ORIGINAL ARTICLE

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To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation

Abstract To balance advantages and disadvantages of group living, some species have fission-fusion social systems in which members of the same group form frequently changing subgroups. This allows flexible responses of group size to external conditions while at the same time retaining group stability. In chimpanzees, subgroup (party) size and composition depend mainly on the presence of receptive females, food availability and the activity of the party. Here we analyse the extent to which fission-fusion parameters are influenced by changes of demographic variables like community size and composition. Data were collected from a habituated West African chimpanzee community (Taï forest, Côte d'Ivoire) over 10 years, during which total community size decreased from 51 to 21, and the number of adult males decreased from 9 to 2. Taï chimpanzees are highly gregarious, as they spend more than 80% of their time with unrelated conspecifics. With decreasing community size, party size, party duration and male-female association increased. Neither activity nor the presence of receptive females or feeding competition could explain the observed changes in grouping patterns. Thus, the decrease in community size led to an increase of party cohesion and also enhanced cohesiveness between the sexes, while general sociality remained unchanged. Therefore, our data support the notion that small communities are more cohesive and have a less flexible fission-fusion system.

Keywords Community size · Fission-fusion system · Daily travel distance · Party size · Party composition

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Introduction

The core issue in socio-ecology is the nature of the relationship between an individual's ecological and social environment. Animal social structures range from solitary systems in which individuals meet infrequently for the purpose of reproduction, as in hamsters (*Cricetus cricetus*), to those systems in which individuals live permanently in groups of hundreds or even thousands, as in some birds. The three main factors suggested to be responsible for the evolution of group living are predation pressure (Van Schaik 1983; Dunbar 1988), access to resources (Krebs and Davies 1993) and cooperation (Caraco and Wolf 1975; Emlen 1991). However, costs and benefits of group living depend on group size and composition, and if a group becomes too large, the disadvantages of intra-group competition for food, mates or other resources may outweigh the advantages of grouping (Krause and Ruxton 2002). Thus, the observed social structure of a species results from an optimisation process in which each individual attempts to maximise its fitness. In this process, group size is interpreted as an adaptive trait that responds to ecological, as well as social, factors.

In populations with long-lived animals in which social organisation is based on individual recognition, maintaining optimal group size may be difficult. For example, groups may be smaller than expected because recruitment of new members is too slow. In addition, the optimal group size may change frequently in response to food patch size. When optimal group size varies largely over short time periods, individuals could benefit from a fission-fusion social organisation (Kummer 1971; Van Schaik and Van Hooff 1983), in which members of a stable community form frequently changing subgroups. This can allow regulation of feeding competition (Kummer 1971), offer greater flexibility in exploiting resources (Dunbar 1988; Symington 1988), or allow males to maximise monitoring of reproductive females (Dunbar 1988). Fission-fusion social systems have been described for some primates, like spider monkeys (*Ateles geoffroyi*;

Klein and Klein 1977) and chimpanzees (*Pan troglodytes*; e.g. Nishida 1968), and in a few other mammals, like bottlenose dolphins (*Tursiops truncatus*; Smolker et al. 1992), whiptail wallabies (*Macropus parryi*; Kaufmann 1974) and spotted hyenas (*Hyaena brunnea*; Owens and Owens 1978). So far, no clear theoretical framework concerning the factors shaping the evolution of this system has been put forward. Nonetheless, fission-fusion systems have often been used to investigate the relation between ecological and social factors and (sub-) group size (Symington 1988; White and Wrangham 1988; Chapman et al. 1995; Matsumoto-Oda et al. 1998; Newton-Fisher et al. 2000), because it is a highly flexible system that can respond quickly to environmental changes. In particular, chimpanzees are one of the most frequently used study subjects (e.g. Sakura 1994; Boesch 1996; Hashimoto et al. 2001).

Chimpanzees live in multi-male, multi-female communities with 20–150 members (Goodall 1986; Nishida 1990; Watts 1998; Boesch and Boesch-Achermann 2000). Subgroup or "party" size varies with several social and ecological factors, including the size and quality of food patches (e.g. Itani and Suzuki 1967; Goodall 1986; Wrangham 1986; Chapman et al. 1994; Matsumoto-Oda et al. 1998; Anderson et al. 2002), predation pressure (e.g. Boesch 1991; Sakura 1994) and the presence of cycling females in a community (Goodall 1986; Matsumoto-Oda 1999; Boesch and Boesch-Achermann 2000; Hashimoto et al. 2001; Anderson et al. 2002; Mitani et al. 2002). Demographic factors like community size and sex ratio may also influence fission-fusion patterns (Goodall 1986; Boesch 1996; Newton-Fisher 1999; Newton-Fisher et al. 2000). However, few studies have investigated how changes in overall community size or composition affect subgrouping (Boesch and Boesch-Achermann 2000), although such a study would give new insight into the evolutionary forces affecting social organisation. In their model of primate social organisation, Van Schaik and Van Hooff (1983) proposed that group size and group cohesiveness are the main links between ecological factors and social organisation. If fission-fusion organisation reduces intra-group competition, parties should be larger and/or more stable when competition is low (because of small community size or high food abundance). Comparative data on wild chimpanzee populations support this argument: relative party size and party duration are inversely related to community size (Boesch and Boesch-Achermann 2000). Thus, community size may directly affect chimpanzee social organisation, both by limiting absolute maximum party size and by reducing the need for flexibility.

