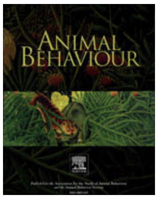
Animal Behaviour 77 (2009) 377–387

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe



Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*

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ARTICLE INFO

Article history:
Received 14 March 2008
Initial acceptance 13 May 2008
Final acceptance 29 September 2008
Published online 25 November 2008
MS. number: 08-00185R

Keywords:
association pattern
chimpanzee
female sociality
grooming
Pan troglodytes
social bond
social network

Patterns of group social structure are often linked to the competitive regime within a social unit and to the availability of kin. In line with this, many studies have shown that the dispersing sex, which is considered to have fewer kin around, is less social, while the philopatric sex has strong social bonds. Chimpanzees were considered to fit well into this scheme with highly social and competing philopatric males and generally asocial and solitary dispersing females. However, recent data suggest that chimpanzee females can indeed be highly social, even though they are unlikely to be related to each other. We studied female sociality in a long-term habituated group living in the Taï Forest, Côte d'Ivoire. Female social relationships as measured by association and grooming preferences were well differentiated and long lasting. Association (and to a lesser extent grooming) bonds were associated with reduced aggression between social partners. In addition, the competitive regime as indicated by group size had a strong effect on female social networks, which were more centralized and less clustered in smaller groups, suggesting that competition may play a major role in shaping female chimpanzee sociality. These findings suggest that strong social bonds can occur even in the absence of a strong network of kin relationships.

Species in many vertebrate taxa live in closed social groups, which are underpinned by individual recognition and repeated social interactions (e.g. guppies, *Poecilia reticulata*: Griffiths & Magurran 1999; babblers, *Turdoides caudatus*: Gaston 1978; elephants, *Loxodonta africana*: Moss & Poole 1983). In most such groups, social interactions are not evenly spread between adult group members, with individuals selectively preferring a few key individuals (e.g. Arnold et al. 1981; Reinhardt & Reinhardt 1981; Packer & Pusey 1987; Mitani et al. 2000; Durrell et al. 2004; Pomeroy et al. 2005). Such nonrandom social biases (social bonds) can either reflect constraints imposed by the physical environment (i.e. distribution of resources) and/or strong site fidelity (Wolf & Trillmich 2007) or can indicate real social preferences in the sense that individuals seek each other out as social partners. Although nonreproductively driven social bonds can exist between the sexes (Palombit 1999), it is the extent and distribution of intrasexual social relationships that has led to extensive research in the past. A number of direct fitness benefits have been suggested to arise from maintaining social relationships with members of the same sex, such as a reduction in contest competition through enhanced cooperation (Blundell et al. 2004) and coalitionary support (e.g. Mitani et al. 2000), increased tolerance from more dominant group members (e.g. Smith et al. 2007) and, among females, social bonds may also provide a benign environment for successfully raising and socializing offspring (Williams 1999).

In addition to these direct benefits of bonding, a number of authors have invoked kin selection theory to explain the variation in the nature and distribution of bonds among adult group members (Hamilton 1964; Griffin & West 2003). Kin selection theory predicts that individuals are more likely to develop a close social bond if their relatedness is higher than the average group relatedness, so that inclusive fitness benefits in addition to the direct benefits can arise. Thus, if social bonds can be established with (closely) related individuals the benefits of these bonds should be greater than those of bonds between unrelated individuals. As a direct result, it is typically predicted that the philopatric sex, which in many species has more kin in the group, will show refined social bonds while the dispersing sex, which has no (or fewer) kin around, will be less social (Sterck et al. 1997). There are obvious exceptions to this 'rule of thumb', for example, when dispersal takes place in kin groups (Mitchell 1994) so that dispersal patterns do not allow the prediction of kinship structure. In addition, some

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doi:10.1016/j.anbehav.2008.09.038

researchers have questioned the existence of social preferences altogether, emphasizing biological market effects instead (Barrett et al. 1999; Bshary & Noë 2003). Nevertheless, the concept of using dispersal patterns as a predictor for same-sex social relationships has been successfully applied to many (primate) species, in which strong social bonds have been shown to exist in the philopatric sex (e.g. Kummer 1968; Kapsalis & Berman 1996; Perry 1996; Silk et al. 1999; Swedell 2002), but not in the dispersing sex (e.g. Kappeler 1993).

Despite this focus on using kin selection as a framework to interpret species-typical sex differences in the extent of their same-sex social bonding, it is important to consider the extent to which both sexes, that is, also the dispersing sex, could benefit directly from maintaining close social bonds with unrelated members of the same sex. This will be especially important for long-lived species, in which dispersal is usually a once-in-a-lifetime event and immigrants subsequently become permanent residents in a social group. In such cases, the competitive regime (rather than kinship) is expected to shape the nature and distribution of social bonds. Previous studies have shown that the competitive regime can interact with kin selection (reviewed in West et al. 2002) and, depending on the nature of the competitive regime, selection for cooperation between relatives and nonrelatives can be affected (e.g. West et al. 2001, 2006).

