territory the limits for 100%, 95%, and 75% of the utilization.

112–226), males: 13.4 km^2 (n = 5, range of number of local positions = 229–453), $U_1 = 28.0$, $U_2 = 50.0$, $p < 0.01$].

Overlap Zone

Overlapping zones of the middle community with the north and south communities were comparable and encompassed 1.75 km^2 (Fig. 3). The overlap zone represented 9.5% of the north community's territory, 7.5% of the south community's territory, and 13.5% of the middle community's territory (with either north or south community). In our simultaneous ranging samples—mainly large parties including males—neighboring communities used the overlapping zones infrequently and at different times. This low correspondence in territory utilization between neighboring communities is indicated by a high negative correlation-coefficient (Spearman-rank-correlation: middle & north: $n = 85$ simultaneous days, $r_s = -0.83$, $p < 0.01$; middle & south: $n = 81$ simultaneous days, $r_s = -0.84$, $p < 0.01$). The middle and the north communities traveled within a mean distance of 3.88 km ± 1.12 km ($n = 1122$ simultaneous local positions) to each other. The middle and the south communities traveled within a mean distance of 4.16 km ± 1.23 km ($n = 1099$ simultaneous local positions) to each other. The middle and the south communities had one direct encounter and four indirect encounters during the observation period. The north and middle communities never encountered each other in the same grid cell, but four indirect encounters occurred (>500 m apart). It should be noted that only interactions between two study communities are considered. However, each community is presumably surrounded by 4–6 neighboring communities, and overlapping zones with all neighbors encompass large areas which might be more frequently and simultaneously used by more than one community than our results indicate. The total number of encounters with all neighboring communities is 53 within the 10-mo study period for the three study communities (north: 29, middle: 11, south: 13 encounters).

Territory Utilization

None of the study communities used their territory randomly but instead showed a slightly clumped distribution (Table III). A few central cells within the territory were used intensively, and most peripheral cells were used with a low frequency (cell use: north: median = 0.8%, range = 0.02–8.9%, variance = 2.6; middle: median = 0.9%, range = 0.07–15.8%, variance = 9.5; south: median = 0.3%, range = 0.03–7.4%, variance = 5.0; Fig. 4). The middle community showed the highest degree of clumping (Table III, GI). However, the overall degree of clumping was very low for all three study communities, considering the values of maximum clumping. Nevertheless, the utilization or dispersion pattern could not be described as random (deviation from a Poisson-distribution: Kolmogorov-Smirnov: north: $d = 0.51$, $p < 0.01$; middle: $d = 0.58$, $p < 0.01$; south: $d = 0.60$, $p < 0.01$).

Table III. Indices of dispersion for the three study communities (expected values for maximum clumping in brackets)

Communities	Index of clumping (IC)	Green's index (GI)
North	29.5 (4469)	0.007 (1)
Middle	26.1 (1344)	0.019 (1)
South	24.6 (3211)	0.008 (1)

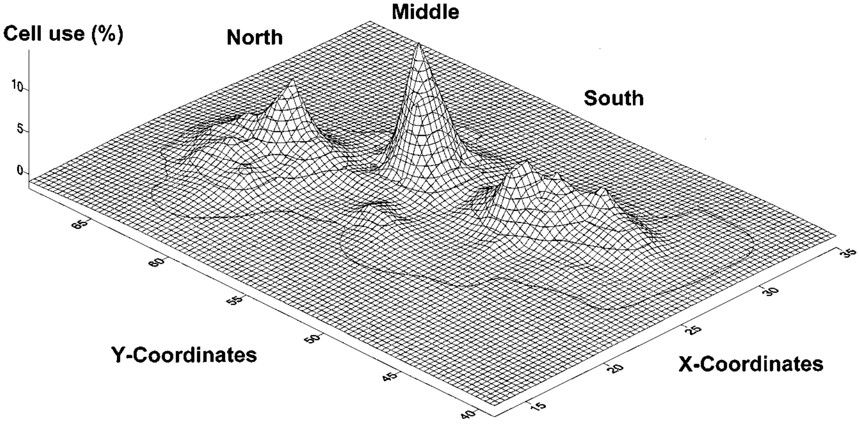

Fig. 4. Territorial utilization of the three study communities (June 96–March 97).

