

Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d'Ivoire

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Group size is expected to be an important factor to predict home-range (HR) size in social animals. In chimpanzees adult males play an important role in defending the HR against neighbors, and therefore it has been suggested that HR size depends on the number of adult males. In this long-term study on wild West African chimpanzees, we analyzed the relative importance of community size and composition on ranging patterns over a 10-year period, using multivariate statistics. Because community size decreased from 51 individuals with 6 adult males in 1992 to 22 individuals with only 1 adult male in 2001, we expected a decrease in HR size, which should be better predicted by the number of males than by community size. We further investigated the effect of fruit availability on monthly HRs over a 4-year period. As predicted, HR size decreased during the first 7 years of our study but increased during the last 3 years. Overall, the number of adult males was the best predictor of HR size, whereas fruit availability did not correlate with HR size. HR use remained stable over the entire study period, with a constant proportion of about 35% of the HR used as core area. High HR and core-area overlap values between different years indicated strong site-fidelity. Although the number of males within the community explained the decrease in HR size, the recent increase in size remains unexplained. This finding suggests that other factors such as relative fighting power of males affect HR size. *Key words:* chimpanzees, community size, core area, center of activity, food availability, home-range size, home-range use, group size, Morista index of similarity, *Pan troglodytes*. [*Behav Ecol* 14:642–649 (2003)]

The home range of an animal is defined as the area the animal traverses during a certain time “in its normal activities of food gathering, mating and caring for young” (Burt, 1943: 351). Since this definition was introduced, many studies have analyzed and modeled the ecological and social factors determining home-range size of different species. Among the most important factors invoked to explain, predict, and understand home-range sizes and ranging patterns within populations are (1) size and distribution of food patches, (2) predation pressure, (3) competition with neighbors for food, mates, or other important resources, (4) group size in the case of social animals, and (5) the availability and distribution of important resources such as water, nest sites, or sexual partners (Anderson, 1984; Barton et al., 1992; for review of factors 1–4, see Adams, 2001; McLoughlin and Ferguson, 2000).

Despite many studies showing clear effects of one factor on ranging patterns, a substantial number of studies have failed to demonstrate a straightforward relationship between the aforementioned factors and ranging patterns (for review, see Adams, 2001; McLoughlin and Ferguson, 2000). Therefore, the observed home range within a species is most likely the result of a combination of various factors acting on different levels (Chapman and Chapman, 2000), and recent studies on use of space indicate a shift from simple, general models toward those incorporating a variety of factors (Gordon, 1997).

For animals living in social groups, the ecological constraints model predicts a strong relationship between three variables: group size, day range/home range, and food availability (Gillespie and Chapman, 2001). For primates, it

has been hypothesized that larger group ranges are the result of low food availability, reduced pressure of neighboring groups, or increased group size (Clutton-Brock and Harvey, 1977; Dunbar 1988).

Besides group size, group composition might be equally important for understanding ranging patterns and home-range size. The socioecological model predicts that female reproductive success is highly dependent on environmental risk and the distribution of resources, while male reproductive success depends on the availability of fertile females (Sterck et al., 1997; Wrangham, 1979a). This has direct consequences on ranging patterns: female home ranges should be more closely linked to food distribution, but male ranging patterns should be more tied to the distribution of receptive females. Given such sex-specific ranging patterns, one can hypothesize that total home-range size and home-range use of group-living animals are also dependent on the number of males and females within a community (van Schaik and van Hooft, 1983).

Here we used data from a long-term study to investigate the effects of group size and group composition on home-range size and use for a wild West African chimpanzee (*Pan troglodytes verus*) community in the Taï National Park, Côte d'Ivoire. Most studies investigating the effects of ecological and social factors on ranging patterns are either experimental (e.g., Boutin and Schweiger, 1988; Desy et al., 1990) or based on interpopulation comparisons (Clutton-Brock and Harvey, 1977; Herbinger et al., 2001; Makwana, 1978), probably because naturally occurring and observable changes of these factors are rare. At our study site, group size as well as group composition have changed during the study period, thereby offering a unique opportunity to directly investigate the effects of these factors on ranging patterns within a social unit in wild animals, avoiding possible disadvantages of interpopulation comparisons.