However, demographic and ecological variation make comparisons across study sites problematic and it may be difficult to differentiate between underlying causes and consequences. Here we analyse the effects of community size and composition on the fission-fusion dynamics of a single West African chimpanzee community over a 10-year period. While community size declined during this period, ecological parameters like food availability and predation pressure remained relatively constant (Lehmann and Boesch 2003). We expected to find that party size and duration increased as community size decreased, and that this effect would remain when we controlled for other factors that can influence party size and duration (food availability, sex ratio, number of juveniles, inter-community aggression rates, the number of oestrous females present and intra-community competition).

Methods

Study site and data collection

The Taï National Park, Côte d'Ivoire, West Africa, comprises approximately 4540 km^2 of evergreen lowland rainforest (for detailed description of the study site, see Boesch and Boesch-Achermann 2000). Data presented in this study were collected from January 1992 to December 2001 on the North Community, which was habituated in 1979 and has been observed since 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 immature (aged between 5 to 15 and 5 to 13 years, respectively) and 14 dependent offspring (aged 0–4 years). Group size subsequently decreased, and by December 2001 the community consisted of 1 adult and 1 adolescent male, 6 adult females, 9 immature and 5 dependent offspring (see Lehmann and Boesch 2003). From 1992 onwards, daily focal animal follows (Altmann 1974) were carried out and data on party size and composition, ranging, social interactions and behaviour of the target animal were collected systematically on checksheets by the field assistants Honora Néné Kpazahi and Grégoire Kohou Nohon. Targets were usually followed from nest to nest or as long as possible (mean daily observation time: 9.7 h±2.1). Daily foraging routes of the focal subjects were plotted on a detailed map of the area. From 1992 to 2001, field assistants plotted 1,962 foraging routes on maps. Five hundred and fifteen follows on adult males and 1,447 follows on adult females were collected. Not all individuals of the study community were followed equally often, and during 1993 and 1994, no male target follows were carried out. Median individual focal days increased from 5 days/year to 21 days/year as community size decreased. However, Taï chimpanzees are very cohesive and often move in large, mixed-sex parties (see Boesch and Boesch-Achermann 2000) so this is not expected to influence yearly averages for party size and duration.

Data analysis

All behavioural data were entered into Taï-Chimp-BehaveBase, our large chimpanzee behaviour database, using Microsoft Access 1997. To measure daily travel distances, daily foraging maps were entered into a Geographic Information System, ArcView (ArcView GIS 3.2), using a digitising tablet (Wacom A3). Changes in day range and grouping parameters were related to changes in total community size, as well as to changes in community sex ratio. Community size was determined by averaging the total number of chimpanzees present on 1 January and 31 December of each year (see Lehmann and Boesch 2003). The average number of adult males (>15 years old) per year was calculated accordingly. It is often assumed that a decrease in community size indicates a decrease in feeding competition. This, however, is only true when home range size does not change to the same extent. Because in Taï, home range size varied (Lehmann and Boesch 2003), we used changes in density (chimpanzees/km^2) as a proxy for intra-community feeding competition. Furthermore, monthly rainfall, an index of forest productivity (Rosenzweig 1968), did not indicate a major shift in food availability across years. It has previously been reported that party size varies with seasons (Doran 1997; Mat-

sumoto-Oda 1999; Boesch and Boesch-Achermann 2000), and therefore it is important to note that the number of observation days was more or less evenly distributed across months per year, with a mean of 16.7±3.1 observation days per month. Two months in the dry season were generally poorly sampled, since chimpanzees are hard to find and to follow during this time; therefore, yearly average party sizes might be slightly overestimated. However, these 2 months are under-represented throughout the whole study period and do therefore introduce a consistent bias across the years in the data set. We checked whether the uneven sex ratio of the target animals had an effect on average party size and duration, since studies on East African chimpanzees have shown that males are more gregarious than females. However, no significant correlation in the expected direction (increase of party size/duration due to more male/fewer female target follows) was found for the number of male and female follows per year and party size/duration (party size: $r_{fem}=0.04$, $n=10$, $P=0.94$, $r_{male}=-0.69$, $n=8$, $P=0.06$; party duration: $r_{fem}=-0.16$, $n=10$, $P=0.66$, $r_{male}=-0.07$, $n=8$, $P=0.87$).

