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ORIGINAL PAPER

Female gregariousness in Western Chimpanzees (*Pan troglodytes verus*) is influenced by resource aggregation and the number of females in estrus

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Abstract Among social animals, group size is constrained by competition over resources. Because female reproductive success is limited by access to food resources, and that of males by access to fertile females, chimpanzee females are proposed to be less social than males and to maintain weak intrasexual relations. Findings from Taï National Park, Côte d'Ivoire, challenged this view, as chimpanzee females were described as generally gregarious, and close intrasexual bonds were common. Here, in a new analysis that focuses on the South Group of chimpanzees in Taï forest, we reevaluate the proposed differences in female association patterns between the Taï and East African populations. We find that mean party size and dyadic association index between females has decreased in Taï, although the level of dyadic associations remains high compared with East African chimpanzees. We attribute the decrease in female gregariousness to the decline in community size over the last 10 years. In addition, we use a multivariate approach to analyze social and ecological factors influencing party size in females. We show that female gregariousness increased when the fruit resources were more clumped and with increased number of females in estrus present. Party size of mothers with sons, however, was smaller with increasing number of sexually receptive females. The results of our model and the reviewed findings of other studies support the socioecological model because food distribution affects female gregariousness, but social and demographic aspects are equally influencing female grouping tendencies.

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Introduction

Living in cohesive social groups presents a paradox for individuals who must compromise between the costs of competition with other group members and the benefits gained from sociality, such as defense against predation and exclusive access to resources (Wrangham 1979; Van Schaik and Van Hooff 1983; Dunbar 1988). Competition over food resources is particularly critical for females whose fertility and fitness are dependent upon sufficient nutrition due to the energetic costs of gestation and lactation (Bercovitch 1987; Gittleman and Thompson 1988; Prentice and Prentice 1988). Thus, according to the socioecological model, female relationships in group-living primates are the result of a trade-off between the potential for feeding competition, which is a function of the quantity and distribution of resources and group size (Isbell 1991; Koenig 2002), and antipredator benefits (Van Schaik 1989). In contrast, male fitness is limited by the number of fertilizations they can achieve, and so male relationships are directly affected by the distribution and fertility of females over time and space (Dunbar 1988). Hence, the optimization of competitive strategies of both sexes shapes social structure (Van Schaik and Van Hooff 1983; Dunbar 1988).

Competition for limited resources can be direct or indirect. Direct (contest) competition occurs when individuals are able to monopolize the access to resources, while indirect (scramble) competition occurs when all individuals have an equal chance of securing some share of the resource (Nicholson 1954). Larger groups may gain advantages over smaller ones in between-group contest competition for food, but within-group scramble competition increases with group size (Wrangham 1979; Davies and Krebs 1993; Janson and Goldsmith 1995).

To resolve the conflict between benefits and constraints of increased sociality, some mammalian species live in a social system with fission–fusion dynamics (some bat species, Kerth and Koenig 1999; Popa-Lisseanu et al. 2008; hyenas, Owens and Owens 1978; Smith et al. 2008; lions, Packer et al. 1990; dolphins, Pearson 2008; Parra et al. 2011; elephants, Wittemyer et al. 2005; spider monkeys, Symington 1990; muriquis, Coles et al. 2011; bonobos, Nishida and Hiraiwa-Hasegawa 1987; Hohmann and Fruth 2002; chimpanzees, Nishida 1968; Sugiyama 1968; Goodall 1986; Boesch and Boesch-Achermann 2000; and humans, Marlowe 2005). This social system allows individuals of one community to travel or to forage in subunits, often called parties that frequently change size and composition in response to activity and current food availability (Kummer 1971). Spotted hyenas (*Crocuta crocuta*) were observed in bigger subgroups when prey was abundant (Smith et al. 2008), and the size of foraging parties in spider monkeys (*Ateles* spp.) fluctuated with fruit abundance. Parties were significantly larger when food availability was high, and during extreme food shortages, spider monkeys reduced the fluidity between fission and fusion and formed smaller, more stable parties (Symington 1988; Aureli et al. 2008; Asensio et al. 2009).

In large-bodied mammals for which predation risk is low (but see Boesch 1991; Boesch and Boesch-Achermann 2000), females may be less gregarious than males in order to avoid within-group feeding competition. Sex differences in association patterns in which female social bonds are weaker than those of males have been described in dolphins (*Tursiops aduncus*) (Connor et al. 2000) and chimpanzees (*Pan troglodytes*) (Pepper et al. 1999; Wrangham 2000; Emery Thompson and Wrangham 2006; Lehmann and Boesch 2008). However, other explanations such as infanticide avoidance and mating strategies have been proposed to explain female grouping tendencies (Sterck et al. 1997). In this respect, chimpanzees are an ideal model species for testing hypotheses on fission–fusion sociality, given the existence of sex differences in associations and of data from multiple studies that encompass a broad range of populations and ecological conditions.

It was originally thought that female patterns of association and space use differed between eastern and western chimpanzees with females from Uganda and Tanzania being more solitary and more attached to specific locations than chimpanzees in the Taï forest (Sugiyama and Koman 1979; Wrangham and Smuts 1980; Goodall 1986; Sugiyama 1988; Wrangham et al. 1992; Pusey et al. 1997; Boesch and Boesch-Achermann 2000; Wrangham 2000; Lehmann and Boesch 2008). Females from East African populations use distinct individual core areas that comprise a mere fraction of the males' territory (Gombe, Goodall 1986; Wrangham et al. 1992; Williams et al. 2002a), and immigrating females compete for group membership and access to foraging (core) areas (Kahlenberg et al. 2008). In this competitive context, higher rank improves access to foraging areas of good quality, which translates to a better diet and thus to fitness advantages (Emery Thompson et al. 2007; Kahlenberg et al. 2008; Potts 2012). In contrast, females from the Taï forest in Côte d'Ivoire are more gregarious and female ranges strongly overlap (at a minimum of 85 %) with those of males (Boesch 1996; Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2005). Even though Taï females do not compete over foraging areas, evidence of feeding competition was found as contest competition over food is prevalent and a linear hierarchy among females was established based on formalized submissive vocalizations (Wittig and Boesch 2003; Gomes et al. 2008).

In this study, we calculated party size, the proportion of time females spent in different party types, and the dyadic association among female chimpanzees of the Taï Forest and compared the results with those from previous studies at Taï and published data from four East African long-term study sites: Budongo (Uganda), Gombe (Tanzania), Kanyawara and Ngogo in Kibale (Uganda). In a second step, we used new data on females of the South Group in Taï to model the effects of several social and ecological factors on female grouping patterns.