In addition to the direct benefits of bonding outlined above, a stable network of social bonds has been shown to enhance individual well-being (Seeman 1996; Taylor et al. 2000) and reduce stress (Engh et al. 2006), so that good social integration may enhance individual survival and reproductive success (e.g. Koenig 1994; Moses & Millar 1994; Lambin & Yoccoz 1998; Silk et al. 2003; Durant et al. 2004; Ruan & Wu 2008). Thus, considering direct benefits of social bonds shifts the attention away from kin selection and back to the dispersing sex, which has, up to now, largely been neglected. Even though a complete picture of population social structure of both sexes is needed to understand fully the evolution of social bonds, very few studies have analysed the extent to which same-sex social relationships exist in the dispersing sex (e.g. Furuichi 1985; Silk 1994; Williams 1999; Fawcett 2000).

We explored the nature and extent of social bonds in the dispersing sex of a long-lived primate, the chimpanzee. Chimpanzees live in large social groups, so-called communities, which can consist of up to 150 individually recognized members (Goodall 1986; Nishida 1990; Boesch & Boesch-Achermann 2000). Males are philopatric, while females normally disperse individually when reaching maturity. Secondary dispersal is rare and adult females can therefore spend up to 40 years within the same group. Because females disperse, adult females within a group are usually not related to each other (Vigilant et al. 2001). In chimpanzees, males form strong hierarchies and intrasexual social bonds (Nishida 1979; Goodall 1986; Watts 1998; Boesch & Boesch-Achermann 2000), while females have often been described as asocial, mostly solitary and lacking clear-cut dominance hierarchies (Goodall 1986; Nishida 1989; Wrangham et al. 1992; Pusey et al. 1997; Fawcett 2000). However, few studies have actually quantified female social relationships in wild chimpanzees and reports from different study sites are mixed (Goodall 1986; Wrangham et al. 1992; Williams 1999; Fawcett 2000; Lehmann & Boesch 2008) while systematic data on social preferences are still largely missing.

We used long-term data on female association patterns and grooming relationships from one group of wild chimpanzees in West Africa, Côte d'Ivoire, to ask the following questions. Do chimpanzee females have preferred same-sex association and grooming partners? If so, how long do such relationships last and what factors determine preferences for particular partners? Are social bonds beneficial in that they reduce aggression between partners? How do social networks derived by these two different, commonly used behavioural measures compare? Finally, we were interested in the effects of intragroup competition on network structure. In line with the theory outlined above, we predicted that a reduced level of intragroup competition (i.e. a smaller group living at a lower density) would lead to a less dense and more centralized social skew in social networks, because the potential benefits that can be gained through close social bonds should be smaller when competition is reduced. Furthermore, there will be fewer highly valuable partners in a small group, so that social networks should become more centralized.

METHODS

Study Site and Population

The Taï National Park, Côte d'Ivoire, West Africa, comprises an area of approximately 4540 km^2 and consists of evergreen lowland rainforest (for a detailed description of the study site see Boesch & Boesch-Achermann 2000). Data presented in this study come from one chimpanzee group, the North Group, which was habituated in 1979 and has been observed continually since its habituation by researchers and field assistants. In January 1992, the group consisted of six adult males (aged $>$ 15 years), 16 adult females (aged $>$ 13 years), 12 adolescents and juveniles (aged 5 years and above) and 13 dependant offspring (aged $<$ 5 years). Since that time, group size has decreased (caused by poaching and diseases) to one adult and one adolescent male, six adult females, nine adolescents and juveniles and five dependant offspring in December 2001 (Lehmann & Boesch 2003). Although home range size varied over the study period, it did not change as much as group size, so that the smaller group lived in a relatively larger home range (Lehmann & Boesch 2003). All chimpanzees live in so-called fission–fusion societies in which the social group as such is rarely found together at one location but rather forms frequently changing smaller subgroups, so-called 'parties' (Sugiyama 1968). Average party size in Taï varies between five and seven individuals, depending on overall group size (Lehmann & Boesch 2004). Females are generally thought to be free to choose the party they want to follow, while males are attracted to sexually receptive females (Anderson et al. 2000). Usually all females in the group reproduce; interbirth interval in Taï is 69 months (Boesch & Boesch-Achermann 2000). Females disperse alone at the age of 11 years before they reach sexual maturity; thus the majority of adult females within the group are immigrants and unlikely to be related (L. Vigilant, personal communication), even though a female occasionally remains in her natal group. In contrast to other study sites, Taï chimpanzee females generally show high levels of sociality, that is, they spend 40% of their time in parties with other females (Lehmann & Boesch 2008) and have highly overlapping home ranges (Lehmann & Boesch 2005), so no specific spatial neighbourhoods exist that could explain partner preferences.

Data Collection

Data presented here start with 1992 for the analysis of association patterns and 1993 for the grooming analyses (data on grooming were not collected systematically on checksheets before 1993). Field assistants made 1447 daily follows of adult females with an average length of 9.7 h per day. All changes in party compositions (from 1992 onwards) and all grooming interactions (1993 onwards) involving the focal subject were recorded continuously on checksheets. All data were entered into 'Taï-Chimp-BehavBase', our large chimpanzee behaviour database, using Microsoft Access. Analyses presented here are restricted to adult females aged 11 years or more.

