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ORIGINAL ARTICLE

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Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*)

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Abstact While male mammals seek to maximize access to potential mates, females maximize feeding efficiency. Ranging patterns are therefore often sex specific. Sex-specific ranging patterns have also been reported for East African chimpanzees and a recent study on female ranging patterns concludes that social organization is best described by a male-bonded community model, where females occupy individual home ranges that are distributed within the boundaries of the male-defended range. In West African chimpanzees, however, such sex-specific ranging patterns have not been consistently observed and a bisexually bonded community model, where both sexes use the entire home range equally, has been suggested to best describe social organization. In this study we analyze 5 years of data on individual ranging patterns of chimpanzees in the Taï National Park (Côte d'Ivoire) to test specific predictions of the different models of chimpanzee social organization. We found that although males in Taï had slightly larger home ranges than females, all individual home ranges and core areas overlapped highly. Small individual home range size differences were entirely due to the use of peripheral areas and were correlated with female social dominance. These findings strongly support the bisexually bonded community model for Taï chimpanzees. Thus, we conclude that there are fundamental differences in the space-use patterns of East and West African chimpanzees and discuss possible factors leading to such differences.

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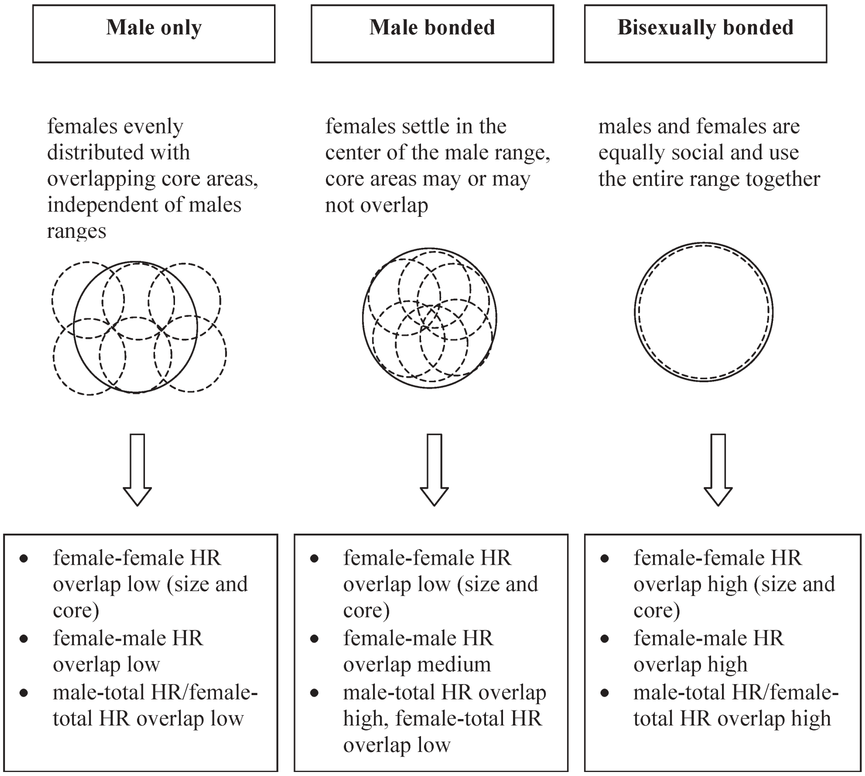
Introduction

The socio-ecological model proposed by Wrangham (1979) and extended by van Schaik (1989) and Sterck et al. (1997) is based on the assumption that male reproductive success is limited by the number of mates a male can find and monopolize, while female reproductive success is closely linked to feeding efficiency (see also Emlen and Oring 1977). Therefore, space use is expected to differ between the sexes and the observed ranging patterns in males should be dependent on the costs and benefits of defending receptive females versus searching for more mates (Dunbar 1988). In line with this, male ranging patterns often change in response to the distribution and the density of receptive females (e.g. voles: Ims 1988; Nelson 1995) while female ranging patterns are more influenced by the availability and distribution of food resources (e.g. Gehrt and Fritzell 1998; Lurz et al. 2000). Other factors, such as predation risk or the risk of infanticide, however, may affect female social relationships and ranging patterns, so that the predicted sex differences in association and ranging may not always be found (Sterck et al. 1997). Nevertheless, male and female space use and ranging patterns can be regarded as a key factor in the evolution of a species' social organization (Ims 1988; Clutton-Brock 1989; Komers and Brotherton 1997; Fisher and Owens 2000) and studying species differences in ranging patterns provides information about the factors influencing social organization. Furthermore, intra-specific variations in ranging patterns will help to understand the degree of flexibility in the social organization of group-living animals.

In line with the socio-ecological model is the often reported finding across many taxa that male home ranges are larger than female home ranges, thereby giving the male access to more than one female. This is especially true for species in which females are solitary and sparsely



females evenly distributed with overlapping core areas, independent of males ranges

females settle in the center of the male range, core areas may or may not overlap

males and females are equally social and use the entire range together

- female-female HR overlap low (size and core)
- female-male HR overlap low
- male-total HR/female-total HR overlap low

- female-female HR overlap low (size and core)
- female-male HR overlap medium
- male-total HR overlap high, female-total HR overlap low

- female-female HR overlap high (size and core)
- female-male HR overlap high
- male-total HR/female-total HR overlap high