A multivariate analysis is especially useful because social and ecological factors presumably influence female grouping patterns synergistically. Resource availability, for example, has been found to influence grouping patterns depending on social factors such as dominance rank and the presence of females in estrus (Anderson et al. 2002; Riedel et al. 2011). We tested both ecological and social factors in one model that included not only overall food abundance but also measures of food distribution. We expected food abundance and distribution, quantified by density and an index of aggregation of fruit trees, to influence females differently depending on their reproductive states. We expected that overall food abundance and the degree of fruit tree aggregation would have a stronger impact on the gregariousness of pregnant and lactating females, because of their high energy demands, than that of cycling females (Key and Ross 1999). Finally, we included the number of estrous females as a control predictor, because it was previously shown to have an important influence on female gregariousness (Anderson et al. 2001; Riedel et al. 2011) We also used the number of dependent offspring as a predictor to investigate if their presence would influence female gregariousness as it was previously suggested that mothers are restricted in their association pattern by scramble competition and would therefore avoid large parties (Wrangham 2000).

We extended our question regarding offspring to test if offspring sex and age would influence female gregariousness. Williams et al. (2002b) proposed that females with male offspring would be more inclined to join parties in order to provide their male offspring with the opportunity to familiarize themselves with the males from the community. In this respect, the best context for male offspring to get acquainted with male and female behavior alike would be in mixed parties with estrus females. Thus, we predicted that females with male offspring would spend more time in larger groups when females in estrus were present.

Methods

Behavioral data collection

The first author (LW) collected data on 12 adult females from the South Group of the Taï National Park in Côte d'Ivoire over 19 months between December 2007 and November 2009 (for a detailed description of the study site, see Boesch and Boesch-Achermann 2000; Boesch 2009). At the beginning of the study, the group consisted of 39 individuals: seven adult males, three adolescent males, fourteen adult females, one adolescent female, and fourteen juveniles and infants. Over the course of the study period, we witnessed five births, the immigration of one subadult female into the community, the disappearance of one male and two adult females, and the death of one female from a leopard attack. Our analysis is based on 2,446.3 h of focal observations (range=125.1–274.3 h/female). LW used continuous focal sampling to record social and feeding behavior. For feeding, the plant species and parts eaten were noted. During focal follows (N=264), LW noted party size and composition, party duration, as well as the presence of females in estrus. A party was defined as all independently from their mother traveling individuals older than 5 years of age, visible within approximately 25 m of the focal individual. Changes in party size and composition were recorded whenever individuals joined or left the party. During periods of rest, the observer moved around the party to ensure that all individuals had been recorded and correctly identified.

To assess monthly fruit abundance, a research assistant trained in botany walked phenology transects and visually inspected the fruit yield of 40 tree species that are known to be important in the chimpanzees' diet (Anderson 2001; Anderson et al. 2002). The quantity of fruit in the crown was scored from 0 to 4, where 0 indicated the absence of fruit, 1 indicated 1 to 25 % of the tree crown to bear fruit, 2 indicated 26 to 50 %, 3 indicated 51 to 75 %, and 4 indicated 76 to 100 %. Each tree species was represented by 3 to 25 individuals with a diameter at breast height (DBH) larger than 10 cm (Anderson et al. 2005). In order to assess the aggregation of tree species in the chimpanzee territory, Goné Bi collected data in vegetation plots to calculate tree density as well as the aggregation index for tree species (Goné Bi 2007).

Measurements of gregariousness

Party association

We calculated the percentage of time females spent in lone female parties which included their dependent offspring, all-female parties which consisted of presumably unrelated adult females (Langergraber et al. 2009), and mixed parties which included at least one male (Goodall 1986; Wakefield 2008). Percentages of time spent in each of these party types were recalculated for Budongo, Gombe, and Ngogo based on the total party scans that contained females. Lone male and all-male party scans were excluded from the total amount of scans, as were uncategorized associations (Wakefield 2010). As a result, percentages presented here reflect only female data and thus differ from the published ones.

Dyadic association

The proportion of time individuals A and B were observed in one party is expressed by the dyadic association index (DAI). In order to compare the DAI across studies and communities, we calculated this index according to the commonly used formula (Nishida 1968; Cairns and Schwager 1987):

$$\mathrm{DAI_{AB}} = \mathrm{AB} / (\mathrm{A} + \mathrm{B} - \mathrm{AB})$$

where A is the total time individual A was observed, B is the total time individual B was observed, and AB is the total time both individuals were observed in the same party.

Party size

To measure the gregariousness of female chimpanzees, we calculated the daily mean weighted party size (DMWPS) as follows:

$$\mathrm{DMWPS} = \sum\nolimits_{\mathrm{p=1\ to\ n}} (\text{party size} * \text{party duration} / \text{total observation time})$$

where n is the total number of different parties per day in which the focal individual was a member, and p is the total number of parties. Party duration is the length of time a party size remains unchanged and total observation time is the amount of time the individual was observed during 1 day. DMWPS was log transformed to archive normally distributed and homogeneous residuals.

We classified factors predicted to influence party size as either social or ecological. Social predictors included

1. *Dominance rank*. Rank was determined by the direction of greeting vocalizations between female pairs (Wittig and Boesch 2003) using MatMan 1.1.4 (Burfield et al. 2003). We were able to describe dominance relationships among females with a linear hierarchy although the improved linearity index (h') (De Vries 1995), which corrects for unknown relationships, was low ($h'=0.54$, $p=0.0016$). The hierarchy was not stable over the course of the entire study and to account for the disappearance of three females, we calculated rank for the periods from December 2007 to August 2008 and from December 2008 to November 2009. We normalized rank between one (highest rank) and zero (lowest rank) and took the square roots of the normalized values to approach a uniform distribution for model fitting.
2. *Reproductive state*. Three different states were distinguished: cycling, pregnant, and lactating. We determined the duration of the pregnancy by counting back 226 days from the estimated date of an infant's birth. We considered females to be lactating until they either started cycling again and/or their offspring reached 2.5 years of age. Infants start to solicit solid foods from their mother at the age of 6 months (Nishida and Turner 1996) and by the age of two and a half they obtain a good proportion of their nutritional needs from solid food items, which lessens the energetic burden of lactation on the mother (Silk 1979; Moebius and CB, unpublished data).
3. *Number of females in estrus*. We considered females to be in estrus when the swelling of the perineum, a morphological cue of the periovulatory period, was full and showed signs of maximal tumescence, including shine and lack of wrinkles (Dahl et al. 1991; Deschner et al. 2003). When swellings occurred during pregnancy or within 2.5 years after giving birth, they were not counted as sexual swellings.
4. *Number of dependent offspring*. We classified infants (individuals under 5 years of age) and juveniles (individuals over 5 years of age and older that still traveled with their mothers over 50 % of the observation time) as dependent offspring (Boesch and Boesch-Achermann 2000).
5. *Number of male offspring*. We included male offspring less than 10 years of age because they still travel and forage with their mothers at times and therefore may influence their mothers' grouping behavior.
6. *Age of offspring*. We calculated the age of offspring in days since birth.