Analysis of Association Data

Because chimpanzees live in a fission–fusion society, association preferences are based on subgroup (party) composition, that is, two females were associated if they were found within the same party. We translated continuous data on party composition into 30 min scans, which allowed us to quantify the frequency with which two particular individuals were associated within the same party. Because such frequencies are dependent on demographic variables as well as on observation schedules, we used a permutation test, which allowed us to evaluate whether certain dyads were observed more frequently than expected by chance given the frequency with which each individual was recorded in the data set. We analysed our data using Socprog 2.0 (Whitehead 1999), which implements a test for preferred long-term associations, based on a procedure introduced by Bejder et al. (1998). The general null hypothesis is that individuals associate equally with all other individuals given their availability in the data set within the observation period. Because we were primarily interested in long-term preferences we tested the null hypothesis that there were no preferred association partners between focal days (using all focal days within a given year), given the frequency with which each individual was recorded during each focal day. Using a modification of the Manly (1995) and Bejder et al. (1998) procedure, we permutated the elements of the symmetric association matrix (30 000 permutations) for each sampling period, keeping row and column totals constant (Whitehead 1999).

As an association index we used the twice-weight index of Cairns & Schwager (1987), which is implemented into Socprog. This index (DAI) was calculated for each dyad in the data set by using the following equation:

$$\mathrm{DAI} = \frac{ab}{ab + a_{\mathrm{withoutb}} + b_{\mathrm{withouta}}}$$

with ab being the number of 30 min bins in which A and B were present in the same party and $a_{\mathrm{withoutb}}/b_{\mathrm{withouta}}$ being the number of 30 min bins in which A or B was observed in a party without the other partner being present. Because group composition changed dramatically between years (owing to death or disappearance of individuals), we analysed all data on a yearly basis, that is, all association preferences within a given year were determined independently of those in the following year. Thus, for each year we determined the number and identity of those female–female dyads whose real association index within that year was greater than 97.5% of their random association index (see Whitehead 1999). Such dyads were termed preferred association partners. If these dyadic preferences persisted for at least 3 of 4 consecutive years (see also Silk et al. 2006b) we termed such dyads long-term association partners. We also compared the number of preferentially associating dyads to the number expected under random associations: even if individuals associated randomly the permutation test would be expected to produce a certain number of significant results, as the permutated values followed a normal distribution. Thus by using a P value of 0.05, we would expect that 2.5 of 100 possible dyads have a significantly higher, and 2.5 of 100 possible dyads have a significantly lower, association index. Our comparison of observed versus expected numbers ensures, therefore, that the effect we observed is indeed a characteristic of chimpanzee association patterns and not simply based on random effects. For subsequent analyses we coded dyadic relations as either 0 (no preferred partners), 1 (preferred association partners) or 2 (long-term association partners). This allowed us to create matrices of social bonds, which were used in subsequent analyses.

Analysis of Grooming Interactions

Data (frequency, duration, direction and partner) on all grooming interactions involving the focal female were available from 1993 to 2001. Because of the very different nature of grooming data compared to association data (grooming is a dyadic activity and its recorded frequency is highly dependent on association patterns) the analysis of grooming interactions differed from that of association patterns (Socprog is designed to analyse primarily association data). A grooming interaction was only included if it lasted for at least 1 min. Mutual grooming was treated as two grooming events, one for A grooms B and one for B grooms A. As for association preferences, data were analysed on a yearly basis. To correct for dyadic association time (i.e. two partners can only be observed to groom each other when they are within the same party), we calculated grooming time as the proportion of dyadic association time (of that particular dyad) that was spent grooming. Because group size and number of available partners (variables that have been shown to affect the general amount of time committed to grooming) varied between years, we standardized grooming effort by using a z transformation (Abdi 2007) to determine preferred grooming partners. Dyads with z scores larger than 1 were termed preferred grooming partners. If the preferences persisted for at least 3 of 4 consecutive years (analogous to association preferences) the dyads were termed long-term grooming partners. For subsequent analyses, all dyadic grooming relations within a given year were coded as 0 (no preferred partners), 1 (preferred grooming partners) or 2 (long-term grooming partners). To assess whether individual females preferred the same partners for grooming and association, we used MatMan (Noldus 1998) matrix correlation analysis (2000 permutations).

Infant Age and Rank Similarity

To test whether preferences among certain dyads could be explained by the presence of similarly aged infants or by individual rank similarity, we used matrix correlation between these variables and the association and grooming matrices described above. Because the matrix correlation procedure required dyadic data, we created infant age–distance matrices in which the age of the younger infant was subtracted from the age of the older infant for each dyad (only positive distance values). If one of the dyad partners had no infant the cell remained empty.

Similarly, we used rank distance data, which we calculated by subtracting the rank of individual A from the rank of individual B. Rank distances were then expressed as positive values, so that A–B and B–A yielded the same distance values. Rank calculations were based on greeting behaviour, using data on pant-grunts and greeting-hoos available from 1994 onwards. Rank relationships were obtained directly from Lehmann & Boesch (2005) and Wittig & Boesch (2003). By using rank distances we tested only whether rank similarity determines preferences. To analyse whether high-ranking females in general had more preferred partners (or were chosen more often as a preferred partner), we counted the preferred association partners for each female year and correlated this with absolute rank, using Spearman rank correlations.