Core Area

Core areas of the three study communities encompassed less than a third of the total territory size, regardless of the method applied (Table IV). Less than two-thirds of the core areas was used exclusively by the territory owners. Exclusive core areas covered on average only 10% (75% MCP) or 7% (50% MCP) of the total territories, and the three study communities spent on average 54% or 31% of their time in this area.

Territory Shift

Seasonal Territory Utilization

To a large extent the north community used the same areas during different seasons. However, the middle and the south communities used

Table IV. Core area sizes (in km^2) of the three study communities and their percentages of the total territory (in brackets), calculated with 2 different methods (MCP = minimum convex polygon method, Fourier = Fourier method; June 96–March 97)

Community	MCP 75%	MCP Exclusive 75%	MCP 50%	MCP Exclusive 50%	Fourier 50%
North	4.9 (29%)	2.3 (14%)	2.0 (12%)	2.0 (12%)	2.3 (31%)
Middle	2.3 (19%)	0.5 (4%)	0.6 (5%)	0.3 (2%)	0.7 (23%)
South	5.3 (20%)	3.5 (13%)	2.1 (8%)	1.5 (6%)	2.3 (24%)

Key: exclusive = only utilized by territory owners, no neighboring community has been observed in this area.

Table V. Territory sizes (in km^2) of the three study communities for the rainy and dry seasons and the degree of overlap for territory use (grid cell method)

	North		Middle		South	
Season	Rain	Dry	Rain	Dry	Rain	Dry
n	2547	1923	544	801	1309	1903
Territory Size	17.5	17.0	12.0	8.0	22.0	16.8
% Overlap	93	96	58	88	71	93

Key: n = local positions, % overlap = indicates how many % of the territory that is used in the rainy season is also used in dry season and vice versa.

only approximately two-thirds of their territory in both seasons and occupied more peripheral areas in the rainy season than in the dry season (Table V). Territory utilization tended to be weakly influenced by different seasons, as indicated by low positive correlation-coefficients (Spearman-rank-correlation: north: $n = 52$, $r_s = 0.23$, $p > 0.05$; middle: $n = 34$, $r_s = 0.26$, $p > 0.05$; south: $n = 49$, $r_s = 0.28$, $p > 0.05$).

Monthly Territory Utilization

Monthly territory overlap within the north and south communities was on average 59% and 54%, respectively. The percentage of overlap was equally distributed for all paired months (CFA, $p > 0.05$). Monthly territories of the middle community overlapped on average 59% from October to March, but between September and October the overlap only reached 7% (CFA, $p < 0.01$). This minor correspondence between September and October was probably the result of an observation bias at the beginning of the study period, when the middle community was mainly followed in the western periphery of their territory where they heavily consumed fruits of *Sacoglottis*.

Activity Center

Activity centers were relatively stable, both between seasons and successive months (Table VI). Shifts of the center ranged from 500 m to 2061 m for the three study communities (north: $\bar{x} = 693$ m, maximum = 1000 m; middle: $\bar{x} = 829$ m, maximum = 2061 m; south: $\bar{x} = 402$ m, maximum = 707 m). The south community shifted their activity center the least. The comparatively larger mean shift of the middle community's activity center for successive months and between seasons was influenced by the low correspondence in their territory utilization during September and October.

Table VI. Shift of the activity centers for the three study communities in % of the territory diameter between seasons and successive months

	North	Middle	South
Period	Shift (%)		
Rainy/Dry season	15	25	12
June/July 1996	22	/	/
July/August	22	/	/
August/September	22	/	/
September/October	15	74	17
October/November	15	25	12
November/December	22	18	0
December/January	31	18	12
January/February 1997	22	25	0
February/March	22	18	17
Monthly Mean	21	30	10

Key: / = no calculation due to small sample.