Ecological predictors

7. *Weighted mean DBH of fruit tree species consumed per day*. We derived mean DBH of fruit species from individual trees on the phenology transect (see above). The mean DBH gives an indication of the size of the species (Leighton and Leighton 1982; Chapman et al. 1992). Since party size as response variable was averaged over the day, we proceeded in the same way with the ecological predictors and calculated the daily weighted mean DBH as follows:

$$\text{Daily mean DBH} = \sum\nolimits_{p=1\text{ to }n} \left[\left(T_{sp} * DBH_{sp} \right) / \; T_{total} \right]$$

where T_{sp} is the time fruit species was eaten, DBH_{sp} is the mean DBH of the species consumed, and T_{total} is the total amount of time an individual spent eating fruit during the day. The values were square root transformed to achieve approximate symmetry before the model was fitted.

8. *Daily weighted mean density of species consumed* (*DMD*). This predictor was calculated as follows:

$$DMD = \sum\nolimits_{p=1\text{ to }n} \left[\left(T_{sp} * density_{sp} \right) \; / \; T_{total} \right]$$

where T_{sp} is time fruit species was eaten, $density_{sp}$ stands for the density of the species consumed, and T_{total} is the total amount of time spent eating fruit during the day. The predictor was log-transformed to approach a symmetrical distribution before the model was fitted.

9. *Spatial aggregation of fruit trees*. The Moran's Index is a measure of spatial autocorrelation and is used to quantify the statistical significance and intensity of aggregation of trees from fruiting species among nearby locations in space. Values of Moran's Index range from minus one to one. If the correlation between counts of trees of one species in adjacent plots with a given distance is high, Moran's Index approaches one, indicating a clumped distribution of the species. If the species is evenly spaced, Moran's Index will approach minus one. The expected value in the absence of a significant spatial autocorrelation is zero (Cliff and Ord 1973). The 350 vegetation plots sampled (10× 20 m) were placed along transects in north–south and east–west direction with a distance of 20 m between adjacent quadrants and covered a length of 400 m/transect. The Moran's Index values were calculated as follows (Sokal and Oden 1978; Anderson 2001):

$$I = \left[n \sum \sum w_{ij} \left(y_i - \hat{y} \right) \left(y_j - \hat{y} \right) \right] / \left[W \sum \left(y_i - \hat{y} \right)^2 \right]$$

where n is number of quadrants across transects, y_i and y_j are the numbers of trees in adjacent quadrants of vegetation plots; $\hat{y}$ is the mean number of trees per quadrant over the area; w_{ij} is assigned a value of 1 when the pair (i, j) pertains to the adjacent quadrant, and otherwise is assigned a value of 0; W is the number of pairs of quadrants used in computing the coefficient. A daily mean Moran's Index (MMI) was calculated weighing the species specific Moran's Index for the time individuals were eating the fruit of a species:

$$\mathrm{MMI} = \sum\nolimits_{\mathrm{p}=1\ \mathrm{to}\ \mathrm{n}} \left[\left(\mathrm{T_{sp}} * \mathrm{Moran's\ I_{sp}}\right) / \mathrm{T_{total}}\right]$$

where T_{sp} is time fruit species was eaten, Moran's I_{sp} is the value of the Moran's Index for the fruit species in the South territory, and T_{total} is the total amount of time spent eating fruit during the total observation time. We transformed the raw values by subtracting the minimum so that all values were positive and then used a square root transformation to attain a roughly symmetrical distribution before the model was fitted.

10. *Fruit availability index* (*FAI*). We calculated the FAI of species with ripe fruit per month using the formula:

$$\mathrm{FAI} = \sum\ _{\mathrm{sp}=1\ \mathrm{to}\ \mathrm{n}} \left(\mathrm{D_{sp}} * \mathrm{T_{sp}} * \mathrm{DBH_{sp}}\right)$$

where D_{sp} is the density of species, and T_{sp} stands for the proportion of fruiting trees of the sampled individuals of species. $\mathrm{DBH_{sp}}$ is the mean diameter at breast height of species. To include the estimate of ripe fruit yield per tree of each species sampled in the calculation of the FAI, we included the scoring of ripe fruit observed in the tree crown in the formula,

$$T_{\mathrm{sp}} = \left(0.25 \times N_{\mathrm{sp}(\mathrm{score}\ 1)} + 0.5 \times N_{\mathrm{sp}(\mathrm{score}\ 2)} + 0.75 \times N_{\mathrm{sp}(\mathrm{score}\ 3)} + 1 \times N_{\mathrm{sp}\ (\mathrm{score}\ 4)}\right) / N_{\mathrm{sp}}$$

where T_{sp} is the sum of the percentage of a species per month with fruit weighted according to their fruit yield, included here as a score from 1 to 4, corresponding to an estimated percentage of how much of the crown is covered with ripe fruit (Goné Bi 1999). This index provides a relative measure of fruit availability for species consumed by chimpanzees that changes from month to month. The FAI values were log-transformed before model fitting to achieve an approximately symmetrical distribution.

Statistical analyses

We tested our data using two different models. The first model tested whether ecological and social factors significantly influenced general party size averaged over 1 day of observation. In the second model, we reduced the data to mothers and tested if sex and age of offspring influence the gregariousness of mothers under certain ecological and social conditions. We used General Linear Mixed Models (GLMM) with a Gaussian error function (Crawley 2005; Baayen 2008a; Bolker et al. 2009). This allowed us to test for the effects of social and ecological factors simultaneously while controlling for factors already known to influence female gregariousness. To account for repeated measurements on the same individuals and for between-subject variation, we included in both models the identity of the focal female as a random effect (Laird and Ware 1982; Jaeger 2008; Bolker et al. 2009). We tested for temporal autocorrelation of data points and included an autocorrelation term in all models. The autocorrelation term was derived by first calculating the residuals of the full model and averaging for each data point residuals of all others from the same respective individual. We weighted the residuals according to their distance in time before calculating their mean. The derived autocorrelation term was then included as an additional predictor in the model. The weight function was shaped as a normal distribution with a mean of zero (i.e., a maximal weight at time lag=0) and had the standard deviation that was obtained by maximizing the likelihood of the full model with the autocorrelation term included.