Fig. 1 The three models of chimpanzee social systems. Modified and extended following Wrangham 1979. The models lead to clear predictions in terms of home range (*HR*) overlaps

distributed, such as raccoons (Gehrt and Fritzell 1998) and red squirrels (Lurz et al. 2000) but the same has been found in group-living species, such as chimpanzees (Goodall 1986; Williams et al. 2002). The socio-ecological model predicts further that if home range quality varies across a habitat, females should compete for home ranges of high quality. Indeed, variations in home range sizes within a population can sometimes be explained by differences in rank, with high ranking individuals occupying better quality and/or larger home ranges as compared to lower ranking ones (Holmes et al. 1996; Huhta et al. 1998). In chimpanzees (*Pan troglodytes)*, for example, it has been found that newly immigrated and therefore low-ranking females occupy home ranges close to the periphery (Nishida 1989). Peripheral areas are assumed to be less safe due to the high risk of violent inter-community encounters (Williams et al. 2002) and therefore peripheral home ranges are thought to be of low quality. However, data about chimpanzee social organization suggest large differences between populations. Generally, chimpanzees live in multi-male, multi-female communities of 20–150 individually recognized members (Goodall 1986; Nishida 1990; Watts 1998; Boesch and Boesch-Achermann 2000). Male chimpanzees usually remain in their natal community while most females disperse. Community home ranges are relatively stable over time and can be divided into a heavily used core area and a less frequently visited peripheral zone. Like bonobos and spider monkeys, chimpanzees exhibit a fission–fusion organization and often travel in small subgroups (‘parties’) rather than as a whole group. This allows a flexible adjustment of group size to individual needs, and sex differences in sociality and ranging patterns are expected. A recent long-term study on female chimpanzee ranging patterns in Gombe, East Africa, showed that females spend most of their time alone and occupy small, individually distinct but overlapping core areas (Williams et al. 2002), while males are known to be more gregarious and occupy larger ranges (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986; Wrangham et al. 1992). However, in a study of the West African subspecies of chimpanzee at Taï National Park no such pronounced differences between male and female space use and sociality were observed and so it was suggested that both sexes are equally social and occupy similar home ranges (Boesch and Boesch-Achermann 2000). A similar pattern has also been reported from another West African study site, namely Bossou (Sugiyama 1988; Sakura 1994).

Thus, since sociality and space-use patterns in chimpanzees appear to vary substantially between populations, three models have been proposed to describe chimpanzee social organization (Fig. 1). The ‘male-only community model’ suggests an even distribution of females with overlapping core areas, independent of the males’ range (Wrangham 1979). Ranging patterns like this minimize feeding competition between females and this model was suggested after some peripheral living females in Gombe were observed to stay in that area when the home range of the males shifted (Wrangham 1979). However, the occurrence of violent attacks on females in border areas at some study sites does not support the ‘male-only community model’ (Pusey 1980). Secondly, the ‘male-bonded community model’ hypothesizes that females settle within the male-defended range but use individually distinct home ranges to minimize feeding competition (Wrangham 1979; Smuts and Smuts 1993). Data from Gombe generally support this model (Williams et al. 2004). Thirdly, based on observations in the Taï National Park, Boesch (1991) suggested the 'bisexually bonded community model' in which males and females use the entire community range equally and are equally social. Although the three models refer to social bonding, they lead to distinct predictions in terms of sex differences in home range size and the degree of home range overlaps (see Fig. 1). No one, so far, has tested these predictions explicitly. In the male-only community, males have larger home ranges than females and all home range overlap combinations are generally expected to be low. In the male bonded community, overlap will be low between female home ranges and a medium overlap is expected between the sexes (due to the fact that male ranges are always larger than those of females). However, most importantly, a sex difference should be found for overlaps with the community range, with males showing a higher overlap with the community range than females. Further, males are predicted to have significantly larger home ranges than females. Finally, in the bisexually bonded situation, all overlap combinations should show a high degree of overlap and since males and females use the entire home range in a similar way, either no or only small sex differences in home range size should exist.

In this study we analyze individual male and female ranging patterns of a wild chimpanzee community in the Taï National Park, Côte d'Ivoire, over a period of 5 years, using home range size, core area size, center of activities and home range overlaps to test the predictions described above. Based on previous observations we expected to find support for the bisexually bonded model, i.e. similar ranges for males and females with high overlap values for all combinations. In addition, we tested whether individual differences could be attributed to (1) female reproductive status (Goodall 1986; Williams 1999), (2) social dominance in females (Wittig and Boesch 2003) or to (3) the number of dependent infants, all of which have previously been suggested to influence female ranging patterns (Williams 1999).

Methods

Study site and population

The Taï National Park, Côte d'Ivoire, West Africa, comprises an area of approximately 4,540 km^2 and consists of evergreen lowland rainforest (for detailed description of the study site see Boesch and Boesch-Achermann 2000). Data presented in this study were derived from the north community, which was habituated in 1979 and has been continuously observed since its habituation by researchers and field assistants. Data presented here start with 1997, when the grid cell system used today was introduced, allowing the determination of individual ranging patterns. In January 1997, the community consisted of 2 adult males (aged >15 years), 11 adult females (aged >13 years), 1 adolescent male (aged 9 years), 2 adolescent females (aged between 9 and 13 years), 6 juveniles (aged between 5 and 8 years) and 10 dependent offspring (aged <5 years). Since that time group size has decreased to 1 adult and 1 adolescent male, 6 adult females, 9 immature and 5 dependent offspring in December 2001. No emigrations or immigrations have been observed in any of the communities during the study period. For some comparisons, data from the more recently habituated south community was used. This community consisted of 5 adult and adolescent males, 20–21 adult and adolescent females, 9–13 immature offspring and 16–18 infants.