Daily Travel Distance

Daily travel distances for the three study communities ranged on average between 2 and 4 km (minimum: <0.5 km, maximum: 9 km; Table VII). There is no sex difference in daily travel distance for the habituated north and south communities (t-test for independent samples: north: males:

Table VII. Daily travel distances (in km) of the three study communities for different seasons and months

Period	n	North	n	Middle	n	South
June–March	205	3.59	125	2.11	147	4.20
Rainy Season	118	3.14	51	2.06	62	3.69
Dry Season	87	4.21	74	2.14	85	4.58
June 1996	11	1.52	/	/	/	/
July	15	1.81	/	/	/	/
August	16	1.68	5	2.24	/	/
September	20	4.03	13	2.14	17	3.40
October	28	3.48	16	1.78	20	3.48
November	28	4.39	17	2.31	25	4.16
December	25	4.78	26	2.48	23	4.72
January 1997	24	3.84	22	2.11	25	4.33
February	24	4.34	17	1.93	24	4.71
March	14	3.57	9	1.62	13	4.55
Monthly Mean	21	3.34 ± 1.22		2.08 ± 0.29		4.19 ± 0.55

Key: n = number of days of observation.

3.71 ± 0.42, females: 3.64 ± 0.39, $t = 0.24$, $df = 11$, $p > 0.05$; south: males: 4.28 ± 0.35, females: 4.11 ± 0.77, $t = 0.49$, $df = 16$, $p > 0.05$). The north and the south communities traveled over longer distances in the dry season than in the rainy season (Mann-Whitney-U: north: $z = -4.39$, $p < 0.001$; middle: $z = -0.12$, $p > 0.05$; south: $z = -3.78$, $p < 0.001$).

DISCUSSION

Territory Size

Comparisons among territory sizes of the three study communities in Taï reveal that the south community, which had the most adult males and community members, occupied the largest territory. In comparison to territory sizes of several known chimpanzee communities, the three study communities of the Taï forest occupied large territories (Fig. 5). Several factors may explain why territories in Taï are comparatively large: 1) population density, 2) food availability and 3) territorial activities.

1. Population density

Low population density in Taï in comparison to other chimpanzee populations might account for their large territories [Taï (north, middle, south): $\bar{x} = 1.84$ chimpanzees/km^2; Gombe (Kasakela, Kakombe): $\bar{x} = 2.29$ chimpanzees/km^2; Kibale (Kanyawara): 2.75 chimpanzees/km^2; Mahale (K, M): $\bar{x} = 3.92$ chimpanzees/km^2; sources in Fig. 5] because larger territories have been observed in several primate species with low population densities (Smuts *et al.*, 1987; Dunbar, 1988). Low population densities allow primate groups to enlarge their territories with respect to group size, whereas in habitats with high population densities territories are expected to get reduced in size by the pressure of neighboring groups. However, the north community also occupied large territories when their density was much higher [in 1982: territory size = 21.75 km^2, 74 community members, population density = 3.4 chimpanzees/km^2, in 1989: territory size = 26.25 km^2, 66 community members, population density = 2.5 chimpanzees/km^2 (territory sizes considered for September–December, calculated with the GC method: Boesch and Boesch-Achermann, 2000)]. Low population density in the Taï chimpanzees is probably a recent effect due to epidemics, like Ebola, high predator pressure by leopards, and poaching pressure by humans (Boesch and Boesch-Achermann, 2000).