Party size, duration and composition

A party was defined as all independently feeding individuals (those at least 5 years of age) visible to the observer (and presumably the chimpanzees). This definition was chosen because all individuals older than dependent infants will contribute to the extent of feeding competition within a chimpanzee community. A party was terminated and a new party was recorded whenever a chimpanzee left or joined the previous party. For each observation day, the number of different parties, number of chimpanzees within each party, party duration and party composition were calculated. Parties for which not all individuals could be identified were excluded. We calculated for each year the mean absolute and mean relative party size (absolute party size/community size*100), mean party duration, frequencies with which small parties (less than 5 individuals) and large parties (more than 10 individuals) were observed and the percentage of total observation time at which single-sex parties, mixed parties and individuals travelling alone (which includes mothers with their dependent offspring) were observed. Using yearly averages allowed us to avoid the inter-dependence of data problem, which presents a difficulty when analysing data of short time periods (see Pepper et al. 1999). Because the presence of oestrous females influences party size (Matsumoto-Oda 1999; Newton-Fisher 1999; Hashimoto et al. 2001; Anderson et al. 2002), we included the number of days per year on which at least one oestrous female was observed as a variable in our analysis. Because changes in party size could also be attributed to changes in inter-community competition, we also included yearly inter-community encounter rates (see Lehmann and Boesch 2003) as a proxy for inter-community competition. Because community size decreased over the course of the years, changes in relative party size are expected, even if absolute party size remained constant. Thus, we used the mean party size observed in 1992 and calculated the expected relative party size in percent based on the assumption that absolute average party size remained constant across years. We then determined whether the observed relative party size differed significantly from the expected relative party size.

Changes in fission-fusion parameters could also depend on the number of juveniles, because they do not travel independently from their mothers, and/or on the number of adult males. Both variables were included in our analyses as independent factors, but we were not able to distinguish between the parameters used because overall community size and the number of adult males were highly correlated. Thus, we did the analyses first using community size and then again using the number of adult males.

Activity budgets and feeding competition

Because party size and duration depend on the activity of the party (Boesch 1996; Newton-Fisher 1999), we analysed mean party size, duration and composition separately for feeding, travelling and resting. We also calculated the overall activity budget for each of the 10 years. To test whether food availability limited chimpanzee party size, we calculated the relation of party size to feeding time per food patch by using average party size per uninterrupted feeding event (of the target chimpanzee) per year. Parties with more than 14 individuals were excluded because we rarely found feeding parties of this size and could, therefore, not obtain reliable estimates of feeding durations. We expected to find a negative correlation between party size and feeding time per food patch (Wrangham 1986; Symington 1988; Chapman et al. 1995).

Daily travel distance

Daily travel distance was derived by measuring the length of daily foraging routes of the target animal in ArcView. This value was then corrected for differences in the observation time, resulting in a distance travelled within 1 h. To estimate distance travelled per observation day, we multiplied these values by 12 h. This method certainly underestimates chimpanzee daily travelling route, since short detours cannot be plotted exactly. To quantify the underestimation, we did a 20-day comparative study by plotting foraging routes on maps and by using a GPS device. We could confirm that foraging routes plotted on the maps are comparable to distances resulting from 30 min GPS location recording (mean deviation 0.032 km or 11%). However, when we used continuous GPS readings rather than 30-min readings, the mean deviation from the map data was 1.2 km, suggesting that daily travel distance was underestimated by about 28%.

We calculated average values per individual and month in order to counterbalance for differences in number of observation days per chimpanzee and month, and used these values to determine mean travel distance per year. Only days with more than 4 h of continuous observation were included in this analysis. We expected to find a positive correlation between party size and daily travel distance if food availability was a critical factor.

Statistics

We used Statistica (Statistica 6.0, Statsoft, 1984–2001) for all analyses. Raw data were normally distributed (Kolmogorov-Smirnov and Lilliefors test for normality, all $P>0.2$) and the level of significance was set at $P<0.05$. We used a one-way Anova to test if average yearly party sizes differed between the three major activity categories (feeding, resting and travelling). To analyse whether party size, party duration, party type and observation frequencies were influenced by the decreases in overall community size and in the number of males, we carried out multiple regression analyses, which allowed us to control simultaneously for the influence of other factors, such as chimpanzee density, number of juveniles in the community, number of days with oestrous females and inter-community encounter rates. Best models were chosen using Akaikes information criteria. Since data on inter-community encounter rates were available for only 7 out of 10 years, the effect of encounter rates was tested by using the significant factors of the overall analysis (across 10 years) plus encounter rates. If inter-community encounter rates were not found to be significant, this variable was discarded. Although the procedure used here can normally distinguish between inter-correlated factors, multicollinearity may occur when sample size is relatively small. Multicollinearity of two variables in a model causes unreasonable regression coefficients (Zar 1999), and it is recommended to remove one of the variables from the model. Community size and density were weakly correlated and we therefore re-analysed the model using only one of the two correlated variables in cases where coefficients for these factors were in the opposite direction than expected. Further, because two of the variables used in this study (community size and number of adult males) are highly correlated ($r>0.9$), we used two different models. Model 1, the "community size model", used community size, density, number of juveniles, encounter rates and number of days with oestrous females as re-

gressors, and model 2, the "adult male model" was the same except it used the number of adult males instead of community size.