We constructed the first full model with the daily weighted mean party size as response. Our ecological predictors were Moran's Index, DBH, and the density of fruit species eaten by chimpanzees and controlled for monthly fruit availability. The social factors included number of offspring and reproductive state as main effects controlling for female rank and the number of estrous females, both known to influence female party size (Wakefield 2008; Riedel et al. 2011). Additionally, we fit a three-way interaction between rank, reproductive state, and food availability to test the influence of reproductive state on female gregariousness depending on rank and food availability. The interaction term was not significant and was subsequently removed from the model presented here.

With the second model we analyzed the general party size of mothers to investigate whether sex and age of offspring influenced female gregariousness. We included the same ecological and social predictors as in the first model, but added the age of offspring (and the younger one if females had two dependent offspring). We also included the interaction of sex and the number of estrus females present because gregariousness in mothers may differ when females in estrus are present depending on the sex of their offspring.

For model fitting, we used the function "lmer" provided by the lme4 package (Bates et al. 2011) in the statistical software environment R (R Development Core Team 2011). To fulfill the assumptions of normally distributed and homogenous residuals, we visually inspected histograms of the continuous predictors and applied data transformations (see above) to approach symmetrical distributions. We z-transformed all continuous predictors before fitting the model (mean=0 and SD=

1). To check for absence of collinearity between predictors, we examined the variance inflation factors (VIF) (Quinn and Keough 2002; Field 2005) using the function "VIF" of the R-package "car" (Fox et al. 2012), which we used in combination with a standard linear model (R function "lm") including only the fixed effects. The largest VIF (maximum=3.64) was below a problematic level. Field (2005) suggests that VIFs reaching or exceeding 10 are problematic. During further investigation of collinearity of the predictors with a Spearman rank test we found the daily calculated Moran's Index to be correlated with the density of fruit trees (r=0.8). To test if the collinearity of these two predictors had an effect on the model fit, we ran a model including only one of either density or Moran's Index and compared the results to those of the full model. Using only one of the two predictors did not influence the model fit significantly. We therefore concluded that the collinearity of the two predictors, density and Moran's Index, was not at a level to destabilize the model and we decided to leave both predictors in the model presented here.

We plotted the residuals against the fitted values and used a quantile–quantile plot to check whether they were normally distributed. None of these checks indicated any severe violation of the assumptions. To calculate the effect sizes for the estimates, we used the t values from the mixed effects models to approximate r statistics according to the formula for non-independent data in Nakagawa and Cuthill (2007). To test the overall significance of our models compared to a null model that only included the intercept, the random effect, and the autocorrelation term, we chose a likelihood ratio test (with R function "ANOVA") (Dobson 2002) which compares the deviance of the full models with those of the respective null model. To test the stability of our models, we re-ran each while excluding one data point at a time from the dataset and compared the results for the coefficients derived from this procedure with the coefficients of the full model. They differed only marginally therefore we concluded that no influential cases were present in the data that could destabilize the model fit. We fitted the model using a Maximum Likelihood approach (argument REML of the R-function "lmer" set to FALSE) to increase the reliability of the significance tests (Bolker 2008). We derived p values using a Markov Chain Monte Carlo sampling technique (Baayen 2008b) and generated these using the functions "aovlmer.fnc" and "pvals.fnc" of the "languageR" package (Baayen 2008b).

Results

Party size, percentage of time spent in different party types, and DAI

Mean party size for female focal individuals was 5.2 individuals (mean weighted party size=4.8, median=4, range=1–26, SD=3.8, N=5075) with a skew towards smaller parties. All-female parties had a mean party size of 3.8.

Females in the Taï forest spent 18.3 % alone, 27.5 % in all-female parties, and 54.2 % of the observation time in mixed parties (Table 1). North Group females spent more time in female parties than did South Group females (Table 1), who were observed more often in mixed parties (Lehmann and Boesch 2008). Extending the comparison to populations in East Africa, the differences are not striking (Table 1): the mean size of parties of all parties in which females were present ranged from 5.2 in Taï to 7 at Kanyawara while the mean of female parties ranged from 3.1 at Kanyawara to 3.8 in Taï. Females were observed alone between 18 and 24 % of the observation time (Williams et al. 2002b; Lehmann and Boesch 2008; Wakefield 2008; Pokempner 2010). Note that we excluded the Sonso community of Budongo because observations were done mainly in feeding trees (Fawcett 2000), which could explain the high percentage of time females at Budongo spent in mixed parties. Time spent in all-female parties ranged from 21 % to a high of 40 % in Taï North Group (Lehmann and Boesch 2008). Time spent in mixed parties ranged from 41 % to a maximum of 59 % in Ngogo (Table 1).

In Taï, the mean DAI for 66 female-female dyads was 0.13 (SD=±0.05, range=0.05–0.34). This is much lower than the mean of 0.27 for North Group females (Wittig and Boesch 2003; but see also Boesch and Boesch-Achermann 2000 for lower DAI among females). Female-female DAI mean values for East African populations range from 0.05 at Gombe (Goodall 1986) to 0.09 in Budongo (Fawcet 2000) and thus do not reach the level of dyadic associations of females in the Taï forest.

At least one study at each site for which published data are available reported a positive relationship between food availability and party size (Table 2). However, food availability was measured differently among studies. While most studies considered phenological data (Chapman et al. 1995; Newton-Fisher et al. 2000; Potts et al. 2011; Riedel et al. 2011), Matsumoto-Oda et al. (1998) used feeding time and diversity of food items as proxies for food availability. Methodological differences between studies may have affected the results and therefore lead to inconsistent findings. Aggregation of fruit species had a positive effect on party size in two of three studies that considered the spatial distribution of tree species (Chapman et al. 1995; Newton-Fisher et al. 2000; Anderson et al. 2002). Tree density had a positive effect on party size in Kanyawara, but the number of females in the party was not affected (Chapman et al. 1995). Patch size of eaten fruit species influences feeding party size (Isabirye-Basuta 1988; Wakefield 2010; Potts et al. 2011), but at Kanyawara party size was not significantly correlated with patch size when multiple food species were available simultaneously (Isabirye-Basuta 1988). The number of females in estrous significantly influenced party size at Taï, Ngogo, and

Table 1 Summary of social grouping information of females in six different chimpanzee communities from western (Taï) and eastern Africa

Population	Party type			Party size		Association	
	Alone	All female	Mixed sex	Mean	Mean female	Female social time[a]	Female mean DAI
Taï (North)	18.1[b]	40.2[b]	41[b]	6.4[c]	n.a.	81.2	0.27[d]
Taï (South)	18.3[e]	27.5[e]	54.2[e]	5.2[e]	3.8[e]	81.7	0.13[e]
Gombe	24[f, g]	22[f, g]	54[f, g]	6.1[h]	3.5[f]	76	0.05[i]
Kanyawara	18.3[j]	35.6[j]	46.1[j]	7[j]	3.1[j]	81.7	0.08[j]
Ngogo	20.9[k, g]	20.6[k, g]	58.5[k, g]	6.68[k]	3.4[k]	79	0.06[k]
Budongo	6.9[l, g]	18.6[l, g]	76.6[l, g]	6.36[l]	2.3[l]	93.1	0.09[l]

[a] Females social time is proportion of time females were observed either in an all-female or in mixed parties.