Chimpanzees live in communities of 20–150 individually recognized members (Boesch and Boesch-Achermann, 2000;

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Table 1
Demographic and ranging data for the chimpanzee study community in the Taï forest

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Community size ^a	46.5	41.5	36	32	33	32	31	26.5	22.5	22
Males > 15 years	6	5	3	2	2	1.5	1.5	1.5	1	1
Females > 13 years	16	15.5	13.5	11	10.5	10.5	11	9	7	6.5
Juvenile/adolescent ^b	11.5	9.5	9	8.5	11	11	8.5	7.5	8	9
Infants ^c	13	11.5	10.5	10.5	9.5	9	10	8	5	5.5
Observation days	260	239	222	216	318	308	329	225	224	287
Density (chimps/km ²)	1.76	2.33	1.69	1.99	1.93	2.14	2.23	1.47	1.10	1.03
Encounter rate	—	—	—	39.5	47.9	32.3	43.1	33.5	22.7	17.9
Morista index ^d	—	0.98	0.98	0.94	0.96	0.99	0.94	0.87	0.89	0.97

^a Chimpanzee counts represent average values of the number of chimpanzees present 1 January and 31 December.

^b Juveniles/adolescents are aged 5–13 (females) or 5–15 (males) years.

^c Infants are aged 0–4 years.

^d Morista index of home range similarity: 1 = total overlap, 0 = no overlap.

Goodall, 1986; Nishida, 1990). Like bonobos and spider monkeys, chimpanzees exhibit a fission–fusion organization and often travel in small parties (subgroups) rather than as a whole community. Male chimpanzees usually remain in their natal community, while most females disperse. Home ranges are relatively stable over time and can be divided into a heavily used core area and a less frequently visited peripheral zone. The home range is usually defended by the males of the community against neighboring chimpanzee communities. Thus, it has been suggested that the number of adult males within a chimpanzee community is a crucial factor for home-range size (Boesch and Boesch-Achermann, 2000; Goodall, 1986). In our study community, the number of chimpanzees as well as the number of males within the community has decreased dramatically during the past 10 years of observation. We therefore predicted a decrease in home-range size with decreasing community size as well as with decreasing number of males. Since male fighting power is very important for home-range defense in chimpanzees (Boesch and Boesch-Achermann, 2000; Goodall, 1986), we expected the number of males to be a stronger predictor for home-range size than community size. Male fighting power, however, is only a meaningful variable in relation to the fighting power of neighboring communities. Because we could not directly measure the fighting power of all neighbors, we used intercommunity encounter rates as an indicator for intercommunity competition. Based on findings demonstrating an inverse relation between home-range size and intercommunity competition (e.g., Boesch and Boesch-Achermann, 2000; Boutin and Schweiger, 1988), we expected to find a similar relation in our study.

Another key factor determining home-range sizes is food availability. In this study we used two measures to control for the effects of food availability. First, we used annual rainfall as an approximation for food production (Dunbar, 1988; Rosenzweig, 1968). Second, we used the “fruit abundance index” from a phenological study that was carried out in Taï during 1997–2000 (Anderson et al., 2002) to analyze the effects of fruit availability on yearly and monthly home-range sizes. Other factors such as predation risk and food distribution are assumed to have remained relatively stable over the past 10 years (especially in comparison to the variation between study sites). We also analyzed home-range use because we expected that changes in food distribution as well as changes in intercommunity competition would be reflected in home-range usage patterns.

METHODS

Study site and population

The Taï National Park, Côte d’Ivoire, West Africa, comprises an area of approximately 4540 km² and consists of evergreen, lowland rainforest (for details, see Boesch and Boesch-Achermann, 2000). Data presented in this study derive from daily observations of the north community during the 10-year period 1992–2001. The habituated community could be reliably observed on a daily basis with the help of field assistants. In January 1992, the community consisted of 6 adult males (aged >15 years), 17 adult females (aged >13 years), 14 immatures (aged between 5–15 and 5–13 years, respectively), and 14 dependent offspring (aged 0–4 years). By December 2001 group size had decreased to 1 adult male, 6 adult females, 9 immatures, and 5 dependent offspring (see Table 1). The decrease in community size was mainly due to disease outbreaks in 1992, 1994 (see Boesch and Boesch-Achermann, 2000; Formenty et al., 1999), and in 1999. During the study period, there was no confirmed loss due to poaching, and predation risk appears to have remained constant.