Data collection

Data were collected by field assistants during daily focal animal follows and locations of the target animal are recorded continuously as *x–y* coordinates of a superimposed 500×500-m grid cell system. Between 1997 and 2001, a total of 316 follows on adult males and 703 follows on adult females with an average length of 10.5 h per day were collected. Targets were usually located early in the morning and followed throughout the day. Multiple targets followed by different observers on the same day made up less than 3% of the dataset. Due to the fission–fusion nature of the chimpanzee social system, targets usually do not spend the entire day together in the same party. Similarly, same targets were rarely followed on consecutive days (<7% of all follows). The large bias towards female follows is due to the small number of males in the north community. Not all individuals of the study community were followed equally often. However, Taï chimpanzees are very cohesive and often move in large parties (Boesch 1991; J. Lehmann and C. Boesch, unpublished data), therefore each individual has been observed sufficiently often as either target or member of a party to determine individual home range size. None of the community members appeared to avoid the group for longer periods of time and all subjects were observed a minimum time of 312 h/year. Due to the high cohesiveness in Taï chimpanzees (Taï chimpanzees spend less than 20% of their time alone, see Lehmann and Boesch 2004), sample sizes were too small to reliably calculate 'alone home ranges' for females as was done in a recent study in Gombe chimpanzees (Williams et al. 2002). For males, data on adult and adolescent males were used.

Data analysis

All data were entered into 'Taï-Chimp-BehavBase', our large chimpanzee-behavior database, using Microsoft Access. All statistical tests were two-tailed with a significance level at α=0.05 and were carried out using SPSS for Windows (Release 11.0.1, SPSS).

Individual home range size

Individual home range was defined as the minimum area including every location where the individual has been observed during a given year. The area was established by counting the number of different grid cells an individual has been observed in, multiplied by the area of a cell, i.e. 0.25 km^2. As individually used areas were highly contiguous, the grid cell method is a better estimate of individual home range size than the minimum polygon method. Since we did not have sufficient individual target days per year to analyze home range size reliably based on target days only, we included all locations where a subject was observed either as target or as member of a party. This method could lead to a bias in the data set as more social individuals would be encountered more often and hence be inferred to have larger home ranges. However, we found no correlation between the number of target days per individual and home range size. Furthermore, this method could only lead to an underestimation of individual home range size. If home ranges were indeed larger than those reported here, this would imply that all females use the entire home range like males, which would strengthen our point. Based on findings in Gombe where females that cycled during a given year were observed to have larger yearly home ranges than non-cycling females (Goodall 1986), we also analyzed the effect of estrus cycle on home range size to test if

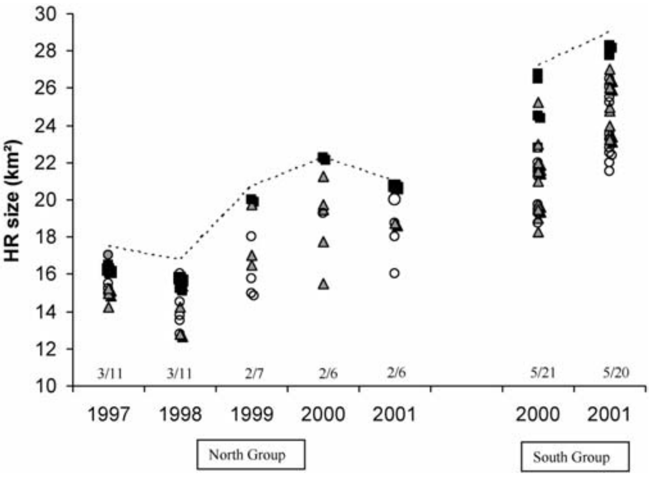


Fig. 2 Home range sizes in km^2 for individual male and female chimpanzees. Males are depicted as *filled squares*, females as *open circles* (non-cycling) and *grey triangles* (cycling), the *dashed line* indicates community home range size. Numbers indicate the number of males and females, respectively. *Shadowed symbols* indicate more than one chimpanzee with the same home range size. Home range size calculation is based on the grid cell method. Note that the scale starts at 10 km^2

inter-individual differences could be attributed to the reproductive state of females. A female was defined as cycling if she was more than 13 years old and had a minimum of two estrus cycles per year. If females in estrus visit areas that are not usually part of their home range, we expect to find larger year home ranges in cycling females than in non-cycling females, as has been reported in Gombe (Goodall 1986). We further included presence or absence of dependent infants in the analysis, since it has been suggested that females with infants travel more slowly and less far and avoid peripheral areas (Williams 1999; Boesch and Boesch-Achermann 2000). Levene's test for variance homogeneity was used to test for home range variance homogeneity across years. Data on home range and core area sizes were analyzed using a linear mixed model procedure. This procedure expands the general linear model to data with correlated and/or non-constant variability (SPSS technical report: Linear mixed-effects modeling in SPSS, http://www.spss.com/registration/premium/). With this analysis we controlled for the effects of individuals across years as well as for the effects of years by including individual as subject variable and year as repeated and random factor while sex, estrus cycle and number of infants/juveniles, respectively, were used as fixed factors. Since the dependent variables (home range and core area sizes) increased over time (Fig. 2), we used the first-order autoregressive procedure to model the covariance (Verbeke and Molenberghs 2000).

Home range overlap, home range use and core areas

Since individuals could have individually preferred areas within their home range (despite using the whole area occasionally), we calculated the amount of time each individual was seen in a particular grid cell as either target animal or accompanying the target. Thus, we obtained durational data for each chimpanzee and location, using these to calculate cell usage intensity as percent of total observation time for each subject. Based on usage data we also calculated individual 75% core areas (following Herbinger et al. 2001), i.e. the minimal number of grid cells accounting for 75% of total individual usage. Data on core area size were analyzed using a linear mixed model procedure as described above. In order to compare individual home range use and core area use patterns we calculated Morisita's index of similarity, which has been suggested to be one of the best measures to analyze 'niche' overlap (Krebs 1999), since it is independent of sample size. This index ranges between 0 (no overlap) and about 1 (total overlap). Even if the same cells had been used as home range in 2 consecutive years but different parts of the home range were used as core areas, the index will result in a low overlap value. Therefore, this index not only provides a measure for the number of different grid cells used in different years but also for differences in cell usage. Yearly home range overlap values (Morisita index) were calculated for each chimpanzee dyad and mean values were calculated per year for each sex combination (female–female, female–male, male–male) as well as for overlap with the community home range (female–total and male–total). To quantify the extent of overlap we used the one-sample T-test and tested values per class and year against 80% overlap. We also calculated the more widely used 'center of activity' to compare home range use between individuals and years. This measure is a theoretical measure based on an average of the x–y coordinates weighted by grid cells usage (Lehner 1996) and was used here to illustrate the high similarities between individuals.