[b] Taï (North): Lehmann and Boesch (2008)

[c] Taï (North): Riedel (unpublished data)

[d] Taï (North): Wittig and Boesch (2003)

[e] Taï (South): this study

[f] Gombe: Williams et al. (2002b)

[g] Percentage recalculated from published data on the basis of parties that contained females. Male associations are excluded

[h] Gombe: Murray et al. (2006)

[i] Gombe: Goodall (1986)

[j] Kanyawara: Pokempner (2010)

[k] Ngogo: Wakefield (2010)

[l] Budongo: Fawcett (2000)

Budongo (Fawcett 2000; Anderson et al. 2002; Mitani et al. 2002a; Wakefield 2008; Riedel et al. 2011). Rank was only tested in Taï (Riedel et al. 2011) where social dominance affected party size during periods of fruit scarcity. Only high-ranking females were able to carry the additional costs of gregariousness. The presence of dependent offspring did not influence the gregariousness of females at Ngogo or Taï (Wakefield 2010; Riedel et al. 2011).

Model of factors influencing female gregariousness (DMWPS) in Taï females

The full model explained variation in female gregariousness in the South Group significantly better than the null model (χ^2= 27.64, df=9, p<0.001). Daily party size was significantly larger when the chimpanzees were feeding on fruit species with clumped distributions (Table 3; Fig. 1) and party size increased with an increasing number of females in estrus (Table 3; Fig. 2). The effect sizes for the significant predictors were moderate (Table 3). Other ecological predictors (DBH, density of fruit trees, and fruit availability) and social predictors (number of offspring, rank, and reproductive state) did not significantly influence party size. The positive relationship between party size and food aggregation might have arisen because the individual is able to participate in larger parties when feeding longer or more often on aggregated fruit species per day because the additional travel cost is buffered by the relative proximity of food patches.

Alternatively, the relationship might have occurred because larger parties sought out fruit with clumped distribution because a larger effective patch is needed to feed all individuals or because the individuals preferred certain species. To differentiate among those alternatives, we ran a GLMM with the Moran's Index as the response variable and party size as a predictor along with density and food availability. None of the predictors influenced the daily Moran's Index, and party size in particular was not correlated with the daily MMI. Therefore, the visited food species were independent of party size of which females where a part of. The variance between the levels of the random factor-here, the subject identity of focal females-was 0, which indicates that individual females did not prefer more or less clumped resources.

Influence of offspring age and sex on female gregariousness

We tested the influence of offspring age and sex on their mother's gregariousness by including only females with offspring in the analysis. The full model was highly significant (χ^2=35.1, df=11, p<0.0001). Again, mothers were found in larger parties when the distribution of consumed fruit was more clumped (Table 4). Furthermore, mothers with male offspring were found in smaller parties when more than one sexually receptive female was present (Table 4; Fig. 3).

Table 2 Summary of the effects of ecological and social factors on party size in different chimpanzee populations

Population	Ecological factors				Social factors		
	Food		Tree				
	Abundance	Aggregation	Density	Patch size	Female rank	# Females in estrus	Offspring
Taï	$+^{a}/+^{b}/+^{c}/\mathrm{ns}^{d}$	$\bullet^{a}/\mathrm{ns}^{b}/\bullet^{c}/+^{d}$	$\bullet^{a}/\bullet^{b}/\bullet^{c}/\mathrm{ns}^{d}$	$\bullet^{a}/\bullet^{b}/\bullet^{c}/\mathrm{ns}^{d}$	$\bullet^{a}/\bullet^{b}/+^{c}/\mathrm{ns}^{d}$	$\bullet/+^{b}/+^{c}/+^{d}$	$\bullet^{a}/\bullet^{b}/\mathrm{ns}^{c}/\mathrm{ns}^{d}$
Mahale	$+^{e}/\bullet^{f}$	$\bullet^{e,\ f}$	$\bullet^{e}/\mathrm{ns}^{f}$	$\bullet^{e}/+^{f}$	$\bullet^{e,\ f}$	$+^{e}/\bullet^{f}$	$\bullet^{e,\ f}$
Ngogo	$+^{g}/\mathrm{ns}^{h}/\bullet^{j}$	$\bullet^{g}/\bullet^{i}/\bullet^{j}$	$\bullet^{g}/\bullet^{i}/\bullet^{j}$	$\bullet^{g}/+^{i}/+^{j}$	$\bullet^{g}/\bullet^{i}/\bullet^{j}$	$+^{g}/+^{h}/\bullet^{j}$	$\bullet^{g}/\mathrm{ns}^{i}/\bullet^{j}$
Kanyawara	$+^{k}/+^{l}/\bullet^{m}/\mathrm{ns}^{n}/\bullet^{o}$	$\bullet^{k}/+^{l}/\bullet^{m}/\bullet^{n}/\bullet^{o}$	$\bullet^{k}/+^{l}/\bullet^{m}/\bullet^{n}/\bullet^{o}$	$\bullet^{k}/\bullet^{l}/+^{m}/\mathrm{ns}^{n}/+^{o}$	$\bullet^{k,\ l,\ m,\ n,\ o}$	$\bullet^{k,\ l,\ m,\ n,\ o}$	$\bullet^{k,\ l,\ m,\ n,\ o}$
Budongo	$\mathrm{ns}^{B}/-^{A,Cp}/+^{q}$	$+^{p}/\bullet^{q}$	$\bullet^{p,\ q}$	$\bullet^{p,\ q}$	$\bullet^{p,\ q}$	$\bullet^{p}/+^{qE}/-^{qF}$	$\bullet^{p,\ q}$
Gombe	$+^{r}$	$\bullet^{r}$	$\bullet^{r}$	$\bullet^{r}$	$\bullet^{r}$	$+^{r}$	$\bullet^{r}$

"+" signifies a statistically positive correlation between predictor and party size, "–" signifies a statistically negative correlation between predictor and party size, *ns* no correlation was found between predictor and party size, "•" signifies that the predictor was not tested

[A] Dataset 1

[B] Dataset 2

[C] Dataset 3

[D] Party size calculated only based on feeding parties

[E] in sexual or all male parties

[F] in mixed parties

[a] Taï: Doran (1997)

[b] Taï: Anderson et al. (2002)

[c] Taï: Riedel et al. (2011)