To test whether observed relative party size differed significantly from the expected relative party, we used a paired sample *t*-test. The relation between feeding time and party size was analysed using partial correlation, controlling for the effect of year. The model for party compositions included community size, number of males, number of juveniles, number of days with oestrous females and inter-community encounter rates. We analysed sex differences in travel distances with *t*-tests, and subsequently analysed travel distances separately for males and females with Pearson correlation analyses because the three factors that were hypothesised to influence travel distance (community size/number of adult males, density, party size) were all highly inter-correlated and therefore not usable in a multiple regression design.

Results

Party size

Absolute, as well as relative party size, generally increased in Taï chimpanzees from 1992 to 2001 (Fig. 1a), despite the decreasing community size. An increase in

a

b
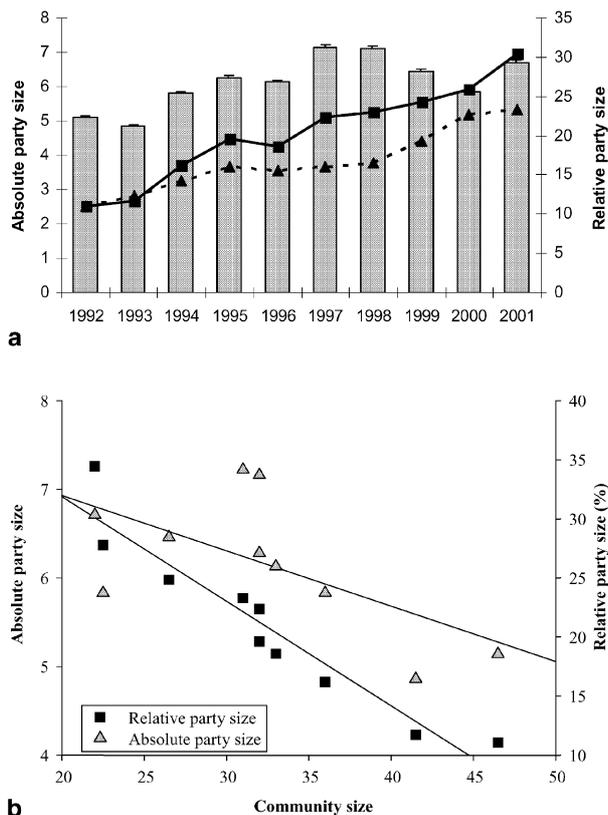
Fig. 1 a Mean (±STE) absolute (*bars*) and relative (*solid line*) party size per year. Relative party size was calculated as percentage of total community size. Since an increase in relative party size is expected when community size decreases, we also calculated expected relative party size (*dashed line*). Observed relative party size was significantly higher than expected relative party size. **b** Relation between community size and absolute (*triangles*) and relative (*squares*) party size. *Lines* represent trend lines; both correlations were significant

relative party size is expected simply due to the decrease in community size, but observed relative party size was significantly higher than the expected relative party size (paired sample *t*-test: $t=4.28$, $df=9$, $P=0.002$; Fig. 1a). Thus, we included both, absolute and relative values in further analyses. Table 1 gives a detailed summary of the results from tests of the two models. There was a significant effect of community size on relative and absolute party size (Fig. 1b, Table 1). In the community size model, the effect of density on absolute party size was significant, but was positive ($\beta=0.65$), and therefore in the direction opposite of that expected (Table 1). As this was probably due to multicollinearity, we re-analysed the model including community size and density, respectively, and found that community size ($\beta=-0.64$, $P=0.044$) but not density ($\beta=-0.03$, $P=0.93$) was significant. No significant influence of density on relative party size was found, nor did the number of days with oestrous females, the number of juveniles, or inter-community encounter rate significantly affect party size measures.
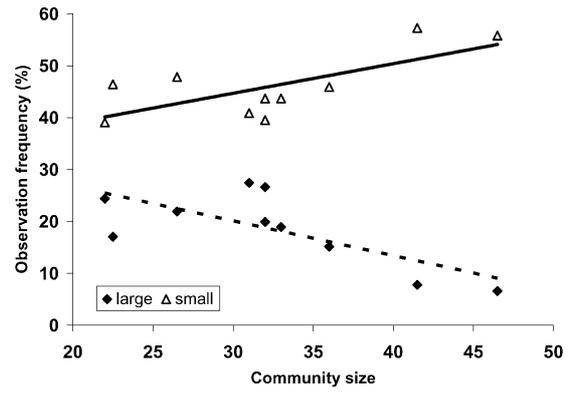
In line with these results, we found a negative effect of community size on the frequency of large parties (more than 10 individuals) and a positive effect on the frequency of small parties (less than 5 individuals, Fig. 2; Table 1). The significant positive effect of density on observation frequencies of large parties was once again due to the problem of multicollinearity, and subsequent analyses revealed that community size ($\beta=-0.73$, $P=0.02$) is the meaningful factor, not density ($\beta=-0.08$, $P=0.83$). The second model showed a significant influence of male number on party sizes and on the frequencies of large and small parties, while the number of juveniles, inter-community encounter rates and number of days with oestrous females did not have significant effects (Table 1).