Data collection

From 1992 onward daily focal animal follows were carried out, and data on group size and composition, ranging, behavior of the target animal, and social interactions have been collected systematically on checksheets by field assistants. Daily foraging routes of a focal subject were plotted on a detailed map of the area. Superimposed on this map is a grid with 500 × 500 m cells, with x-/y-coordinates referring to individual cells. From 1992–2001, field assistants plotted 2628 foraging routes on maps. A total of 563 follows on males and 2065 follows on females, with an average observation duration of 9.6 h per day were collected. Target subjects were chosen in a pseudo-random way, and targets were usually a member of one of the parties followed the previous day. The large bias toward female follows is due to the small number of males in the north community (see Table 1). Unfortunately, not all individuals of the study community were followed equally often, and during 1993 and 1994 no male target follows were carried out. However, since the Taï chimpanzees are very cohesive, that is, they often move in large parties (see Boesch and Boesch-Achermann, 2000), and male and female home ranges are very similar in size (Lehmann and Boesch,

unpublished observation), this bias should not influence our estimates of home-range size or usage significantly.

Data analysis

All behavioral data were entered into a large chimpanzee-behavior database using Microsoft Access 2000. Daily foraging routes were entered into a geographic information system, ArcView (ArcView GIS 3.2), using a digitizing tablet (Wacom A3). We determined community size by averaging the total number of chimpanzees present at 1 January and 31 December each year (Table 1). We estimated home-range size using two different methods, the minimum convex polygon (MCP) method and grid cell analysis. Although both of these methods have been criticized in the past (e.g., Worton, 1987), they have the advantage of not requiring independent data points. Furthermore, they are widely used methods, and thus their results can be compared with those of other studies.

Home-range and core-area size

We defined the community home range as the total of all areas visited by the chimpanzees during the course of a year (1 January–31 December). To calculate core-area size per year grid cell (500 × 500 m) usage frequencies were used. The core area of the home range included the minimum number of grid cells accounting for 75% of total usage frequencies (Chapman and Wrangham, 1993; Wrangham, 1979b). Thus, data are presented in either exact square kilometers, derived from the MCP method (home-range size) or as estimated square kilometers, derived from the grid cell method by multiplying the number of grid cells used by 0.25 km².

Fruit abundance and monthly home ranges

We defined monthly home ranges as the total of all areas visited by the chimpanzees during the course of a month and calculated the ranges using the MCP method. A “fruit abundance index,” incorporating fruit phenology data as well as data on basal area and density of the studied tree species in the community range, was used as a measure of fruit abundance for the period February 1997–December 2000. For details on data collection and calculations, see Anderson et al. (2002).

Average encounter rates with neighbors

Since 1995 encounters with neighboring communities were recorded using ad libitum sampling. Due to the rare occurrence of direct encounters, we pooled the number of days with direct and auditory encounters. The average number of encounters per year, an approximate measure of intercommunity competition, was estimated with corrections for the variable number of sample days per year.

Other variables

Because data from other studies have suggested that females in estrus increase their home range and influence male ranging patterns (Goodall, 1986), we included the number of estrous females observed per year in our analysis as a possible factor to explain variations in home-range sizes. The number of estrous females was determined as the absolute number of individual females that were observed in estrus for at least 9 days during a given year (we counted each female only once). This measure is the most conservative one and minimizes possible biases introduced by uneven observation days per individual.

Between July 1999 and May 2001, playback experiments with chimpanzee calls of neighboring and stranger communities were carried out in the study community. These experiments could have led to an increase of border-

patrolling behavior, thereby extending the borders of the home range. Alternatively, these experiments could have artificially enhanced the pressure from neighboring groups, leading to a decrease in home-range size. We have done several analyses to control for such effects: possible short-term effects of playback experiments on chimpanzee behavior were excluded by excluding experimental days and up to 3 days after each experiment from the analysis, and middle-term responses were controlled for by analyzing home-range size for only those months in which no experiments were carried out (i.e., March–June for years 1992–2000).

Home-range usage

To analyze whether the home range was used in a random, clumped, or uniform way, we calculated the standardized Morista index of dispersion for each year (Krebs, 1999). This index is based on the grid cell usage frequency and relatively independent of population density and sample size. The standardized values range from -1.0 to +1.0 with 95% confidence limits at -0.5 and +0.5 (Krebs, 1999). An index of zero indicates random patterns; clumped patterns are indicated by values above zero, and uniform patterns are indicated by values below zero.