[d] Taï: this study

[e] Mahale: Matsumoto-Oda et al. (1998)

[f] Mahale: Itoh and Nishida (2007)

[g] Ngogo: Mitani et al. (2002a)

[h] Ngogo: Wakefield (2008)

[i] Ngogo: Wakefield (2010)

[j] Ngogo: Potts et al. (2011)

[k] Kanyawara: Wrangham et al. (1992)

[l] Kanyawara: Chapman et al. (1995)

[m] Kanyawara: Isabyre-Basuta (1988)

[n] Kanyawara: Pokempner (2010)

[o] Kanyawara: Potts et al. (2011)

[p] Budongo: Newton-Fisher et al. (2000)

[q] Budongo: Fawcett (2000)

[r] Gombe: Goodall (1986)

Discussion

The re-analysis of general female gregariousness, measured as mean party size and the mean female DAI, reveals that both have decreased compared with previous results from Taï. General association patterns described by the proportion of time spent in different party types remained fairly stable. We attribute the decrease mainly to the effects of demographic change, because party size and DAI are most likely affected by a decline in the number of potential social partners. In contrast, how much time females spent alone versus in subgroups may not depend on the number of conspecifics in the community. The comparison of party size, DAI, and general association patterns to East African populations proved to be difficult due to the methodological and analytical differences among studies. Therefore, no statistical tests between studies were undertaken and instead we only discuss general trends and relative differences.

Party size

The observed change in party size over time in Taï South Group was most likely due to the decline that the community experienced over the past 17 years. Community size

Table 3 Influence of ecological and social factors on general party size in Taï chimpanzees

Main effects	Slope	SE	Lower CI	Upper CI	*p* value	Effect size *r*
Intercept	1.525	0.076	1.357	1.687		
Rank of female	0.015	0.039	−0.078	0.101	0.736	0.026
Reproductive state (pregnant)	0.038	0.137	−0.231	0.315	0.917[a]	0.040
Reproductive state (lactating)	−0.012	0.092	−0.206	0.187		0.025
Number of dependant offspring	0.030	0.045	−0.072	0.120	0.583	0.046
Number of females in estrus	0.087	0.032	0.026	0.153	0.006	0.185
Fruit availability	0.034	0.037	−0.039	0.110	0.369	0.063
DBH	0.032	0.036	−0.039	0.102	0.380	0.060
Density[b]	−0.029	0.057	−0.146	0.081	0.605	−0.035
Moran's Index[b]	0.129	0.053	0.028	0.236	0.015	0.166
Autocorrelation term	0.076	0.030	0.009	0.133	0.027	0.168

Results of a GLMM modeling DMWPS ($n=237$) as a function of number of females in estrus, number of offspring, rank, and reproductive state of the female followed up and ecological predictors including mean DBH, MMI, the mean density of species consumed, and monthly fruit availability of consumed fruit species. Reproductive state is a categorical predictor with three levels (lactating, pregnant, and cycling). The slope, which represents the estimated coefficient, and *p* values were derived from Markov Chain Monte Carlo (MCMC) sampling. Effect sizes (*r*) were calculated from *t* values. The equivalent of a confidence interval for coefficient estimates is presented as Bayesian credible intervals (CI) and exclude zero for the significant predictors

[a] Overall *p* value for the predictor reproductive state with levels pregnant, lactating, and cycling

[b] Since DBH and Moran's Index were correlated, we reran the model with only one of them included at a time. This revealed slightly different results for both (Moran's I estimate=0.1095±SE=0.0523, $p=0.0078$; density, 0.0644±0.058), but the same predictors reached significance therefore both predictors were kept in the model

decreased from 54 individuals in 1999 to a minimum of 34 individuals in 2006 and the number of females decreased from 19 to 11. Before this drastic decline, South Group females were more gregarious (mean general party size in North=6.4, in South=9.4, Riedel, unpublished data). Subtle differences in food abundance and aggregation might have explained this difference: the South Group territory had a higher monthly FAI than the North Group territory (Riedel et al. 2011) and 74 % of 39 fruit tree species showed a slightly more clumped distribution in the South (Fig. 4). Similar small scale spatial ecological differences between neighboring territories within one population or among neighboring populations have been suggested to lead to differences in social structure in other chimpanzee populations (Collins and McGrew 1988; Pusey et al. 2005; Potts et al. 2009).

Percentage of time spent in different association types

The within-population comparison illustrates that North Group females spent more time in all-female parties than South Group females, who seemed to prefer mixed parties (Lehmann and Boesch 2008). Only two males were present in North Group from 1999 to 2001, one adult and one adolescent, whereas South Group had a minimum of five males (two adults and three adolescents) which could explain the observed difference (Lehmann and Boesch 2008).

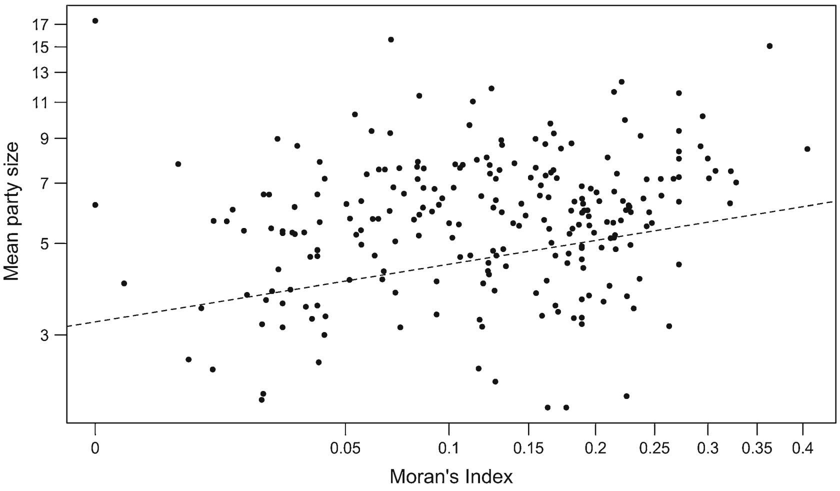

Fig. 1 Taï chimpanzee party size (log scale) as a function of food tree aggregation, measured by the Moran's Index (log scale). The *regression line* shows the estimated intercept and the slope estimate by a GLMM (Table 3)