Home range size and rank

Since in Taï female chimpanzees exhibit a linear hierarchy (Wittig and Boesch 2003), we analyzed whether differences in rank accounted for variations in home range size. Rank calculation was based on directed pant–grunts and greeting–hoohs, all of which serve as greeting vocalizations in Taï chimpanzees (Wittig and Boesch 2003). Since greetings between females are rare, ranks cannot be assessed on a yearly basis. We subdivided the whole study period into two different periods (1997–1998 and 1999–2001) because the death of several community members in 1999 led to several changes in ranks. Data for 1997/1998 were taken from Wittig and Boesch (2003) while data for the second period were calculated directly from 81 greeting vocalizations, using MatMan (Noldus 1998). The relation between female home range size and female rank was analyzed using Spearman rank correlation analysis.

Site fidelity and inter-individual differences

Home range and core area usage can be compared between individuals within each year, to examine individual variation, and between years within individuals, to examine site fidelity. We used dissimilarity indices to calculate average values of between-individual home range dissimilarity within years and within-individual home range dissimilarity between years. Dissimilarity values were obtained by subtracting individual home range similarity values (as derived from the Morisita index of similarity, see above) from 1, which is the highest possible similarity. In a recent study, Williams et al. (2002) calculated 'female alone core area' dissimilarities by using an index based on the distribution of points where a female was seen alone compared to the overall distribution. Since in our study females were rarely observed alone, we based comparisons concerning space use on the time each individual spent in a given location, rather than comparing the distribution of locations. Thus, the index chosen in our study controlled for home range size, location and use. Because of the different nature of the data and a different focus of our study, indices were calculated differentially in these two studies. However, we used the data of Williams et al. (presented in Table 1 in Williams et al. 2002) to calculate 'within-individual and between-years' versus 'between-individual and within-years values'. Although values cannot be compared directly between study sites, we used non-parametric statistics (Mann-Whitney U-test) to analyze for differences between and within years within each study site to obtain information about inter-individual differences and site fidelity within each study site.

Results

Individual home range sizes and sex differences

In 1997 and 1998 individual home ranges were very similar but with increasing community home range in 1999 inter-individual differences also increased (Fig. 2), as shown by the significant increase of variance across years (Levene's test for variance homogeneity: Levene statistic$_{(4,49)}=5.3$, $P<0.01$). Further, we found a small but significant sex difference, with males having larger home ranges than females (mixed model analysis: $F_{(1,12.3)}=4.9$, $P<0.05$). On average, females used 88% of the males' home range. The female with the minimum value in the year 2000 (55%), started to show signs of a disabling illness that limited her ability to move and she died in the following year. Excluding her from the analysis, however, does not alter significance. No significant difference in home range size was found for cycling versus non-cycling females (mixed model analysis: $F_{(1,28.5)}=0.05$, $P=0.83$) nor did the presence of dependent infants affect yearly home range size (mixed model analysis: $F_{(1,27.6)}=0.31$, $P=0.59$). Because our study community has considerably fewer males than other chimpanzee communities, we also depicted individual home range sizes for the larger south community for the year 2000 and 2001. Female home range sizes correlated positively with the number of days they were followed in 2001, and we did not include these values in our statistical analyses. Values presented in Fig. 2 are therefore minimum female home ranges (due to a possible underestimation of female home range size), indicating that also in a community with more males, females use a minimum of 85% of male home ranges. Thus, although there is a significant sex difference in home range size in both communities, absolute values show that male and female home ranges were very similar in size, with females using a high percentage of the males home range.

Home range overlap, home range use and core areas

Both males and females used a similar proportion of the home range as core area (mixed model analysis: $F_{(1,19.2)}=1.79$, $P=0.2$; Fig. 3) and consequently males were found to have a larger core area than females (mixed model analysis: $F_{(1,12.7)}=7.84$, $P<0.05$; see Fig. 3). Overlap values in general are very high (with all values but one above 0.85, see Table 1), indicating that all individuals used the home range in a similar way. The only value below 0.85 occurred for female–male overlap in 1999. This is mainly due to two females (Goma and Fossey) with relatively small home ranges. But average female–male overlap for that year is still significantly larger than 0.75, indicating a high degree of overlap even in this year. Male–male overlap values could not be tested statistically because of the small sample size (only two males in the community in 1999 and 2000 with identical home ranges). To demonstrate that differences in home range size were solely due to differences in the use of the periphery, we calculated for each grid cell in 1999, as the year with the largest inter-individual differences, the percentage of community members that used that grid cell. All inner cells were used by all community members, and only the outermost peripheral cells were used by fewer individuals (Fig. 4). As indicated in Fig. 4, only one cell was used by males only and two cells were used by females only; all other cells were used by both sexes, indicating that sex differences in home range size were not due to differential use of peripheral cells.