To further analyze whether the chimpanzees used the same parts of their home range with high frequencies throughout years, we calculated home-range overlap and core-area overlap between years. For this analysis we used the Morista's index of similarity, which has been suggested to be one of the best measures to calculate niche overlap (Krebs, 1999) because it is independent of sample size. The index ranges between 0 (no overlap) and about 1 (total overlap) and uses the relative frequency with which each grid cell has been used to determine overlap. Thus, even if the same cells had been used as home range in 2 consecutive years but different parts of the home range had been used as core areas, the index would result in a relatively low value because cell usage frequencies would be very different. Therefore, this index not only provides a measure for the number of different grid cells used in different years but also for shifts in cell usage frequencies. We also calculated the more widely used “center of activity” to compare home-range use between years. This measure is a theoretical measure based on an average of the x-/y-coordinates of grid cells weighted by their usage frequency (Lehner, 1996).

Statistical analysis

We used Pearson correlation analysis to determine if the number of observation days or fruit abundance on a monthly basis correlated with home-range sizes. The effect of several other variables on home-range size was analyzed by using a generalized linear model with identity link function and Gaussian error distribution (McCullagh and Nelder, 1989). We used best subset model selection based on Akaike's Information Criteria (AIC) to identify the most important variables. Variables included in the model were community size, number of adult males, number of adult females, number of dependent infants, number of estrous females, and rainfall as an approximation for food availability. Encounter rates were included in a second step because these data are only available for a 7-year period. For that analysis we only used the significant factors from the first model plus the new variable encounter rates to determine if this variable would improve the model. To analyze the effect of fruit abundance ($n = 4$) on yearly home-range size we used (on a more descriptive level) Spearman correlation analysis because all multivariate methods require more than four data points. All analyses are based on two-tailed statistics with

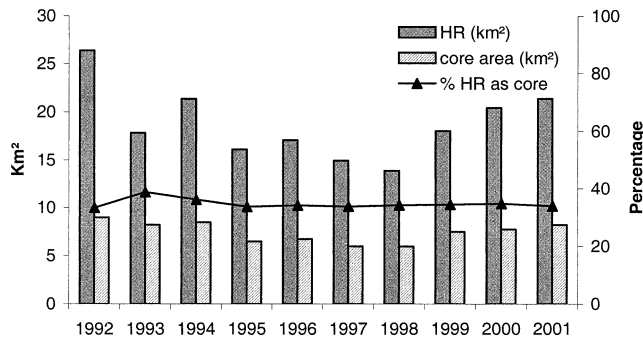


Figure 1
Home-range (HR) size, core-area size, and percentage of home range used as core area from 1992 until 2001. Home-range calculation is based on the minimum convex polygon method, and the core-area measure is based on grid cell method (see text for details).

a significance level of $p < .05$ and were calculated using the program Statistica (StatSoft). We checked adequacy of the model by residual analysis. Residuals were approximately normally distributed and indicated independence of the data by showing randomly distributed residuals.

RESULTS

Total home-range size

Home-range size was calculated based on the MCP and the grid cell method. We found that the grid cell method consistently resulted in higher estimates for home-range size as compared to the MCP method, probably due to the relatively large grid cells we used. However, despite the difference in absolute home-range size (see Herbing et al., 2001), the relative changes between years remained the same regardless of the method used, and further analyses were based on the MCP values.

Because the number of observation days differed between years, we tested for a possible effect of observation days on home-range size. As we found no significant correlation between number of observation days and yearly home-range size ($n = 10, r = -.24, p > .5$), we concluded that changes in home-range size were not due to variations in the number of observation days. Additionally, Herbing et al. (2001) showed that 4–5 months of observation using data collected in a 30-min interval are sufficient to reach the asymptote in the cumulative curve of home-range size in Tai chimpanzees, and the data set presented in the present study is well above these critical values.

Relative home-range sizes did not change when we controlled for the effects of the playback experiments by excluding experimental days plus up to 3 days after the experiment. Furthermore, the increase in home-range size between 1999 and 2001 was still evident when we compared only those months in which experiments were never carried out. Thus, we are confident that the observed changes in home-range size after 1998 are not due to increased border-patrolling behavior caused by playback experiments.

Total home-range size generally decreased from 1992 to 1998 from 26.4 km² to 13.9 km², respectively, but increased from 1999 to 2001 (Figure 1). Community size, in contrast, continued to decrease, while the number of adult males remained relatively stable since 1997 (Table 1). Of the six variables used in the generalized linear model, only two were selected by the best subset method—namely, the number of adult males and the number of adult females. The reduced model using these two factors was significant