For all matrix correlations we used MatMan (Noldus 1998) with a row-wise matrix correlation with 2000 permutations. Because of differences in group composition, analyses were done separately for each year. To obtain an overall result, P values were subsequently pooled by converting all P values into z scores, which were combined using $z_{\mathrm{overall}} = \sum z_i/\sqrt{k}$, where k is the number of tests being combined (Rosenthal 1991). Correlation coefficients were combined using Fisher's z transformation (Fisher 1932). Results were considered significant only if $P < 0.05$ and $r > 0.3$ (Cohen 1988). This restriction is important as matrix correlations are known to produce significant results even though the variance accounted for by the correlation is extremely small. Thus, we used both parameters (P and r) to judge whether a result was meaningful. (Note that $r = 0.3$ explains only 9% of data variance.)

Network Structure and Group Size

The use of social network analysis allowed us to move beyond the dyadic relationship level and to compare networks derived from different behavioural measures. It further allowed assessment of how association and grooming preference networks respond to changes in group size (and hence competitive regime). Our networks were based on association and grooming matrices as calculated above and represented preferred short-term and long-term partners for association and grooming, respectively. Thus, these networks were highly filtered. We calculated three commonly used network parameters, namely density, centrality and clustering, for a time when the group was large (16 females, 1994) and when it was small (7 females, 2001). By using years far apart in time we circumvented the problem of data dependency and pseudoreplication (which is especially important as long-term preferences are by definition based on consecutive years). For that reason we only used data from 2 (far apart) years and thus comparisons between these years remain qualitative, as quantitative comparisons with only two data points are not possible.

Network density indicates the proportion of individuals with association/grooming preferences compared to the total number of preferences possible: density = number of preferences/total number of dyads. We made two estimates, one for the overall number of preferences irrespective of whether or not they were long term and one for long-term preferences only.

Network centrality indicates to what extent the existing preferences were centralized around one particular individual, that is, it provides a measure of how evenly preferences were distributed among individuals. The centrality index ranges from 0 to 100, with 0 indicating that all individuals were equally involved in preference relationships and 100 indicating that one particular (very central) individual was involved in all existing preferences (Wasserman & Faust 1994).

Finally, the network clustering coefficient was used to measure the extent to which subgroups existed within the whole group (i.e. how clustered the network was). Clustering is of interest because it highlights substructures within the network. The clustering coefficient ranges from 0 (no clustering) to 1 (maximum clustering, as in a fully connected network). To allow comparison between networks, we used the weighted clustering coefficient.

Because chimpanzees live in a fission–fusion social system and fission–fusion fluidity decreases in smaller communities (i.e. parties last longer and are generally larger: Lehmann & Boesch 2004), we hypothesized that association preferences would be less pronounced in the smaller group (all individuals spend most of their time together so that preferences as measured by party membership are less likely to arise). This should be indicated by a decrease in network density and clustering and an increase in centrality, as only a few key individuals will still show preferences. Similarly, because of the decrease in feeding competition and the fewer available grooming partners in the smaller group we expected grooming to be more evenly distributed, that is, there would be fewer preferences, as there is a decreased need for close social partners (leading to a decrease in density and clustering and an increase in centralization).

Social Bonds and Aggression

We tested the hypothesis that preferred social/grooming partners showed more tolerance for each other, that is, that these dyads engaged less often in aggressive conflicts than nonpreferred dyads. The following behaviour elements were considered to be aggressive and potentially harmful: displaying, chasing, attacking, pushing, beating and biting. Aggressive interaction rates were calculated on a yearly basis as the number of aggressive interactions between a particular dyad divided by the time this dyad was observed together in the same party, resulting in aggressive interactions per h association time. Only data from 1996 onwards were included because reliable aggression rates were not available from previous years. Two sets of analyses were carried out. First, we used a mixed-model analysis with dyadic aggression rates per year as the dependent variable, social preferences as based on associations and grooming data as fixed factors (with three levels each), and year and female identities as random factors, thereby controlling for female identity and avoiding the risk of pseudoreplication. Comparisons between categories were carried out using a least significant difference (LSD) post hoc test. However, because aggression in female chimpanzees is rare, the dyadic data were skewed and deviated from a normal distribution. Although mixed models are relatively robust against such deviations we also carried out a nonparametric analysis in which we used average yearly aggression rates per preference class (nonpreferred, preferred or long-term partner in grooming and association), resulting in an average yearly aggression rate for each of the three categories. Aggression rates between categories were compared across years using a Kruskal–Wallis test; for post hoc tests we used a Mann–Whitney U test. Because post hoc tests were carried out only when a significant overall effect was found and were used to test the specific hypothesis that social preferences reduce aggression rates, we used one-tailed statistics. Because some females were the preferred partner of several other females, individual females were represented unevenly across preference categories (appearing in 0–3 dyads for preference and long-term categories). In a strict statistical sense these females may bias the results; however, because we were interested in predictors of social bonds, and hence whether particular females were avoided or chosen as preferred partners because they were more or less aggressive than others, the results are still meaningful and interesting.

Statistics

All statistical tests, unless otherwise stated, were two-tailed with a significance level at $P < 0.05$ and were carried out using SPSS for Windows release 11.0.1 (SPSS Inc., Chicago, IL, U.S.A.). Ucinet (Borgatti et al. 2002) was used for network analyses, Socprog in combination with MatLab 7.2 (MathWorks, Natick, MA, U.S.A.) was used to determine association preferences and MatMan (Noldus 1998) was used for matrix correlation analyses. Analysing longitudinal social interaction data will in some cases increase the risk of pseudoreplication. We minimized this risk by using randomization tests and yearly individual averages, so that for most analyses females contributed the same amount of data to each analysis. In cases where pseudoreplication could not be avoided (see above) we made a special effort to ensure that results were not due to a few individuals only.