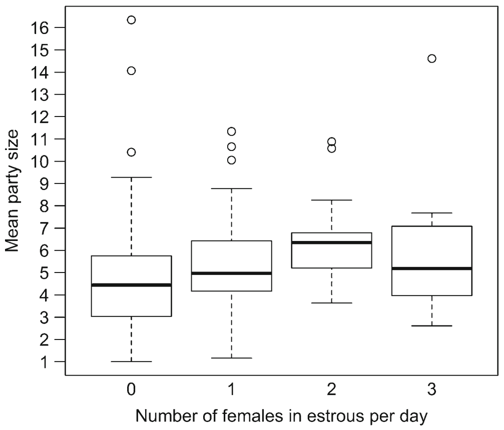

Fig. 2 Mean daily general party size as a function of number of females in estrus in Taï chimpanzees. *Whiskers* indicate the minimum and maximum of the daily mean party size. The *central box* represents the values from the lower to the upper quartile (25 to 75 percentile), and the *middle line* depicts the median. Values that are beyond the quartiles by one-and-a-half of the inter-quartile range are depicted as *open circles* and considered outliers

The between-population differences were less pronounced than expected. Females in Gombe spent less time in all-female parties and almost 30 % more time alone than females of all other populations (Table 1). They forage in individual core areas, which could explain why they spent more time alone than at Taï and less time in all females parties (Lehmann and Boesch 2005). In addition, 50 % of Gombe females did not emigrate but stayed in their natal community and maintained close bonds with their mother even after having established their own core areas (Pusey et al. 1997; Williams et al. 2002a). Since females accompanied by offspring count as "lone" females, these mother–daughter associations are not counted as "all-female" parties (Wrangham and Smuts 1980; Williams et al. 2002b).

Dyadic association

Within-population comparison showed reduced DAIs among females in Taï South Group compared with results of earlier studies. The loss of 11 adult females from 2004 to 2009 (Köndgen et al. 2008) undoubtedly changed the dynamics of dyadic associations between individuals and might have been responsible for the decrease in mean DAI. Long-term relationships between females were disrupted and females seem to establish new social bonds only slowly. Eastern chimpanzee populations exhibit lower female DAIs than those found at Taï. Although some females at Ngogo maintained exceptionally strong dyadic social bonds (Wakefield 2008; Langergraber et al. 2009), Ngogo females show social sub-structuring, and Wakefield (2008) found that those within association cliques had higher mean DAIs than females at Taï. Clique members often groomed with each other and they showed reciprocity in grooming (Wakefield 2010). At over 180 individuals, Ngogo is the largest chimpanzee community studied thus far and structuring in association cliques may help to maintain strong individual relationships in a large community (Mitani and Amsler

Table 4 Influence of ecological and social factors on general party size of mothers in Taï chimpanzees

Main effects	Slope	SE	Lower CI	Upper CI	*p* value	Effect size *r*
Intercept	1.777	0.065	1.647	1.920		0.023
Rank of female	0.009	0.025	−0.051	0.068	0.819	−0.052
Reproductive state (lactating)	−0.060	0.028	−0.223	0.108	0.774[a]	−0.028
Reproductive state (pregnant)	−0.044	0.026	−0.266	0.181		−0.041
Age	−0.019	0.080	−0.086	0.051	0.627	0.068
DBH	0.028	0.109	−0.029	0.083	0.344	−0.040
Density	−0.024	0.032	−0.102	0.060	0.575	0.175
Moran's Index	0.095	0.028	0.020	0.167	0.011	0.061
Fruit availability	0.028	0.041	−0.033	0.090	0.381	0.141
Autocorrelation term	0.049	0.024	−0.001	0.093	0.049	−0.200
Interaction[b]/number of estrus females × number of male offspring	−0.088	0.030	−0.145	−0.026	0.004	0.023

Results of a GLMM modeling daily weighted party size (n=223) as a function of factors influencing the sociality of mothers. Ecological factors included mean DBH, MMI, the mean density, and monthly fruit availability of consumed fruit species, while social factors included reproductive state and dominance rank of the focal female, age of the younger offspring, and the interaction of number of females in estrus with number of male offspring younger than 10 years of age. The slope describes the estimated coefficient. The respective p values are derived from MCMC sampling. Effect sizes (r) were calculated from t values. The equivalent of a confidence interval for the coefficient estimates is presented as Bayesian credible intervals (CI) and exclude zero for the significant predictors

[a] Overall p value for the predictor reproductive state

[b] Both predictors are not presented in the table as main effects because they are included in the interaction term and thus their coefficients and respective p values as main effects should not be interpreted

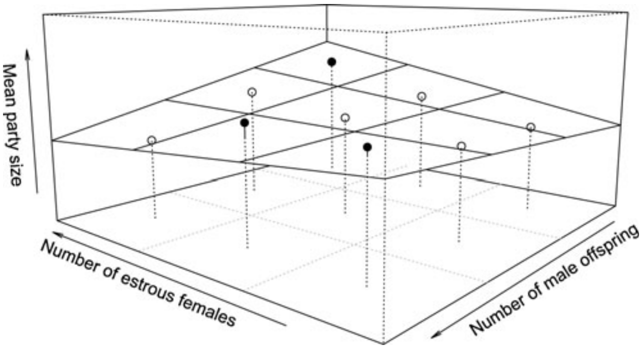

Fig. 3 Influence of the number of females in estrus and the number of male offspring of mothers on general party size in Taï chimpanzees. The model was built based on 223 data points which, for clarity here, were binned to the mean value according to counts in cells. The *surface* represents the predicted values calculated by the GLMM; the *circles* represent the means of grouped data; *filled circles* depict the data points that exceed the estimated values; *open circles* represent data points that fall below the estimated values. For mothers of female offspring, party size increased with an increasing number of females in estrus. Mothers with sons, however, decreased their participation in large parties with increasing number of sons (Table 3). DMWPS was log transformed, while number of females in estrus and number of male offspring were *z*-transformed

2003; Wakefield 2008). However, the mean DAI for females is lower than in Taï (Wakefield 2008).

Social and ecological influences on party size

Taï female chimpanzees were more gregarious on days when they fed longer or more often on fruit species with a clumped distribution and when more females where in estrus. However, mothers of sons were found in smaller parties with increasing number of females in estrus.

Feeding on species with clumped distributions should reduce the path lengths between patches and should therefore lessen the costs of each additional individual in a party (Clutton-Brock and Harvey 1977; Janson 1988; Isbell 1991; Chapman et al. 1995; Janson and Goldsmith 1995). Finding food trees of the same species in relative proximity would also enable party members to split up to feed in different trees and reunite after the feeding event, which reduces contest and scramble competition while allowing females to remain more gregarious (Wrangham 1977). Even though food distribution appears to shape female grouping patterns in accordance with the socioecological model (Isbell and Young 2002), female gregariousness was clearly influenced by the presence of females in estrus, as party size increased with an increasing number of females in estrus. This finding corroborates previous results from Taï (Anderson et al. 2002; Riedel et al. 2011). Riedel et al. (2011) found also that dominance rank influenced gregariousness when ripe fruit was scarce which supports contest competition as one of the main drivers of female sociality (Murray et al. 2006; Riedel et al. 2011). Given that the South Group lost almost half of their female community members, it is possible that fruit availability did not constrain gregariousness because of relaxed competition between individuals or that fruit scarcity was not severe enough during this observation period for rank affects to emerge.