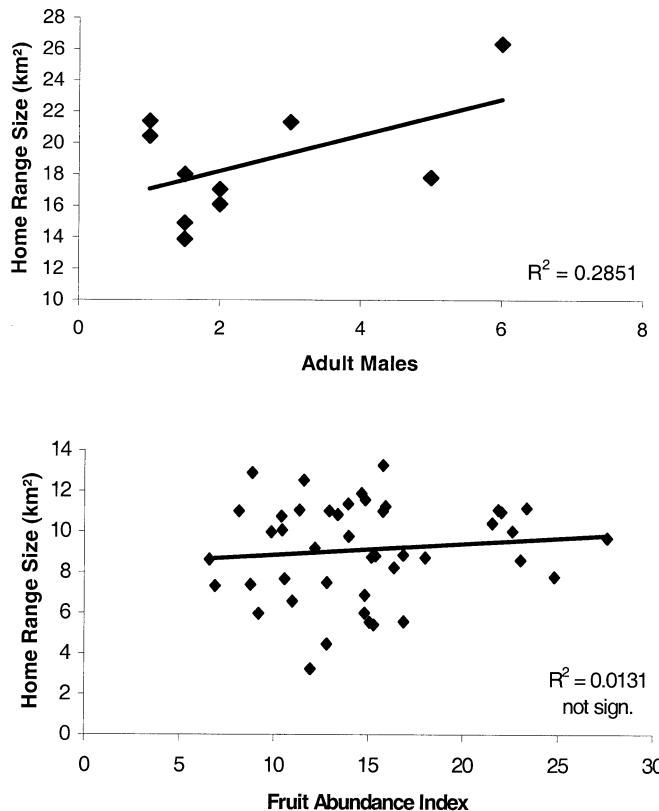


Figure 2
(a) Relation between home-range size and number of males aged >15 years. The line represents the trend line. (b) Relation between monthly home-range size and fruit abundance. The line represents the trend line. No significant correlation was found between these two variables.

(Model_{males+females}: $n = 10, df = 2, AIC = 48.64, \chi^2 = 10.96, p < .005$; Model_{full}: $n = 10, df = 6, AIC = 56.03, \chi^2 = 11.57, p > .07$). The effect of number of adult females, however, was negative (standardized $\beta = -2.27$) and therefore in the direction opposite to that expected. This is due to the fact that the number of adult males and the number of adult females are highly correlated ($r = .92$).

Multicollinearity of two variables in a model is known to cause unreasonable regression coefficients (Zar, 1999), and it is suggested to remove one of the variables from the model. We therefore used the simple regression within the generalized linear model analysis to analyze the effects of the number of adult males and the number of adult females separately and found that the model using only the number of males reached significance ($n = 10, df = 1, Wald \chi^2 = 3.99, p < .05$), whereas the model using number of females did not ($n = 10, df = 1, Wald \chi^2 = 0.63, p > .4$). Thus, we consider the number of adult males as the only meaningful factor to explain variations in home-range sizes (see Figure 2a). However, when including encounter rate ($n = 7$) in the model, the model improved as compared to the model using number of males only (Model_{males+encounter rate}: $n = 7, df = 2, AIC = 32.2, \chi^2 = 6.8, p < .04$; Model_{males}: $n = 7, df = 1, AIC = 33.3, \chi^2 = 3.7, p < .06$). No significant correlation was found between home-range size and fruit abundance ($n = 4, Spearman r = -.4, p > .6$).

Fruit abundance and monthly home range

Monthly home ranges did not correlate with either number of observation days ($n = 44, r = -.03, p > .8$) or fruit abundance index ($n = 44, r = .11, p > .4$; Figure 2b).

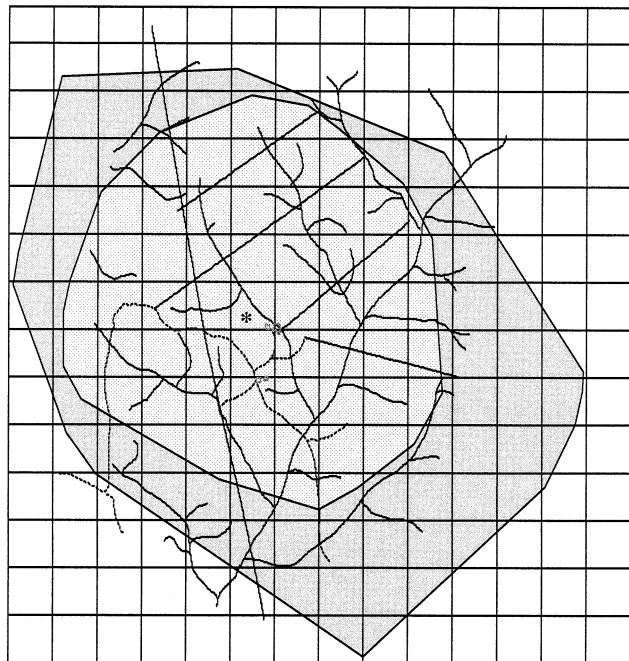


Figure 3

Maximum (shaded area) and minimum (dotted area) home ranges of the north community during the study period from 1992 to 2001. Largest home range in 1992 was 26.39 km² and smallest range in 1998 measured 13.89 km². Grid represents 500 × 500 m cells. Lines are rivers and paths in the forest. The asterisk refers to the central grid cell in Figure 4, in which the majority of the activity centers was found (1992–1997).