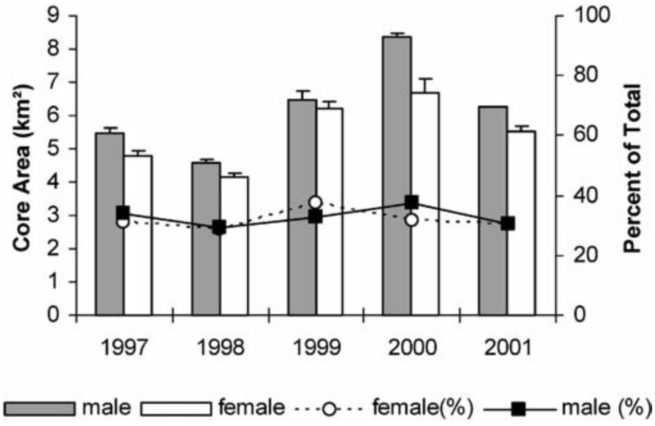


Fig. 3 Core area size in *km*^{2} and relative proportion (%) of individual home range used as core area for male and females chimpanzees

Center of activity

All individual center of activity were within a maximal distance of 400 m within years (Fig. 5), which is less than 7% of the largest home range diameter. Individual centers

Table 1 Yearly home range use overlap values for sex dyads. Overlap was calculated using the Morisita index of niche overlap. The index ranges between 0 (no overlap) and 1 (total overlap). Values are mean±standard error of the mean. The last column indicates the number of males (*m*) and females (*f*) used in the analysis

Year	Male–male	Male–female	Female–female	Male–total	Female–total	*n* (m/f)
1997	0.98±0.001	0.94±0.001	0.94±0.001	0.97±0.003	0.96±0.003	3/11
1998	0.98±0.007	0.94±0.005	0.94±0.004	0.97±0.005	0.95±0.09	3/11
1999	0.99	0.78±0.021	0.85±0.012	0.96±0.002	0.86±0.015	2/7
2000	0.98	0.90±0.016	0.86±0.012	0.95±0.006	0.91±0.018	2/7
2001	1.00	0.97±0.03	0.97±0.002	0.98±0.00	0.98±0.002	2/6

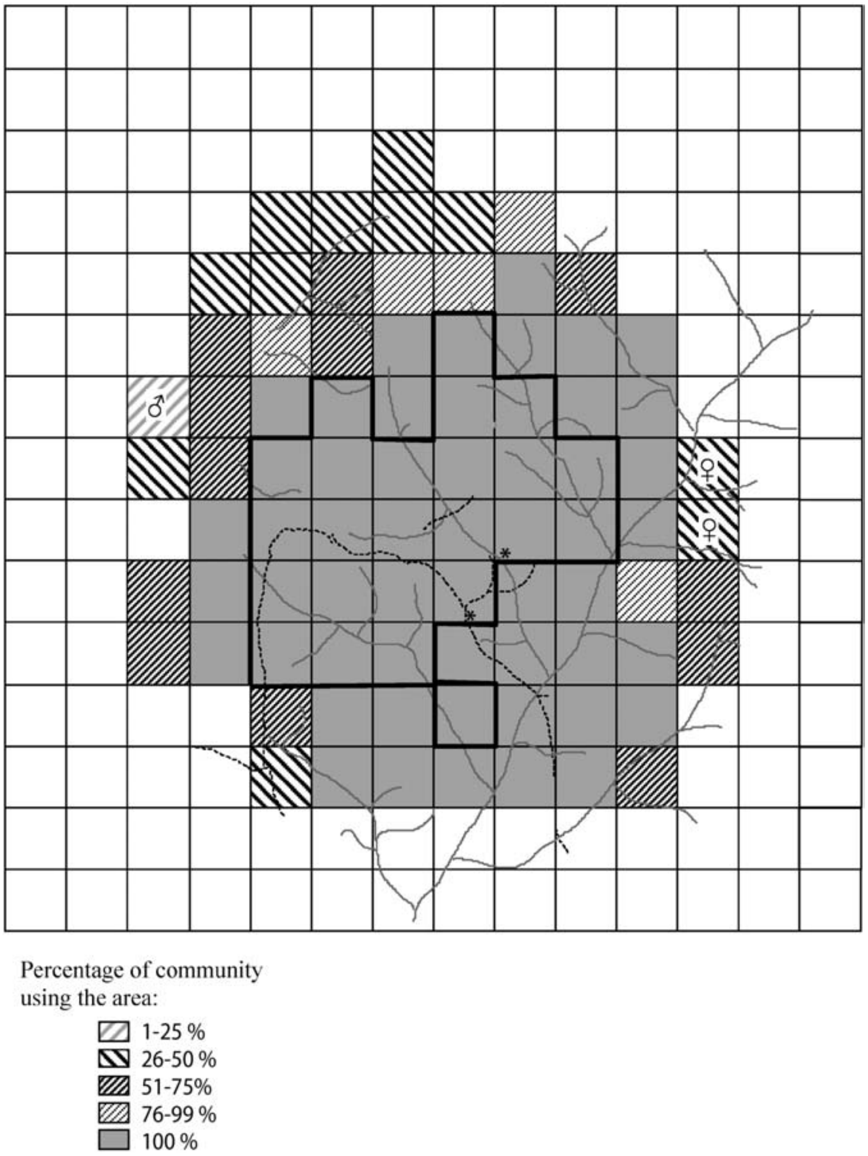


Fig. 4 Home range use of the Taï chimpanzee north community in 1999. *Shading* indicates the proportion of community members (%) that used each of the grid cells. The community core area is indicated by the *bold line*. This figure demonstrates that differences in home range size are entirely due to a difference in the use of the periphery. ♂ and ♀ *symbols* indicate cells that were used by males and females only, respectively. 1999 was chosen because it was the year with the largest inter-individual differences

cluster more closely together within years than between years. The maximal distance between two centers of activity was 800 m, indicating that over the period of 5 years the home range was used in a very similar way and center of activity did not shift dramatically.