RESULTS

Association Preferences

Overall, significantly more dyads than expected by chance showed association preferences (Mann–Whitney U test: $z = -3.8$, $N_1 = N_2 = 11$, $P < 0.0001$), indicating that chimpanzee females did not simply associate at random but preferred particular partners (Table 1). On average (averaged across all years), only 14% of all possible dyads associated preferentially. Figure 1 depicts all females

Table 1
Association and grooming preferences across years

Year	Females in group	Association				Grooming			
		Possible dyads	Preferred dyads	Females with preferred partner	Females with long-term partner	Possible dyads	Preferred dyads	Females with preferred partner	Females with long-term partner
1992	16	120	10	10	7	240			
1993	16	120	15	15	10	240	69	16	0
1994	16	120	17	12	13	240	76	16	4
1995	12	66	13	10	9	132	40	12	3
1996	12	66	9	12	9	132	45	12	5
1997	11	55	8	10	6	110	37	11	5
1998	11	55	10	10	10	110	37	11	3
1999	11	55	8	10	7	110	31	11	3
2000	7	21	4	6	4	42	19	7	0
2001	7	21	5	6	5	42	10	7	0
2002	6	15	2	4	2	30			

Counts of adult females within the group, the number of possible dyads, the number of dyads preferring each other and counts of females with preferred and with long-term association and grooming partners are shown. In the case of grooming, twice as many dyads are possible because grooming is a directional activity while association preferences are by definition symmetrical.

and their preferred long-term association partners over the duration of the study. Thus, it indicates on a year to year basis those dyads that associated preferentially for at least 3 of 4 consecutive years, the overall duration of this preference and whether or not this preference was ended by the death or disappearance of the preferred partner. The majority of all adult females (84%) had at least one preferred partner and most of these preferences (78%) were maintained for at least 3 of 4 consecutive years (Fig. 1). In most cases (86%) long-term association dyads ended by the death or disappearance of one of the partners (Fig. 1).

Grooming Preferences

Results are summarized in Table 1 while Fig. 2 depicts all females and their preferred long-term grooming partners over the duration of the study. Thus, it indicates which dyads showed consistent grooming preferences for at least 3 of 4 years, the overall duration of this preference and whether or not this preference was ended by the death or disappearance of the preferred partner. Grooming was biased towards a specific partner in 31% of all possible dyads and all females showed a preference for a specific partner within a year. However, only 22% of all females maintained their preferences for at least 3 of 4 or more consecutive years, and only 5% of all possible dyads were classified as a long-term grooming partner (Fig. 2). Of these long-term relations 57% were ended by the death of one of the partners (Fig. 2). Thus, in contrast to association patterns, long-term grooming partner preferences were much less frequent and of shorter duration.

The correlation between grooming and association preferences was extremely weak within and across years (see Table 2 for results of matrix correlations; although the combined P value is less than 0.05, the correlation coefficient is extremely low), indicating that females did not groom preferentially those individuals with which they associated preferentially.

Rank Similarity and Infant Age

Table 2 gives the matrix correlation results within and across years. Neither rank similarity nor the presence of similarly aged infants significantly explained partner preferences (although the relationship between grooming preferences and rank reached a combined P value of less than 0.05, the combined correlation coefficient is too small to be regarded as biologically meaningful). In addition, there was no significant correlation between absolute rank and the number of association and grooming partners (see Table 3 for statistical values), indicating that high-ranking individuals were not generally preferred as social partners.

Preference Networks and Group Size

Figure 3 depicts an example of the preference (as defined above) sociogram of adult female chimpanzees for a year in which the group was fairly large (16 adult females) and for a year in which the group was much smaller (7 females). Even though no female appeared to be truly isolated on a dyadic level, most dyads were actually unconnected (because grooming is a directed activity the maximum number of grooming dyads is twice as high as for association preferences). Very few of the preferences for grooming and association overlapped but, when both networks were combined, almost all individuals were interconnected, thereby representing a close social group. Table 4 gives network density, centrality and clustering indices for the 2 years. Network analysis allowed us to compare grooming and association networks with each other as well as to assess the effects of group size on these networks. This analysis moves beyond the dyadic level (as used above) by assessing the effects of dyadic relationships on overall social structure. The results closely mirror the results from the dyadic level. The association and grooming preference networks were almost identical in the large group (1994): both networks showed low levels of density (only 12–13% of all possible relations existed) and medium levels of centrality (26 and 33, respectively). In contrast to association, grooming preferences were directional (Bel groomed Ven preferentially but Ven did not prefer Bel, preferring Per instead) and therefore the maximum number of possible dyadic relations was much higher than in the association network. Because of this, the network density was almost identical, although there seem to be many more connecting lines in the grooming sociogram. The low level of centrality means that neither association nor grooming preferences centred on a few key individuals but involved almost all of the group members. This further supports the notion that high-ranking females were not overall preferred association or grooming partners in this group, which is in line with the fact that there was no significant correlation between rank and individual degree centrality values (Spearman rank correlation: $r_S = 0.29$, $N = 12$, $P > 0.3$). However, association networks appeared much more clustered than grooming networks (0.52 versus 0.15), supporting our view that association preferences lead to small subgroups (e.g. the trio of Mys–Pou–Bij and Her–Ven–Fos) in the network that are not necessarily connected to other individuals, whereas the grooming network appeared much more interconnected, integrating the group as a whole (see also Fig. 3). Grooming and association networks also differed when we only considered long-term preferences; in that case association networks were much more dense than grooming networks,