Taï chimpanzees spent, on average, 50% of observation time feeding, 19% travelling, and 31% resting, with annual percentages remaining fairly constant. For this analysis, data from 1992 were excluded as the recorded feeding time was unusually high due to difficulties in identification of party members, leading to an overall smaller sample size as compared to other years. Because individual identification becomes easier during feeding (because chimpanzees remain longer in one place) recorded party sizes in 1992 could be biased towards feeding party sizes. Travelling parties tended to be smallest and resting parties largest, but using yearly averages these differences were not significant (Anova $F_{2,26}=0.907$, $P=0.417$). Changes across years were almost identical for all activities (mean deviation in percent between years and activities: 3.2%±1.7%), indicating that the observed changes in overall party sizes were independent of activity and affected all behaviours in a similar way.

To assess whether increases in party size led to increased feeding competition, we calculated the mean party size for each uninterrupted feeding event and found that feeding duration and mean party size were positively correlated when we controlled for the effect of year (partial correlation: $r=0.50$, $df=137$, $P<0.001$, Fig. 3).

Table 1 Statistical values of multiple regression analyses for the models analysed; *n.c.* means "not chosen" and indicates that this variable was not chosen to be included in the model by the best subset (ss) method, using Akaikes information criteria. Asterisks indicate significant results

|	Community size model							Adult male model						
	adj r^2	$B_{com. size}$	$\beta_{density}$	$\beta_{no. oestr. days}$	$\beta_{no. of juv}$	$B_{enc. rate}$	Model stats (best ss)	adj r^2	$\beta_{no. ad. males}$	$\beta_{density}$	$\beta_{no. oestr. days}$	$\beta_{no. juv}$	$\beta_{enc. rate}$	Model stats (best ss)
Mean party size	.65	−1.1*	0.65*	−0.37	n.c.	n.c.	$F_{3,6}=6.7$, $P=0.024$	.73	−0.92**	0.33*	−0.25	n.c.	n.c.	$F_{3,6}=9.29$ $P=0.011$
Relative party size	.93	−0.97***	n.c.	−0.12	n.c.	n.c.	$F_{2,7}=60.5$ $P=0.0001$	.88	−0.79***	−0.30*	n.c.	n.c.	n.c.	$F_{2,7}=34.1$ $P=0.0003$
Party duration	.85	−0.93***	n.c.	n.c.	n.c.	n.c.	$F_{1,8}=53.0$ $P=0.0001$	.75	−0.64**	−0.42	n.c.	n.c.	n.c.	$F_{2,7}=14.4$ $P=0.0045$
Observation frequency small parties	.51	1.01*	−0.46	n.c.	n.c.	n.c.	$F_{2,7}=5.7$ $P=0.034$	.72	0.88**	n.c.	n.c.	n.c.	n.c.	$F_{1,8}=24.2$ $P=0.0012$
Observation frequency large parties	.77	−1.2**	0.65*	−0.28	n.c.	n.c.	$F_{3,6}=11.02$ $P=0.0075$	.82	−1.0**	0.31	n.c.	n.c.	n.c.	$F_{2,7}=21.4$ $P=0.001$
% mixed parties	.48	−0.74*	-	n.c.	n.c.	n.c.	$F_{1,8}=9.4$ $P=0.0153$	.23	−0.56	-	n.c.	n.c.	−0.85*	$F_{1,5}=12.6$ $P=0.0165$
% single-sex parties	.33	0.64*	-	n.c.	n.c.	n.c.	$F_{1,8}=5.5$ $P=0.0471$	.07	0.42	-	n.c.	n.c.	n.c.	$F_{1,8}=1.8$ $P=0.2214$
% alone	−.04	n.c.	-	n.c.	−0.26	n.c.	$F_{1,8}=0.6$ $P=0.4664$	−.04	n.c.	-	n.c.	−0.26	n.c.	$F_{1,8}=0.6$ $P=0.04664$

Fig. 2 Relation between community size and observation frequencies for small (less than 5 individuals) and large (more than 10 individuals) parties. Observation frequencies are expressed as percentages of total observations. *Lines* represent trend lines; both correlations were significant
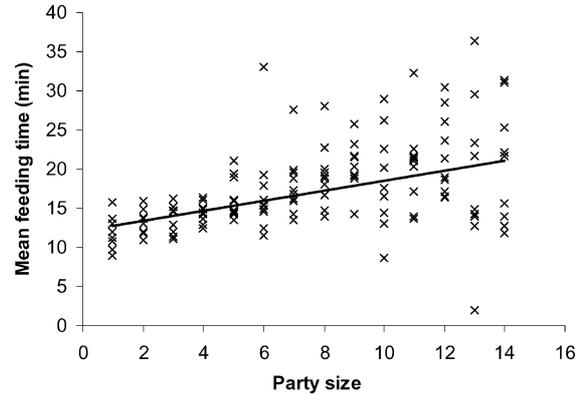
Fig. 3 Relation between party size and duration of uninterrupted feeding. Data were calculated as average party size for each uninterrupted feeding event in a given year. *Line* represents trend line; the correlation was significant