Home range size and rank

Taï chimpanzee females showed a linear hierarchy in both periods (P97/98: Wittig and Boesch 2003; P99/01: h'=0.75, $\chi^2_{23.3}$=37.3, P<0.06). There was a significant correlation between rank and home range size for the first period but not for the second period analyzed (Spearman rank correlation: r_S=−0.81, n=14, P<0.001; r_S=−0.663, n=8, P<0.08), demonstrating that high ranking individuals used larger home ranges than low ranking subjects. The non-significant result for the second period was entirely due to one female, Perla, who seemed to have moved from a mid-rank position to the bottom of the hierarchy, while her home range remained mid-sized (see Fig. 6). Exclusion of Perla from the analysis of the second period would lead to a significant correlation (Spearman rank correlation: r_S=−0.955, n=7, P<0.001). The generally larger home ranges of high ranking females were entirely due to the fact that they used more peripheral cells than lower ranking females.

Site fidelity

Figure 7 depicts mean values of home range dissimilarities for Gombe (Williams et al. 2002) and Taï within individuals but between years and within years but between individuals. The former is a measure of site fidelity, the latter for inter-individual differences. Although the absolute values can not be compared directly since dissimilarities were calculated in different ways, it is obvious

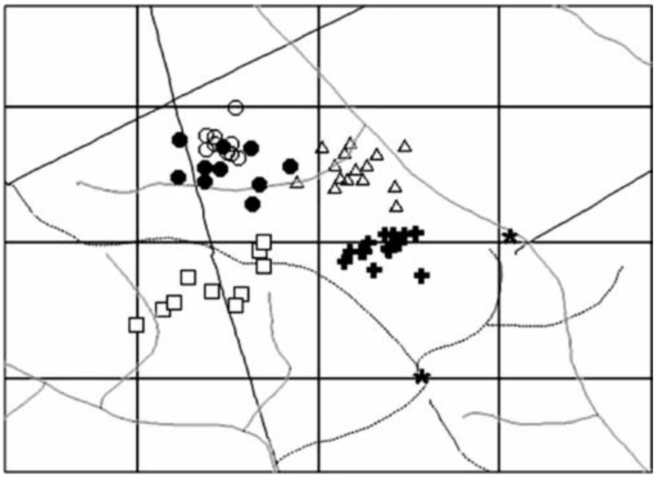


Fig. 5 Individual centers of activity within and between years. *Crosses* 1997, *triangles* 1998, *squares* 1999, *filled circles* 2000, *open circles* 2001. *Grid cells* are 500×500 m. For spatial orientation we used *asterisks* to indicate the same cells in Fig. 4 and Fig. 5

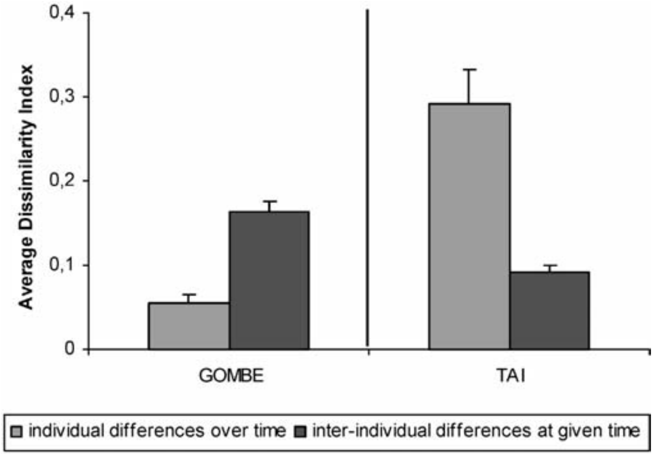


Fig. 7 Mean values of individual home range dissimilarities among female chimpanzees in Gombe and Taï. Individual differences over time indicate site fidelity by comparing individual home range use within animals between years, while inter-individual differences at a given time indicate home range usage between individuals within a respective year. Data from Gombe are taken from Williams et al. (2002). Since the indices were not calculated the same way, a direct comparison between the sites is not valid

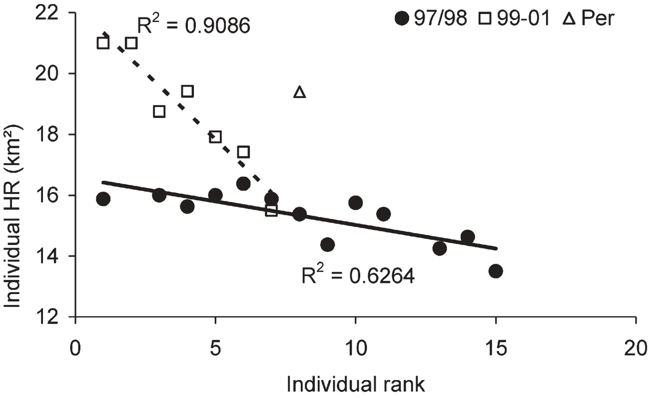


Fig. 6 Relation between chimpanzee rank and individual home range (*HR*) size for two different periods (1997/1998 and 1999–2001). Rank 1=highest rank. The *triangle* symbolizes an outlier, the female Perla (see text). n=13 in 1997/1998, n=8 in 1999/2000

from the graph that females in Gombe display strong site fidelity relative to their inter-individual differences whereas the opposite is the case for Taï. Differences between individual home range dissimilarities within and between years are significant for both sites (Mann-Whitney U-test: Gombe: z=–3.5, n=19, P<0.001; Taï: z=–3.1, n=7, P<0.01) but in opposite directions (Fig. 7).

Discussion

In summary, our data on Taï chimpanzee ranging pattern demonstrate that despite a significant sex difference in home range size, all chimpanzees used the community range in a very similar way. This was supported by high values for individual home range overlap and for overlaps with the community range. Further, all individual centers of activity were highly clustered within the same area and no sex difference was found in the proportion of the home range used as core area. Inter-individual differences in home range use within a given year were smaller than differences between years. Additionally, individual differences in home range sizes were entirely due to the different usage of peripheral areas, and were correlated with rank. Differences in female home range size could not be attributed to female reproductive state or the presence of dependent infants. Thus, our data support the hypothesis that the social system of Taï chimpanzees is best described by the bisexually bonded model, for which high inter-individual similarities in space use are expected (see Fig. 1). Our data further strengthen the suggestion that social organization in chimpanzees varies between study sites and that Taï chimpanzees differ in their space-use pattern from East African chimpanzees.