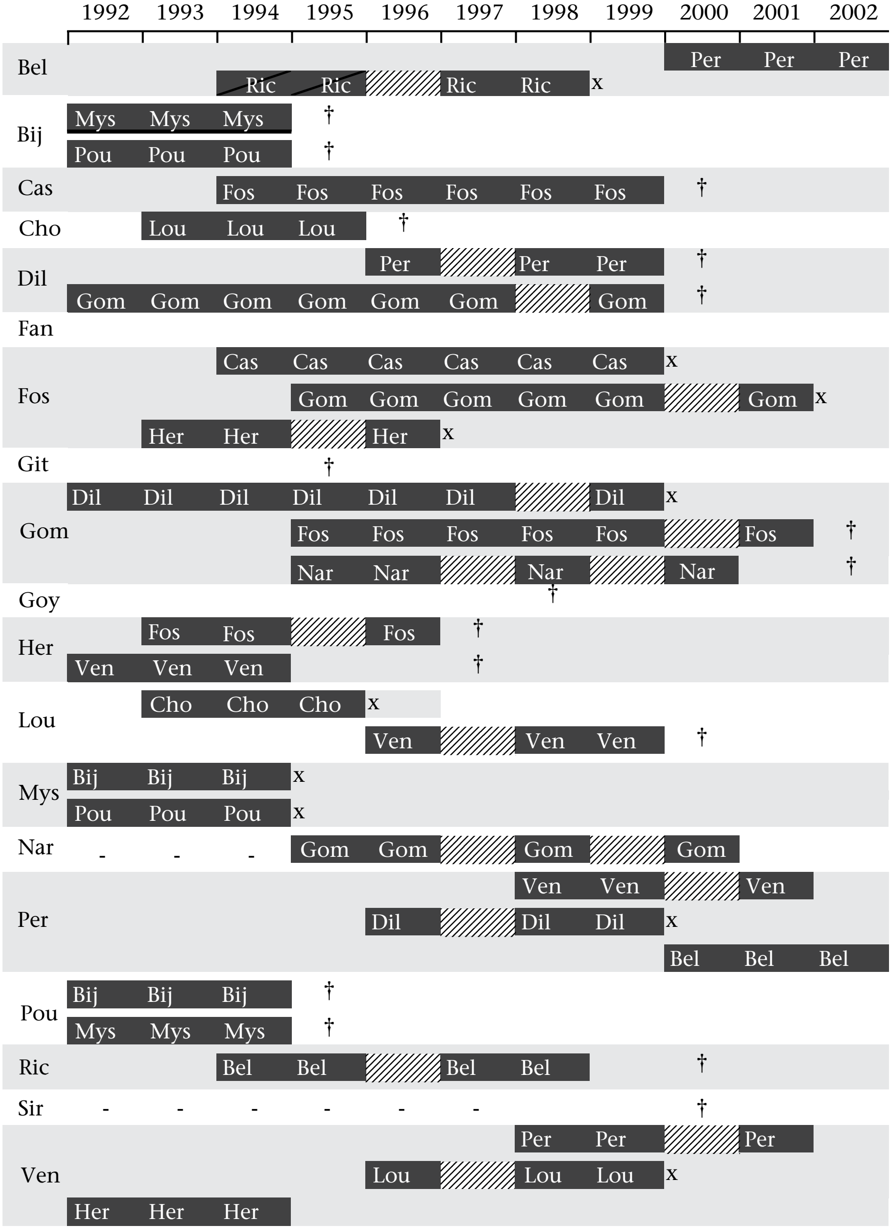

Figure 1. Preferred long-term associations in adult female chimpanzees. Three-letter codes identify individual adult females (rows); black bars indicate long-term association partners for the respective years; hatched bars indicate years during which association data with a previously preferred partner did not reach significance. X indicates the death or emigration of the partner; † indicates the death or emigration of the individual (row); Sir did not reach adulthood until 1998 and therefore was not included in the data set before 1998.

mirroring the finding that association preferences were much more likely to last over many years than were grooming preferences.

The decrease in group size appeared to affect grooming and association preference networks differently. Contrary to our predictions, association preferences became more pronounced in the smaller group (medium-term as well as long-term preferences), as reflected by the increase in network density. On the other hand, grooming network density remained stable (including all preferences) or decreased (in the case of long-term preferences). In contrast to the network from 1994, the centrality index was much higher for both networks, indicating that a large proportion of these relations were centred on a few key individuals, such as Per (association network) and Bel (grooming network). Exclusive subgroupings above the dyad level, however, no longer existed (the clustering coefficient was 0 for both networks).

This analysis highlights the fact that association preferences were more likely than grooming preferences to persist for several years. The fact that both association and grooming tended to be more centralized and less clustered in smaller communities probably reflects a decrease in partner choice and the increase in spatial cohesion, which makes exclusive subgroupings more difficult (at least in the case of association preferences). In addition, the results suggest that (1) a differentiated social structure exists between chimpanzee females (irrespective of group size) and (2) group size (and therefore competitive regime) has a strong effect on the nature of the social structure.