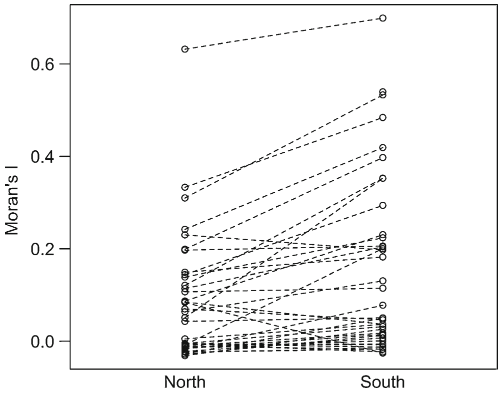

Fig. 4 A Comparison of Moran's Index values of fruit tree species between South and North Group territories in Taï National Park. A majority (75 %) of fruit species show a more aggregated distribution in South territory (Wilcoxon signed-rank test, V=632, p<0.0001)

In contrast to our expectation, mothers with sons were found to be in smaller parties as the number of sexually receptive females increased. Juvenile and adolescent males are attracted to females with sexual swellings, who are usually monopolized by adult males. On days with more than one estrus female present, juvenile males might get a chance to associate with one of the estrus females who is less attractive to adult males. However, our findings did not support this prediction. When more than two females were in estrus simultaneously, parties split up and mean party size was smaller on days when there were three estrus females present versus two (Fig. 2). We speculate that mothers with sons may avoid large parties with estrus females to protect themselves and their offspring from aggression from displaying males (Muller and Wrangham 2004; Muller et al. 2009). However, we did not collect data on male aggression towards adolescent and juvenile males and thus we cannot address this question.

A comparison of social and ecological influences on party size across chimpanzee research populations (Tables 2 and 3) indicates that food and the presence of estrous females are most important. Consistent with previous studies (Goodall 1986; Matsumoto-Oda et al. 1998; Fawcett 2000; Anderson et al. 2002; Mitani et al. 2002a; Wakefield 2008; Riedel et al. 2011), the presence of estrous females (when tested) increases party size in all communities. It is less clear why food availability has a significant influence on party size in some populations but not in others (Table 2). But even minor differences in the density of an important tree species can have strong effects on demography, which in turn can influence association patterns and thus gregariousness (Potts et al. 2009, 2011). Furthermore, the level of aggregation of fruit species, and therefore the relative distance between food patches, affected party size at Taï, Kanyawara, and Budongo (Chapman et al. 1995; Newton-Fisher et al. 2000). Thus, the effect of food quantity is likely to be modulated by its spatial distribution. Not only spatial but also temporal aspects of fruit abundance and quality define habitat differences which may influence association patterns (Watts et al. 2012). In the Taï National Park, ripe fruit is particularly scarce for two to four months per year during these months, the chimpanzees forage more solitarily and the intake of non-fruit items in the diet increases (Doran 1997; Anderson et al. 2005; Polansky, unpublished data). In Taï, the seasonal limitation of ripe fruit appears to be short and occurs during the rainy season. In Gombe, however, the dry season is the time of fruit scarcity and lasts for at least 6 months (Clutton-Brock and Gillett 1979). During this time, individuals lose weight (Pusey et al. 2005) and party size is significantly smaller (Murray 2006). This comparison suggests that food scarcity in Taï is not as pronounced as for example in Gombe and may also explain some of the observed differences between eastern and western populations.

Food distribution has been found to positively influence party size in other mammal species living in social systems described as fission–fusion such as spider monkeys (Symington 1988) and brown hyenas (Owens and Owens 1978). Group size of female lions in the Serengeti, Tanzania, however, was larger than predicted for small prides during periods of prey scarcity. This may be because the benefits of sociality for lions such as cooperative territory defense and offspring protection outweigh the energetic benefit of solitary hunting (Packer et al. 1990). Bottlenose dolphins at Shark Bay, Australia, adjusted their group size to activity, habitat type and seasonal predator presence. They foraged in smaller groups but increased group size when hunting in shallow waters where biomass of prey species was higher and seasonal predator presence was more likely (Heithaus and Dill 2002). These examples, including our analysis, demonstrate that the distribution and availability of food plays an important role in determining group size in species with a fission–fusion social system but other factors such as protection from predators, demography or social benefits need to be considered simultaneously to fully understand the underlying mechanisms of grouping patterns.

Moreover, in fission–fusion species with female based philopatry such as elephants, bats, dolphins, lions, and hyenas, female–female association patterns are largely explained by matrilineal kinship (Packer et al. 1990; Holekamp et al. 1997; Archie et al. 2006; Kerth and Van Schaik 2011). Chimpanzees, bonobos, and woolly spider monkeys, however, are characterized by female dispersal (Strier 1990; Kanō 1992; Mitani et al. 2002b). Therefore associations within females can only be explained by benefits independent of relatedness and thus social and ecological factors need to be included in models regarding social relationships between females. Furthermore, female sociality of the genus *Pan* may provide us with some insight into the nature of female relationships of the common ancestor of *Homo* and *Pan* as the majority of human societies practice female migration which is likely to be an ancestral trait (Foley and Lee 1989; Seielstad et al. 1998; Langergraber et al. 2007).

The comparison of general association patterns of females within Taï illustrates variation in female gregariousness over time and emphasizes their behavioral flexibility in response to demographic change. After a decline in community size, we observed a decrease in general mean party size and a weaker dyadic association among females. Our results complement recent findings from East Africa (Wakefield 2008, 2010; Langergraber et al. 2009; Pokempner 2010) and call into question the simple dichotomy of sociality between eastern and western female chimpanzees and underscore that the variation in gregariousness is driven by site-specific ecological and social conditions. Of many potential ecological and social factors, food aggregation, and number of sexually receptive females had the strongest influence on female gregariousness of the Taï population. Females in the South group might have experienced relaxed feeding competition because the number of potential competitors was low and therefore general food availability did not constrain participation in parties. We conclude that both social and ecological factors drive female sociality, and that a change in one can affect the influence of the other. It is therefore warranted to consider social and ecological aspects of sociality simultaneously when describing the dynamics of fission–fusion social systems.

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Ethical Standards This research complies with the ethical guidelines for research projects of the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany and was conducted in accordance with the animal care regulations and national laws of Côte d'Ivoire and Germany.

Conflict of interest The authors declare that they have no conflict of interest.

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