Home-range use

Morista index

All indices for habitat use were between 0.501 and 0.508 and showed with 95% confidence a clumped distribution. This reflects a clumped use of the home range, with a highly used core area and a less visited peripheral area. However, food abundance does not follow a similar pattern (Anderson et al., 2002).

Core area

The size of the core area changed proportionally to changes in home-range size (Figure 1). The proportion of the home range used as a core area was about 35% of the total home range and remained stable across different years (Figure 1).

Home-range and core-area overlap

The Morista index of similarity provides an indication of home-range/core-area overlaps between consecutive years. Values were extremely high (mean ± standard deviation: home range_{overlap} 0.95 ± 0.04, core area_{overlap} 0.88 ± 0.06; Table 1). These high values demonstrate the strong site fidelity of the chimpanzees, not only in terms of area of the forest used but also in terms of specific places visited most frequently. The strong site fidelity of the Taï chimpanzees despite large changes in home-range size as well as in community size and composition is also depicted in Figure 3, which shows the largest and the smallest home range of the study period.

Center of activity

The center of activity across years remained stable, indicating that areas of heavy use did not shift much during the study

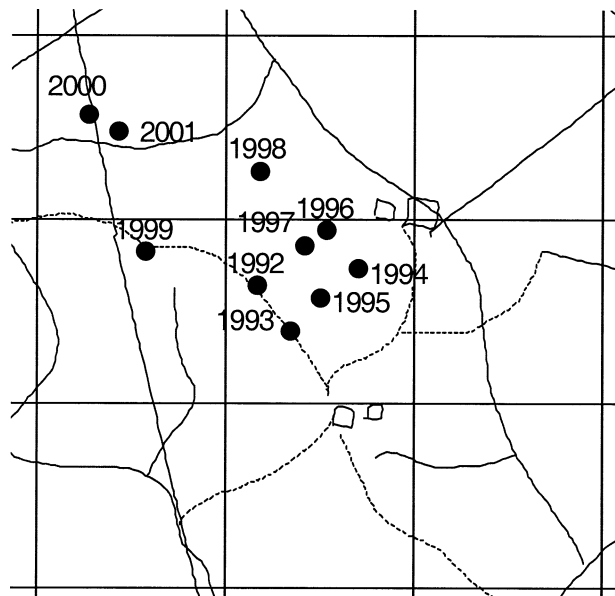


Figure 4

Centers of activity from 1992 to 2001. Grid cell size is 500 × 500 m. The grid cell in the center of this figure is marked with an asterisk in Figure 3.

period (Figure 4). The largest distance between the centers of activity of 2 consecutive years occurred between 1999 and 2000, where they were 0.4 km apart. The largest distance over the whole study period was 0.8 km (1994/2000). In a home range of an average size of 18.5 km² this distance is probably negligible, and the data support the high degree of site fidelity indicated by the high values of the Morista index of similarity.

DISCUSSION

In this study of long-term ranging patterns of Taï chimpanzee we have demonstrated that, although home-range size varied considerably between years, home-range use remained remarkably stable. Using multivariable analysis, changes in home-range size were largely attributable to the number of adult males present in the community as well as to the number of intercommunity encounters. Total community size changes did not sufficiently explain changes in home-range size, which is mainly due to the fact that home-range size increased in recent years despite decreasing community size.

In primates as well as in many other species, group size has been found to be a good predictor of home-range size (e.g., Davidge, 1978; Ikeda, 1982; Suzuki, 1979; Takasaki, 1981). However, although it has been reported that larger chimpanzee communities occupy larger home ranges (see Figure 5), it has been suggested that community size alone is not a sufficient predictor for home-range size in chimpanzees (Boesch and Boesch-Achermann, 2000; Goodall, 1986). This is also demonstrated in the present study where home-range size decreased with decreasing community size over a period of 7 years (1992–1998), but the increase of home-range size in recent years (1999–2001) cannot be explained by changes in community size.