Party duration

Average party duration increased from 7.5±16.26 min in 1992 to about 41.6±63.4 min in 2001. Multiple regression analyses revealed a significant negative effect of community size/number of adult males on party duration (Fig. 4) but not of density, number of juveniles, intercommunity encounter rates or number of days with oestrous females (see Table 1). Because larger parties last longer (Boesch and Boesch-Achermann 2000), we analysed the effect of average party size on party duration to rule out the possibility that the increase in party duration is simply a side effect of increased party size. Interestingly, party size had no effect upon party duration (multiple regression analysis, using party size and community size as regressors: party size n.s. (*P*=0.42), community size *P*<0.001; Fig. 4). Analysis using the number of adult males rather than community size gave a similar result (Table 1).
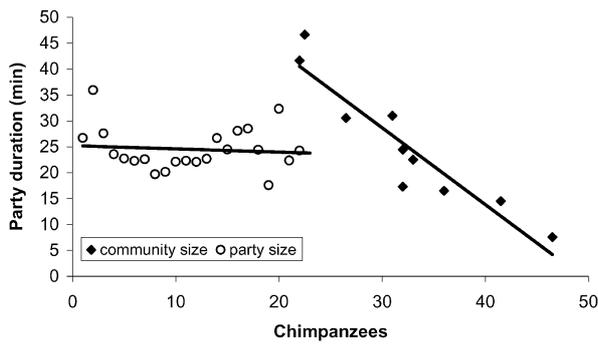
Fig. 4 Relation between average party duration and average party size (*unfilled circles*) and community size (*filled squares*), respectively. *Lines* represent trend lines; only community size revealed a significant effect
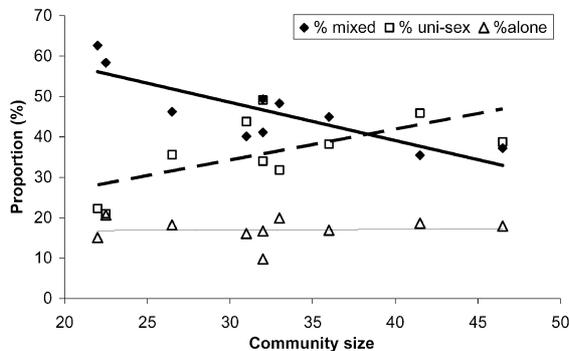
Fig. 5 Relation between community size and percent observation time spent in different party types. *Lines* represent trend lines; correlations were significant for single-sex and mixed parties

## Party composition

On average, chimpanzees spent 46.4% of their time in mixed parties, 36% in single-sex parties, and 17.6% alone or with their offspring only. Community size significantly affected the time spent in mixed parties (Fig. 5) and in single-sex parties, while the number of juveniles and the number of days with oestrous females did not (Table 1). This emphasises the increased attraction between males and females as the number of males declined. Furthermore, the number of adult males did not affect any of the party composition measures. Using a subset of 7 years, inter-community encounter rates had a significant negative effect on the time spent in mixed parties in the adult male model (Table 1). However, this may be due to the strong positive correlation between community size and encounter rates ($r=0.89$), so that the exclusion of community size in the adult-male model might have led to the significant effect of encounter rates on party composition. Time spent alone was not significantly affected by any of the tested factors (Table 1).
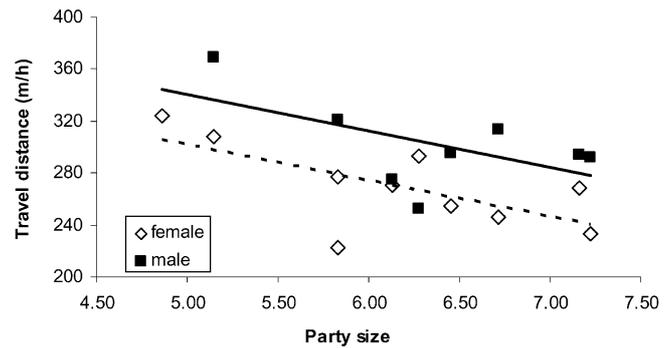
Fig. 6 Male and female travel distances in relation to mean yearly party size. In 1993 and 1994 no male target follows were carried out. To correct for unequal observation times, travel distances are given as m/h. *Lines* represent trend lines; a significant correlation was found for females but not for males

Daily travel distances

Average daily travel distance decreased from 1992 to 2001. There was no significant sex difference for average male and female travel distance ($t=2.00$, $df=16$, $P=0.063$), but males tended to travel farther than females (Fig. 6) and the lack of significance is most probably due to the small sample size ($n=8$ for males and $n=10$ for females). Thus, we analysed male and female travel distances separately, using Pearson correlation coefficients. For females, but not for males, travel distance was significantly positively correlated with community size and with number of adult males (females: community size $n=10$, $r=0.85$, $P=0.002$, number of males: $n=10$, $r=0.84$, $P=0.002$; males: community size: $n=8$, $r=0.37$, $P=0.362$, number of males: $n=8$, $r=0.63$, $P=0.09$). Contrary to our expectation, daily travel distance and average yearly party size were not positively correlated for either sex (males: $n=8$, $r=-0.59$, $P=0.137$; females: $n=10$, $r=-0.67$, $P=0.035$). Density was also not significantly correlated with male ($n=8$, $r=-0.38$, $P=0.351$) or female travel distance ($n=10$, $r=0.55$, $P=0.098$).