Generally, sex differences in space-use patterns have often been related to differences in social structure, parental care and mating systems. In the monogamous beaver, for example, males and females occupy and use territories of almost identical sizes (Herr and Rosell 2004), while in polygynous voles males have larger ranges than females, enabling them to obtain access to multiple females during the breeding season (Ims 1988). Furthermore, it is widely believed, that in mammals males have generally better spatial abilities than females (Jones et al. 2003), which has been linked to mating-oriented extensive ranging often found in males (for discussion see Ecuyer-Dab and Robert 2004). This study together with the data from Gombe (Williams et al. 2004), however, suggests a strong ecological component to sex differences in ranging pattern (see discussion below). Nevertheless, Tai chimpanzees do show a small but significant sex difference in range size, which is in line with the predictions of the socio-ecological model, predicting that

Table 2 Sex differences in home range (*HR*) size, home range use and home range overlap in wild chimpanzees at four different study sites. Percentages indicate the percentage of the males range used by females. Values are taken from Chapman and Wrangham (1993) for Kibale, from Hasegawa (1990) for Mahale, from Williams et al. (2002) for Gombe and from this study for Taï.

Sex differences in	Kibale (Kanyawara)	Mahale (M group)	Gombe (Kasakela)	Taï (North group)
HR size	♂ > ♀	♂ > ♀	♂ > ♀	♂ > ♀
HR overlap (♀ to ♂)	65%	75%	56%	90%
HR use	No sign. sex differences	♂ use HR evenly, ♀ have individually preferred zones	♂ use HR evenly, ♀ have individually preferred areas	No sig. sex differences
Community size	41+	89–98	32–60	22–32

males have larger ranges than females to maximize their access to reproductively active females (Clutton-Brock 1989). Most other chimpanzee study sites have reported such a sex difference (see Table 2), although those differences are not always so clear-cut and/or often due to differential use of peripheral areas (Hasegawa 1990; Chapman and Wrangham 1993; this study). Only in Gombe is there evidence that male chimpanzee home ranges encompass several of the more dispersed living female ranges (Wrangham 1979), so that an increase of a male's home range could result in access to an increased number of females. However, contrary to most other chimpanzee populations, the study group in Gombe has neighbors on only two sites. Furthermore, a recently published study from Gombe (Williams et al. 2004) suggests that an expansion of the community range does not lead to an increased number of females but it may enhance female reproductive success by providing more food resources to resident females. By expanding their range at the periphery of the community home range males could also increase their access to extra-community females. Extra-group paternity in Taï has been shown to occur in about 12% of the infants born (Vigilant et al. 2001; Boesch et al. unpublished data), thus males may enlarge their home range towards peripheral areas not only to increase food availability but also to seek opportunities for extra-group copulations.

Apart from sex-specific reproductive strategies described above, sex differences in ranging patterns can also be attributed to home range defense strategies. In chimpanzees, all adult males of the community cooperate to defend the home range against neighboring groups by patrolling the border regions of their range (Goodall 1986; Nishida 1990; Boesch and Boesch-Achermann 2000). Females, on the other hand, have been reported to avoid these regions, presumably because of the high risk imposed to them by inter-community encounters through infanticide (Nishida et al. 1985; Boesch and Boesch-Achermann 2000). Hence, males may have larger home ranges than females, as was observed in Taï, where individual differences in home range sizes are mainly due to the use of peripheral areas (Fig. 4). That peripheral areas are indeed costly to the females is supported by the finding that in Gombe, females occupying peripheral home ranges, have lower reproductive success (Williams et al. 2002). However, in contrast to other reports, some females in Taï have repeatedly been observed to patrol together with the males in border regions (C. Boesch, unpublished observation) and peripheral areas are not exclusively used by males (see Fig. 4). Indeed, some of the most peripheral cells were used exclusively by females. Furthermore, the presence of dependent offspring did not correlate with home range size, indicating that mothers do not avoid peripheral areas. This minimizes the potential for sex differences in home range size in comparison to other study sites, where females have been reported to avoid the periphery (see Table 2). There are several possible explanations for this observation. First, since the visiting of peripheral cells is a rare event, it may simply be that we missed occasions when the males visited these places. Second, as suggested above for males, females also may use peripheral areas to seek extra-group mates and may go there without the males. However, annual home range size was not affected by the reproductive state of females and peripheral areas were used by both cycling and non-cycling females and not primarily by cycling females, as one might expect if females were seeking extra-group copulations. Third, females may be attracted to the periphery because they find valuable food resources there and fourth, females, like males, may use peripheral cells to defend the community range against neighboring communities. Interestingly, higher-ranking females used more peripheral cells than low ranking females. A similar effect for males has been reported from an East African study site, namely Kibale, where dominant males used peripheral cells more frequently than subordinates (Chapman and Wrangham 1993). Since in Taï, females have been observed to participate in border patrols (Boesch and Boesch Achermann 2000) it might be that high ranking females are more likely to participate in patrols than low ranking females, which stay more often in the safer core area. Inter-individual differences were found to increase when community size and the number of males decreased in Taï, and this particular behavior may be linked to the recently unusual small number of males in the study community. Finally, the decrease in community size of the study community and at least one of the neighboring communities (Lehmann and Boesch 2003) may have led to reduced between-group competition, thereby relaxing relations between communities. Thus, the use of peripheral cells may be less risky in Taï as compared to other study sites, where chimpanzee density is higher and the risk of inter-community encounter might be greater. However, as we only know the chimpanzee density of one of the neighboring communities, this line of argument remains speculative.