2. Food availability

In several primate and bird species, comparatively larger territories characterize groups occupying habitats with low food availability (Dunbar,

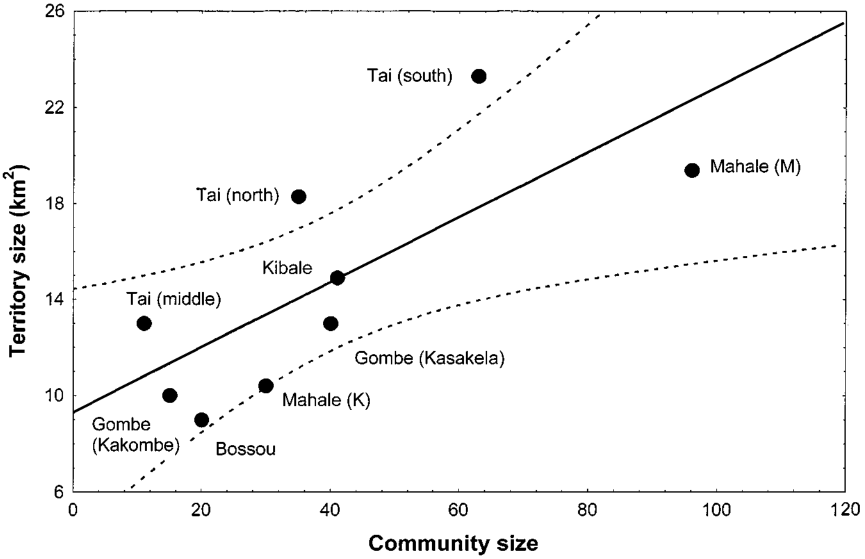

Fig. 5. Territory size (km^2) in relation to community size for various chimpanzee communities ($r_s = 0.90, n = 9, p < 0.01$, 95% confidence interval indicated by broken line). Sources: Bossou: Sakura (1994); Gombe: Wrangham (1979), Goodall (1986); Kibale: Chapman and Wrangham (1993); Mahale: K-community: Nishida (1979), M-community: Hasegawa (1990); Taï: this study. In Gombe, Mahale and Taï territory sizes were calculated with the grid cell method (cells 400–500 km^2). For Bossou the method was not indicated. For Kibale we included the larger territory size calculated by the minimum convex polygon method instead of the grid cell method, as there was little evidence of an asymptote in the cumulative plot of home range size versus number of sightings in Chapman and Wrangham (1993). Moreover, complete habituation of the middle community revealed a larger territory than previously noted (19.5 km^2 instead of 13.0 km^2).

1988; Eberhard and Ewald, 1994). However, several factors indicate that Taï is presumably a comparatively rich habitat, and low food availability cannot explain their larger territories.

a. The annual rainfall (used as an index of the primary production of vegetation and therefore as an indirect measure of food availability) is at the upper range in comparison to other chimpanzee habitats in eastern Africa [1700–1800 mm in Taï (Roth *et al.*, 1979; data from the Taï Monkey Project) versus 1600–1800 mm in Gombe, Mahale, Kibale (Goodall, 1986; Nishida, 1990; Chapman and Wrangham, 1993)].
b. Chimpanzees in Taï consume more plant species (223, unpubl. data Boesch; Goné Bi, 1999) in comparison to other communities [Gombe: 141 (Wrangham, 1975), Mahale: 198 (Nishida and Uehara, 1983), Bossou: 200 (Sugiyama and Koman, 1992)].

c. Descriptions of a heterogeneous distribution of food resources in space and time are available for Gombe, Mahale and Kibale (Goodall, 1986; Nishida, 1990; Wrangham *et al.*, 1996). In times of food scarcity chimpanzees at Gombe suffer weight loss, sicknesses, increased mortality and a reduced reproductive effort (Goodall, 1986; Wallis, 1992, 1995). Wrangham *et al.* (1996) also suggested that a marked period of fruit scarcity is responsible for the relatively low reproduction rate of the Kanyawara community in Kibale. In Taï marked bottlenecks in food availability do not seem to occur, and chimpanzees do not appear to suffer physically from reduced energy intake when fruit becomes less abundant. Even in the relatively lower food rich rainy season, large tree species, such as *Klainedoxa gabonensis*, *Nauclea diderichii*, *Pycnanthus angolensis* and *Sacoglottis gabonensis* come into fruit and are consumed by the chimpanzees. Towards the end of the rainy season their regular hunting activities on colobus provide an additional high nutritional benefit.

d. Taï chimpanzees form larger mean party sizes than other chimpanzee communities (Boesch, 1996). If Taï were a poor habitat, chimpanzees would be expected to form smaller parties, in order to reduce intracommunity competition.