Discussion

Our data demonstrate that, as previously reported (Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2003), Taï chimpanzees are very gregarious and spend only about 18% of their time alone or only with their offspring. Furthermore, the amount of time that individuals associate with others does not depend on community size or the number of males, as indicated by the fact that the time spent alone or only with offspring hardly changed over the study period. However, as predicted, grouping patterns are highly dependent on total community size and on the number of males. With decreasing community size and fewer males, the chimpanzees formed larger parties more frequently, stayed longer in each party, and spent more time in mixed parties and less time in single-sex parties. When smaller, the community showed increased

cohesiveness between the sexes and decreased fluidity in the fission-fusion system. Other possible influences on party size, including the number of oestrous females, chimpanzee density, the number of juveniles in the community, inter-community encounter rates or activities, could not explain these changes. Also, daily travel distance was positively correlated with community size but, contrary to expectations, it decreased as mean party size increased, at least for females.

Our results are consistent with findings from a small chimpanzee community with only one adult male at Bossou (Sugiyama and Koman 1979), and support Boesch's (1996) hypothesis that community size directly affects fission-fusion dynamics. The finding that both, the number of males and community size, explain observed changes in grouping patterns equally well does not allow us to attribute the effects to only one of these variables. However, to simplify the following discussion, we refer to community size as the variable responsible for the observed effects. We do this because Boesch and Boesch-Achermann's (2000) comparison among different chimpanzee communities demonstrated the importance of community size for fission-fusion parameters, but we note that the effects reported here could also be due to changes in community composition.

The finding of high general sociality of Taï chimpanzees contrasts with reports from East African chimpanzees, where females spend most of their time alone or with their offspring, while males are more gregarious (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986; Pepper et al. 1999). These differences in sociality are probably due to differences in food competition and predation pressure, such as relatively higher food availability and predation pressure in Taï (Boesch 1991, 1996; Doran 1997). However, more comparative data on feeding competition and predation pressure from multiple study sites are needed to fully understand why chimpanzee populations differ in overall sociality.

In this study, we demonstrate that demographic variables can have a strong effect on social organisation, namely on fission-fusion parameters such as party size and duration, within one chimpanzee community. The underlying causes for this type of social organisation have not yet been well studied, although subgrouping as in the chimpanzee fission-fusion system can be found in a variety of species. The most common assumption is that fission-fusion parameters strongly depend on ecological variables, as well as on the reproductive strategies of the species. Our data demonstrate how demographic changes affect subgrouping patterns in the absence of ecological changes. Our finding of an inverse relationship between party size and community size is consistent with what Boesch and Boesch-Achermann (2000) found in their inter-community comparison of relative party sizes. Ecological factors like predation pressure and food competition, however, are more likely to influence absolute than relative party size. Given that a certain absolute number of chimpanzees provide optimal protection against predators, absolute party size should remain constant despite decreasing community size, as long as neither predation pressure nor food availability changes. This would then automatically result in higher relative party sizes for smaller communities. If, however, larger party sizes were advantageous (due to high predation pressure, for example), parties should be absolutely larger in large communities simply because they can form larger parties. Therefore, our finding that party size and duration increased with decreasing community size adds importantly to our understanding of social organisation in chimpanzees, since it shows that chimpanzee social organisation directly responds to demographic variables by decreasing the flexibility of the fission-fusion system when the community is very small. Because in this study, ecological parameters remained relatively constant, these findings further suggest that chimpanzees may gain social, not just ecological, benefits from greater gregariousness (see Wrangham 1986).

So why does a decrease in community size lead to an increase in party size and to a reduction of the fission-fusion fluidity? Three main factors could be responsible for these effects: (1) party size was previously limited by food competition, (2) the increase in party size reflects a change in mating strategies due to small community size, or (3) increased predation or inter-community encounter risk (due to the decreased number of males) leads to an increase in party size to improve individual protection. If the first factor, food competition, had limited party sizes previously by allowing only a certain number of individuals to feed at a certain patch before it is depleted, we would expect party size to be negatively correlated with chimpanzee density and feeding time (Wrangham 1986; Chapman et al. 1995), which was not the case. Additionally, contest feeding competition is expected to take place primarily within a party (rather than on community level), so that chimpanzees in larger parties should experience more food competition, which in turn should lead to increased travel distances and decreased feeding times per food patch (assuming that food patches are nearly depleted, see Chapman et al. 1994). In our study, however, travel distance was—if at all—negatively correlated with party size (for females) while there was a positive correlation between feeding time and party size. Both results indicate that food availability per food patch did not limit party size. This is further supported by the finding that the time a chimpanzee spends alone does not decrease with decreasing community size. A general increase in food availability, which could explain the observed changes as this would reduce the costs of large parties, seems unlikely (see Lehmann and Boesch 2003) and an increasing number of studies demonstrate that food abundance and party size are not always closely linked (Newton-Fisher et al. 2000; Hashimoto et al. 2001). This indicates that other factors than feeding competition may also have a strong influence on chimpanzee—and presumably other species'—grouping patterns.