Based on the socioecological model, it has been suggested that group composition in general, and in the case of chimpanzees, the number of adult males within a community might be a better predictor of home-range size than total community size (Boesch and Boesch-Achermann, 2000;

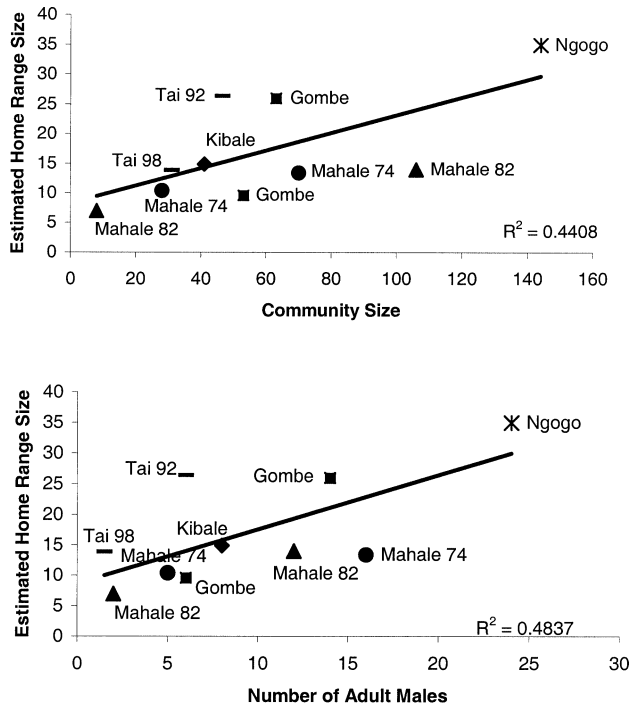


Figure 5 Home range sizes and demographic variables reported from various chimpanzee study sites. The upper graph depicts home range in relation to community size; the lower graph depicts home ranges in relation to the number of adult males. Values are mainly estimates and taken from Goodall (1986) for Gombe; Chapman and Wrangham (1993) for Kibale; Nishida (1979) for Mahale 1974, Hasegawa and Hiraiwa-Hasegawa (1983) for Mahale 1982, and Watts and Mitani (2001) for Ngogo. Data for Tai are from the present study (largest and smallest home range in 1992 and 1998, respectively). The lines represent trend lines.

Goodall, 1986). Findings from East African chimpanzee populations in Gombe (Goodall, 1986) and Mahale (Hasegawa and Hiraiwa-Hasegawa, 1983; Nishida, 1979), where smaller home ranges are associated with fewer males (Figure 5), support this hypothesis. However, in Gombe as well as in Mahale, communities with fewer adult males were also smaller, and it is difficult to separate the effect of community size from that due to the number of adult males within the community. Furthermore, recent work on Gombe long-term data did not reveal a significant effect of number of adult males on home-range size (Williams, 1999). In Tai, on the other hand, the number of adult males but not community size predicted home-range size significantly, supporting the hypothesis that male fighting power is more important in chimpanzees than absolute community size. However, the relation between home-range size and number of males is not so straightforward because the increases in home-range size since 1999 cannot be explained by the absolute number of adult males in the community. Furthermore, an intercommunity comparison in the Tai forest also does not support the male hypothesis. In 1997, the smallest community (11 chimpanzees) with 4 adult males used a home range of 12.1 km² (see Herbing et al., 2001) while the study community (data presented here) with only 1–2 adult males ranged over almost 15 km². Additionally, earlier data from Tai demonstrate that home-range size can increase despite a decrease of the number of adult males: in 1982 Boesch and Boesch-Ackermann (2000) found that the community with a 9 adult males used a home range of 18.1 km², but in 1989 when only 6

males were present the home-range size was 23.7 km². Thus, number of males within a community (i.e., intrinsic fighting power) is an important but not sufficient factor to explain within- and between-community home-range size variations.