Therefore low food availability does not explain large territories in Taï chimpanzees as Taï seems to be a very rich habitat for chimpanzees.

3. Territorial activities

In Taï, high food availability could allow for a) increased territorial activities and b) economic defense of territories, which might make it worthwhile for and enable communities to occupy and keep large territories. Large territories have been predicted to occur when there is high food availability in breeding territories, where sexual selection favors males with large territories, because of enhanced mating success (Andersson, 1994). Enhanced mating success for male chimpanzees occupying large territories is likely because female immigration patterns seem to be influenced by a) the number of males within a community and b) the total size of a community (both factors correlate with territory size: Nishida *et al.*, 1985; Goodall, 1986; Boesch and Boesch-Achermann, 2000). Taking into account high food availability in Taï, time saved foraging for food could be invested in increased territorial defense, such as patrolling territorial borders and encountering neighboring communities. Boesch and Boesch-Achermann (2000) analyzed territorial activities of the north community over a 13-year period ($n = 129$) and observed that at least twice per month males invested time and energy to defend their territory or to locate neighboring communities. A large percentage (29%) of the territorial activities of the north community consisted of males actively patrolling territorial borders and searching for signs of neighboring communities. In only 26% of the patrols did they actually find neighbors, which indicates that patrols instead serve to gain information about the location of neighbors rather than to actually engage in a direct encounter. Since a patrolling party mostly consists of males and therefore is smaller than the average party size in Taï (about ten individuals), chances of being outnumbered when encountering neighbors are high and make direct confrontations risky (Boesch and Boesch-Achermann, 2000).

Besides patrols, five different attack strategies have been identified for the north community: frontal-, back-and-forth-, lateral-, rearguard-attack and commando (Boesch and Boesch-Achermann, 2000). Their application mostly depends on the number of adult males present in the attacking party. The north community engaged in encounters three times per month and the middle and the south communities encountered neighbors once or twice a month. The lower encounter rate for the middle community is presumably influenced by their lower habituation, whereas the comparatively lower rate for the south community might be due to their large territory.

In a habitat where food is abundant, energy spent in intercommunity encounters can readily be regained. Consequently, Taï chimpanzees might experience lower defense costs than those of chimpanzees in poorer habitats. Comparatively higher food availability might also improve fighting abilities because of better physical condition and could allow territory owners to be more persistent in direct intercommunity encounters. Comparing territorial behavior between Gombe and Taï, Boesch and Boesch-Achermann (2000) found no difference in patrolling frequencies between the two sites (5% of observation time), but neighboring communities were heard or seen much more frequently in Taï than in Gombe (11.6% in Taï versus 5.5% of observation time in Gombe). In Taï, Boesch and Boesch-Achermann (2000) observed that once auditory contact with a neighboring community has been established, the north community advanced towards their opponents in 86% of the cases and came into visual contact in 48% of the cases. If encounters were restricted to auditory contact, opponents usually gave drumming displays for up to an hour, which probably served to mark their territory and to estimate the number and the strength of their opponents. The small sample size of encounters among the three study communities did not allow us to identify clear dominance relations, but there was a tendency for the middle community to avoid the larger south community more than the north community. Higher encounter rates in Taï than in Gombe are presumably influenced by ecological factors, since the large buttress trees that chimpanzees use to drum are more common in Taï than in Gombe and sound carries further because of a comparatively flat topography (Boesch and Boesch-Achermann, 2000).

However, lower visibility and population density make encounters in Taï less likely than in Gombe and probably compensate for better drumming conditions. The fact that in Taï, other communities are heard frequently could allow neighboring communities to coordinate their territorial use with respect to one another. Our results suggest that overlap zones are rarely used simultaneously by more than one community. Given high food availability, ecological and social benefits of occupying a large territory and sharing parts as overlap zones might still offset the costs of not using a smaller territory more exclusively.