Reproductive strategies have been hypothesised to influence sociality and grouping patterns of social animals. For chimpanzees, several studies have shown that

the number of cycling females influences grouping patterns (Newton-Fisher 1999; Boesch and Boesch-Achermann 2000; Newton- Fisher et al. 2000; Anderson et al. 2002; Mitani et al. 2002). In our study, however, the large-scale changes in fission-fusion patterns could not be explained by the number of days on which oestrous females were present. Males, however, may change their reproductive strategy depending on community size (Dunbar 1988). Males seek out females to monitor their reproductive states, but they may find it harder to encounter females when community size is small and only a few parties with females are around. Thus, males might adjust their reproductive strategy to the size and composition of the community by increasing the amount of time they spend with each female when community size is small rather than searching frequently for new parties (Dunbar 1988). Our finding of an increased proportion of mixed-sex parties with decreasing community size could support this hypothesis, although this could also be due to other mechanisms (see below).

Predation and inter-community encounter risk should affect party size in similar ways, because both can pose life-threatening risks (Tutin et al. 1983; Symington 1987; Boesch 1991; Sakura 1994). We found that party size was not significantly influenced by inter-community encounter rate, although this may not sufficiently measure the risk involved with each encounter. Relative measures, such as strength differences between communities, may provide better measures, but were unavailable in our study (Williams et al. 2002; Lehmann and Boesch 2003). Furthermore, the effects of inter-community aggression on party size may be only temporary and not long enough to be measured by yearly averages. Boesch (1991) found that chimpanzee party size decreased in response to increased predation risk, presumably because smaller parties are less conspicuous. Alternatively, enhanced predation risk can also lead to increased party sizes, since larger parties offer better defence mechanisms and enhance the dilution effect (Hamilton 1971), although this effect is stronger for very small parties than for larger ones. Although we do not have direct data on leopard density in the Taï forest, we believe that it is unlikely that predation risk changed systematically over the last 10 years. One could, however, hypothesise that female chimpanzees perceive an increased predation risk (or risk in general) with decreasing number of males in the community. Males protect females—for example, by chasing leopards (C. Boesch, personal observations)—and increased predation pressure during one period led to an increase in mixed and all-male parties (Boesch 1991). In our study, it was mainly the number of males that decreased over time (leading to a more female-biased sex ratio); thus, if females actively seek the proximity of males for protection, party size should increase when only two males are present in a community (and these two males spent most of their time together), which is in line with our findings. Finally, whether males seek proximity to females for monitoring their reproductive status or females seek the proximity to males for pro-

tection, both scenarios will lead to an increase in mixed-sex parties, party size and party duration as fissioning becomes less advantageous in a small community, given that food availability is sufficiently high. None of the above factors alone is sufficient to explain the frequent changes in party size and composition found in large communities; thus, chimpanzee social organisation most probably is adapted to several needs (Boesch 1996), including social benefits such as socialising of offspring (Chapman et al. 1994; Newton-Fisher 1999; Williams et al. 2002).

This study demonstrates for the first time that community size and composition influence grouping patterns even if ecological parameters remain relatively constant. All of the factors discussed above are not specific to chimpanzees but are important for the evolution of sociality in general (e.g. Sterck et al. 1997; Connor et al. 1998; Clutton-Brock et al. 2002). Thus, our demonstration of an interaction between demographic variables and ecological parameters such as predation pressure and feeding competition may have implications for studies on social mammals in general, as it indicates that demographic variables have to be taken into account when comparing different populations within and across species, and when looking at the evolution of sociality. For group-living animals, it may be important to gain regular information about other community members, to monitor their social status and coalitions (Dunbar 1988; Newton-Fisher 1999). This, in turn, could explain the constant mingling among the members of a group, and community size would be expected to play in important role for the fission-fusion fluidity. Smaller communities need fewer turnovers (and therefore fewer fission-fusion events) to enable all members of the community to meet, which is also in line with the observation of prolonged party duration in a small community.

In conclusion, we have shown that demographic changes can affect the social system of a species. In our study, we found that the general level of gregariousness in chimpanzees does not depend on demographic variables but fission-fusion fluidity does. Parties last longer and are larger in a smaller community, and it is unlikely that the observed effects are solely due to a decrease in feeding competition. Other factors, such as reproductive strategies, predation risk and/or social parameters, like the "need" to encounter all community members on a regular basis, may have contributed to the observed effects of demographic variables on the chimpanzee social system. These results indicate that demographic variables interact with ecological parameters and play an important role in animal social organisation.

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