One reason for this could be that the number of adult males within a community is only an approximation for intrinsic fighting power, which may not always be a correct measure for absolute fighting power of that community. Absolute fighting power is expected to vary with individual characteristics (such as fear or border patrolling strategies), which might be especially important when only a small number of males is present. Additionally, females can take a more active part in border patrolling, as has been observed in Tai (Boesch, personal observation), which may then increase the community's fighting power. But not only absolute strength is important but also the relative fighting power of one community as compared to the strength of neighboring communities. In Gombe, the number of adult males relative to external threats (a measure derived from unexplained disappearances, injuries, and intercommunity encounters) was significantly correlated with home-range size (Williams, 1999), indicating the importance of relative fighting power and intercommunity competition. This is also supported by our study, where intercommunity encounter rates were an important variable in the model obtained to explain home-range size changes. The increase of the home range in recent years occurred during a time when intercommunity encounters decreased. This finding is in line with the negative correlation between intercommunity encounters and home-range size, which was reported by Boesch and Boesch-Ackermann (2000) when analyzing monthly home ranges. However, our finding of a stable home-range use and a stable relative core-area size suggests that home-range size was not constrained by territorial activities of neighboring communities in previous years.

One other explanation for the recent expansion of the home range in Tai could be a decrease of overall chimpanzee density, which would also explain the decrease of intercommunity encounters. Unfortunately, direct data on overall population densities in the Tai National Park are not available. Boesch and Boesch-Ackermann (2000) reported a density of 4.1 chimpanzees/km² in 1989, while today we find around 1 chimpanzee/km², but the reported densities are derived from one or few habituated communities only and do not necessarily reflect overall population densities in the area. However, for Tai, we cannot exclude the possibility that the epidemics in 1996 and 1999 may have affected a major part of the chimpanzee population in the Tai forest, thereby leading to a general decline in chimpanzee population density. One neighboring community, which was habituated in 1995, has decreased in size and is currently close to extinction (1 male, 2 females). However, although our study community expanded their home range, the expansion did not occur into the home range of this small community.

Another factor that has been shown to influence ranging patterns is food availability. Comparisons between populations living in different habitats have shown that, for example, chimpanzees living in dry woodlands have much larger home ranges than chimpanzees living in rainforest habitat (Baldwin et al., 1982). In a recent paper on the generality of the ecological-constraints model, Gillespie and Chapman (2001) emphasized that the model predicts a strong relationship among group size, ranging patterns, and food availability but not necessarily between any two variables alone. Thus, the increase of home-range size in Tai chimpanzees despite decreasing community size could be due simply to a decrease in food availability. For the past 4 years average fruit abundance index did not change markedly, and we did not

find a significant correlation of fruit availability and home-range size for either monthly home ranges (Figure 2) or for the available data points on yearly home range. This was also supported by the lack of a significant correlation of home-range size and the annual amount of rainfall, which in general has been considered to be a good predictor of overall forest productivity (Dunbar, 1988; Rosenzweig, 1968). Furthermore, if the home range had been expanded due to a decrease in food availability, we would expect to see an increase of daily travel distance and/or changes in home-range use. However, daily travel distance increased only marginally in recent years (Lehmann and Boesch, unpublished observation), and home-range use as well as the proportion of the home range used as core area remained remarkably constant, indicating that the variations in home-range sizes observed in the Taï chimpanzee community are most probably not due to alterations in food availability. Therefore, we feel confident that fruit availability is not responsible for the observed changes in home-range size.

Several other studies have demonstrated a lack of an effect of food availability and ranging patterns (for review see Adams, 2001). As the observed changes in home-range size cannot be explained by changes in fruit abundance, it appears unlikely that home-range size in this study simply reflects the metabolic needs of the group, as suggested by optimality models for home-range size (Maher and Lott, 1995; McNab, 1963, see also McLoughlin and Ferguson, 2000). For chimpanzees it may instead be important to extend their home ranges above their metabolic needs to either secure access to additional food resources or to increase the number of mates. Data from Gombe suggest that male territoriality might be strongly driven by aiming at increased access to food resources rather than attracting female mates (Williams, 1999). The former may be closely related to the latter because females might be attracted to increased food supply and female reproductive success might be enhanced in larger home ranges (Williams, 1999).

In summary, our long-term study on chimpanzee ranging patterns demonstrates that home-range size could be significantly predicted by the number of adult males and by intercommunity encounter rates but not by community size, supporting the hypothesis that community composition has a strong influence on ranging patterns. Food availability did not help to predict variations in home-range size. However, none of the factors used here to predict home-range size can sufficiently explain the recent expansion of the range. Thus, we conclude that the observed home-range size is most likely the outcome of a (not necessarily linear) combination of several factors, including food, mate attraction, community size, and relative fighting power, and the predictive value of any of these factors depends on the status of the other factors. The fact that overall home-range use and core-area size has scarcely changed over the past 10 years indicates that factors other than community size and composition determine home-range use. To what extent social behavior, including individual ranging patterns, have been influenced by the dramatic decrease in community size is currently under investigation.

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