Potential Benefits of Social Bonds

Overall aggression rates between females were low with, on average, one aggressive interaction between females every 60 h of

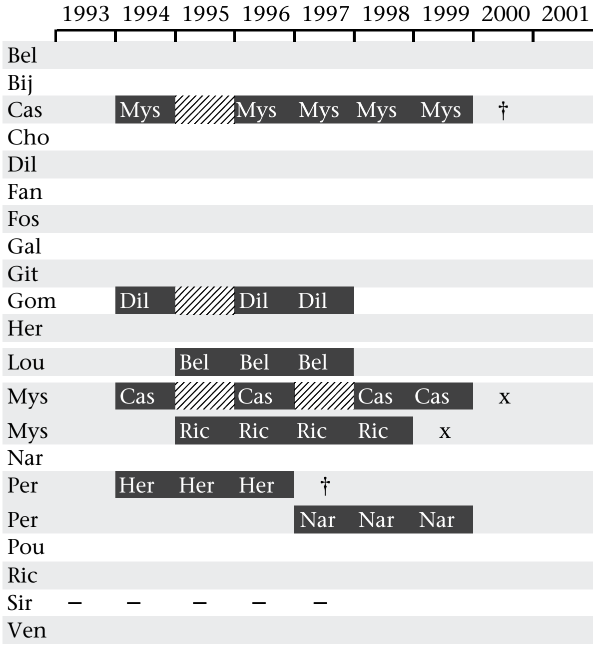

Figure 2. Long-term grooming relationships of adult female chimpanzees. Three-letter codes identify individual adult females (rows); black bars indicate long-term grooming partners for the respective years; hatched bars indicate years during which a previously preferred partner did not reach criterion. X indicates the death or emigration of the partner; † indicates the death or emigration of the individual (row); Sir did not reach adulthood until 1998 and therefore was not included in the data set before 1998.

observation. Figure 4 depicts average aggression rates between nonpreferred, preferred and long-term association and grooming partners. The mixed-model analysis revealed that aggression rates were not significantly different between grooming preference categories ($F_{2/495.4} = 1.84$, $P > 0.15$), while association preferences were marginally significant ($F_{2/503.1} = 2.98$, $P < 0.053$). Post hoc comparisons of association preferences indicated that aggression rates were significantly lower in preferred association partners than in nonpreferred dyads ($df = 496.97$, $P < 0.05$), while long-term preference partners did not differ significantly from either of the other two categories ($df = 505.5$, all $P > 0.12$). Using the nonparametric approach, we found very similar results, that is, there was a significant overall effect of association partners (Kruskal–Wallis chi-square test: $\chi^2_2 = 6.8$, $N = 18$ (6 years with 3 categories each), $P < 0.05$); no such effect was found for preferences based on grooming data ($\chi^2_2 = 3.9$, $N = 18$, $P > 0.1$). Post hoc analyses on association data indicated significantly lower aggression rates in preferred than nonpreferred partners (Mann–Whitney U test: $Z = -2.3$, $N_1 = N_2 = 12$, exact $P = 0.011$), while the reduction in aggression rates in preferred long-term partners was marginally significant ($Z = -1.6$, $N_1 = N_2 = 12$, exact $P = 0.054$). Preferred and long-term association partners did not differ significantly in their aggression rates ($Z = -0.8$, $N_1 = N_2 = 12$, $P > 0.2$).

Table 3
Spearman correlations between absolute rank of individual females and the total number of association and grooming partners

	Association		Grooming given		Grooming received	
	r_S	*P*	r_S	*P*	r_S	*P*
1994	−0.10	0.79	−0.15	0.64	0.23	0.36
1995	−0.18	0.57	0.01	0.97	0.31	0.33
1996	−0.19	0.56	0.32	0.30	0.26	0.41
1997	0.27	0.42	0.15	0.65	0.36	0.28
1998	0.07	0.85	*−0.53*	*0.09*	**−0.72**	**0.01**
1999	0.29	0.39	*−0.59*	*0.07*	−0.11	0.75
2000	0.59	0.17	0.10	0.83	0	1
2001	0.06	0.91	−0.46	0.36	—	—
Combined	0.11	0.77	−0.16	0.48	0.02	0.11

Bold type indicates significant, and italics near-significant, correlations.

Thus, both sets of analyses indicate that aggression rates may be reduced in preferred association partners but not between preferred grooming partners.

DISCUSSION

Our findings are among the first to demonstrate strong and long-lasting preferences for specific partners in adult chimpanzee females, using two behavioural measures: grooming and association patterns. While female preferences for same-sex association partners were maintained over many years and were independent of rank and presence or age of infants, existing preferences for grooming partners were of a less long-lasting nature. The fact that both types of preferences were affected by demographic conditions (but not to the same extent) is likely to reflect different kinds of social investment for various purposes.