In conclusion, higher food availability in Taï in comparison to other chimpanzee populations may enable Taï chimpanzees to defend their territories in a comparatively economical and coordinated way, which might account for comparatively large territories in this population.

Territory Utilization, Core Area and Overlap Zone

Although territorial utilization has been studied in several chimpanzee communities, most researchers did not quantify the pattern of territory use (Wrangham, 1979; Kawanaka, 1984; Goodall, 1986; Hasegawa, 1990; Sakura, 1994). At Kibale, ranging patterns for females and males have been identified as uniform by applying the index of dispersion (Chapman and Wrangham, 1993; average ID for both sexes = 0.82, equals IC = −0.18, IC = ID − 1). It indicates that at Kibale the difference between time spent in the core area and time spent in the periphery is not significant.

At Taï, clumped territorial utilization (core areas being used more than peripheries) is unlikely to reflect a clumped food distribution. Food abundance per unit area is not significantly greater over time within the core area than in the periphery (Anderson, unpubl. data). It is more likely that social factors, such as the distribution of neighboring communities, influenced territory utilization. This interpretation is supported by the following observations:

a. Exclusive core areas encompassed only a very small central part of the territories.
b. Overlapping zones with all neighboring communities included highly-frequented areas.

Therefore, we suggest that central parts of the territories were used preferentially because, to some extent, they represented safe refuges for the territory owners where the communities could range without facing intercommunity competition for either food or mates—exclusive core areas (Table IV).

At Kibale, the uniform territorial utilization suggests that either intercommunity pressure is less strong than in Taï, or Kibale chimpanzees simply cannot afford to preferentially use small central areas of their territory because of the relatively lower food availability. Although intercommunity encounters seem to be relatively infrequent in Kibale, chimpanzees nevertheless respond to border areas, e.g. females avoid the periphery, larger parties are formed in bordering areas, and two adult males have been killed in intercommunity interactions (Wrangham, pers. comm.). Further comparisons with chimpanzee communities in Mahale, Gombe and Bossou show, on a more descriptive level, that central core areas, which account for <30% of the territory, and overlapping zones that reach well within intensively used parts of the territories are common characteristics also in other chimpanzee populations (Kawanaka and Nishida, 1974; Nishida, 1979; Goodall, 1986; Wrangham, 1986; Hasegawa, 1990).

Territory Shifts

The three study communities showed rather stable territorial utilization, with respect to shifts of activity centers and areas used over seasons and months. Minor differences among the study communities are comparable to the variation that occurred within one community. The middle and south communities seemed to compensate more than the north community for reduced fruit availability in the rainy season by ranging more in peripheral parts of their territories. The reduced daily travel distances of the north and south communities in the rainy versus the dry season were therefore not due to a more efficient use of the core area, as was suggested by Doran (1997) in a study that also revealed reduced travel distances in times of food scarcity. In times of relatively low food availability the benefit of finding other food sources in peripheral areas probably outweighed the costs of encountering neighboring communities to a larger extent than in times of high food availability. This indicates that food availability nevertheless influenced territorial utilization of the Taï chimpanzees. However, considering descriptive data from the communities in Gombe and Mahale, we suggest that territorial utilization in those communities reflects stronger seasonal influences, indicated by seasonal migrations within the territory with major shifts of activity centers (Nishida and Kawanaka, 1972; Goodall, 1986).

To understand differences in territorial utilization among chimpanzee communities, it is important to consider not only ecological factors, such as food availability and distribution but also social factors, such as intercommunity relationships. For chimpanzees in Taï, intercommunity relations seem to have a stronger impact on territorial utilization than food availability and distribution and seem to explain more of the observed characteristics of territories. To assess the importance of both factors on territorial use, it will be necessary to quantify food availability and distribution as well as intercommunity interactions and relations in the various chimpanzee study sites in a comparable way.

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