Generally, group size and composition are expected to affect space use in social mammals and one can therefore hypothesize that the differences between study sites are due to variations in community size and composition (see Table 2). However, with time the chimpanzee community in Taï has undergone dramatic changes in size and composition without fundamentally changing individual ranging pattern. The concept of a bisexually bonded chimpanzee community was introduced by Boesch (1996), based on the finding that Taï chimpanzees spend most of their time in mixed-sex parties and are generally very socially cohesive. At that time community size was around 76 chimpanzees. Boesch (1991) also reported that more than 80% of the individuals of both sexes were seen foraging together over the course of the day when the Taï community consisted of 66–80 individuals, strengthening our finding of a high level of home range similarity in Taï chimpanzees, irrespective of community size and composition. Furthermore, the larger south community shows a similar high similarity between male and female home ranges. The finding of highly clustered individual centers of activity throughout the 5 years (see Fig. 5) further supports these results. However, a general increase of inter-individual differences in home range sizes was found from 1999 onwards. In this year, an epidemic disease led to the death of 10 individuals, including the former alpha male and the community was left with only one adult male. Also, since the community range expanded at the same time (Fig. 2, see also Lehmann and Boesch 2003), it may well be that the unusually low number of adult males has led dominant females to contribute more to home range defense, thereby using more peripheral areas. Alternatively, peripheral areas in Taï as compared to other study sites with higher overall chimpanzee densities may impose less risk on females. The central part of the home range, however, was used evenly throughout the study period by all individuals and this appears to be independent of changes in community size and composition. Our finding of enhanced inter-individual differences in peripheral cell use in Taï is somewhat in contrast to findings in Gombe, where females were reported to become more social and ranging patterns became more bisexually bonded, when chimpanzee density decreased (see Williams et al. 2002). Thus, it seems unlikely that all differences in social organization and space use observed between various chimpanzee study sites are solely a consequence of differences in community size and/or composition (Table 2). Chimpanzee space-use patterns are rather determined by a variety of ecological and social factors, including community size and composition.

As more data on chimpanzee social organization and space use are collected and analyzed it becomes clear that there are fundamental differences between the study sites (Table 2). Large sex differences in space use were found in Kibale (Chapman and Wrangham 1993) and Gombe (Wrangham 1979; Goodall 1986; Williams et al. 2002), while in Mahale (Hasegawa 1990), Bossou (Sugiyama 1988) and Taï sex differences are less pronounced. In Gombe, females show high individual site fidelity across years, while in Taï we found strong community site fidelity (Fig. 7). Similarly, in Gombe chimpanzee ranging patterns seem to be best explained by the male-bonded community model, while in Taï social organization is best described by the bisexually bonded model, which assumes high levels of gregariousness between the sexes (Boesch 1996; J. Lehmann and C. Boesch, unpublished data). How can these differences be explained? The two major factors that have been suggested to influence social organization and space use are predation pressure and food availability. High predation risk has been demonstrated in a variety of taxa to lead to an increase in sociality and group size (Dunbar 1988; Boesch and Boesch-Achermann 2000; Hass and Valenzuela, 2002), and thereby to high home range similarity. While in Gombe predation risk is virtually non-existent (Goodall 1986) and females can safely travel alone for a large part of their day (minimizing feeding competition), in Taï, chimpanzees frequently encounter leopards and suffer a high risk of predation (Boesch 1991; Boesch and Boesch-Achermann 2000). Thus, traveling alone may be too risky for a female in Taï, which in turn leads to higher sociality and cohesiveness in Taï chimpanzees. The cost of this behavior, however, is an increase in feeding competition. Indeed, a recent study on female contest competition in Taï indicates a high degree of contest competition (Wittig and Boesch 2003), especially in comparison to Gombe chimpanzees. Ecological differences between the study sites could, however, also facilitate high female sociality in Taï and the costs of large parties can be reduced by a richer environment and by the existence of a linear hierarchy in female chimpanzees (Wittig and Boesch 2003). In Gombe and Kibale low food availability and/or smaller food patches may force females to forage alone in small, well-known ranges, while a richer environment would allow the formation of larger groups. Variation in food availability and in food competition within sites has previously been shown to affect aspects of chimpanzee social organization, such as party size (Boesch and Boesch-Achermann 2000; Doran 1997). Although studies on food availability have been carried out at several sites (Ghiglieri 1984; Chapman et al. 1995, 1999; Furuichi et al. 2001; Anderson et al. 2002; Mitani et al. 2002), comparative data are still lacking. High sociality in Taï chimpanzees may also be further facilitated by the fact that chimpanzee density is much lower in Taï (1.03–2.14 chimp/km^2, Lehmann and Boesch 2003) than in Gombe (>5 chimps/km^2, Williams et al. 2002), although density estimates are based on only a few habituated communities and may not reflect overall population density. In addition, other benefits may arise for female chimpanzees when traveling together, such as social benefits based on the possibility to observe other group members or the availability of playmates for offspring, so that females will join parties if the ecological conditions allow them to do so.

In conclusion, this study suggests that chimpanzee ranging patterns are highly flexible and most probably adapted to the specific ecological conditions of the habitat. While high food availability may facilitate high levels of gregariousness, predation risk is probably the most important factor shaping chimpanzee social organization by favoring large parties whenever predation is a deadly threat to chimpanzees. The different findings from various study sites emphasize the flexibility with which chimpanzees adapt their social organization to environmental conditions. In Taï, chimpanzee space use is best predicted by the bisexually bonded community model, with highly similar male and female ranges. Small individual differences found in home range sizes were positively correlated with rank and might be related to communal home range defense strategies. Enhanced access to resources, i.e. number of females for males and access to food for females, respectively, does not seem to be a likely explanation. These data demonstrate that individual space use in chimpanzees can differ substantially between populations and more comparative data are needed to shed light on the underlying causes.

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