Grooming and Association

Social investment can take different forms and is likely to fulfil more than one function. In many primate studies, grooming and association preferences are used to quantify social bonds between individuals, assuming that both variables are measures of a similar

Table 2
Matrix correlation results and combined *P* values across years

	Association preferences with				Grooming preferences with				Association with grooming	
	Infant		Rank		Infant		Rank			
	Tau	*P*	Tau	*P*	Tau	*P*	Tau	*P*	Tau	*P*
1992	−0.03	0.65	—	—	—	—	—	—	—	—
1993	−0.02	0.65	—	—	−0.06	0.86	—	—	0.01	0.41
1994	−0.02	0.6	0.02	0.44	−0.07	0.91	0.08	0.22	0.13	0.06
1995	−0.26	0.98	0.05	0.33	0.003	0.5	0.07	0.19	0.01	0.45
1996	0.08	0.78	−0.04	0.65	−0.1	0.86	0.11	0.12	0.13	0.12
1997	−0.2	0.97	0.07	0.27	0.04	0.3	0.07	0.2	0.03	0.38
1998	−0.07	0.75	−0.01	0.56	−0.11	0.88	−0.08	0.19	0.07	0.25
1999	−0.04	0.66	−0.08	0.76	0.11	0.11	−0.01	0.58	0.1	0.22
2000	−0.11	0.76	−0.11	0.72	0.17	0.19	0.1	0.33	0.16	0.25
2001	−0.03	0.56	−0.31	0.95	0.04	0.44	0.03	0.51	−0.06	0.6
2002	−0.07	0.42	0	0.6	—	—	—	—	—	—
Combined	−0.071	0.99	−0.047	0.8	0.003	0.73	*0.046*	*0.046*	*0.065*	*0.04*

The first two lines indicate the matrices used for the row-wise matrix correlation (2000 permutations). ‘Infant’ indicates the presence of similarly aged infants and ‘rank’ indicates rank similarity. The two significant combined *P* values (in italics) have a very low correlation coefficient and are therefore not regarded as biologically meaningful.

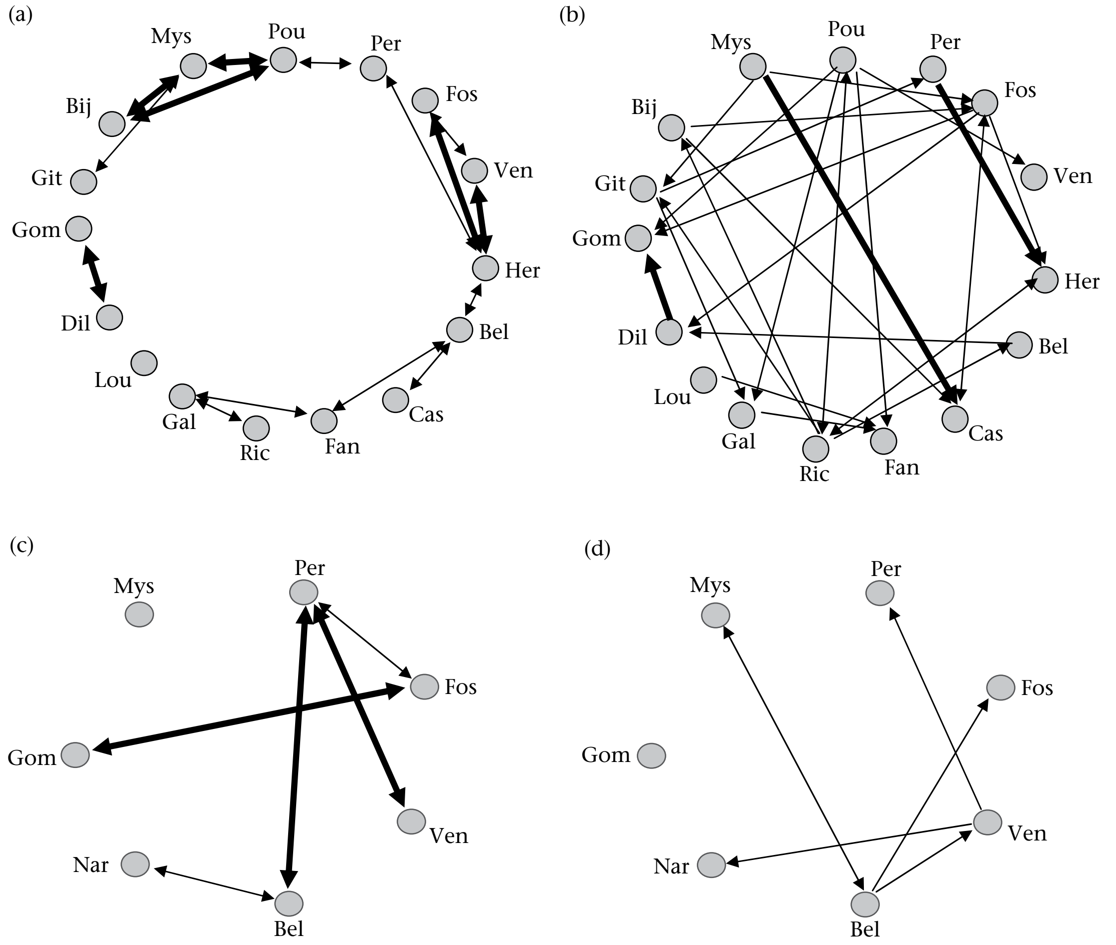

Figure 3. Social preference networks based on (a, c) association preferences and (b, d) grooming preferences for (a, b) 1994, when there were 16 females in the group and (c, d) 2001, when the number of females was reduced to seven. Lines indicate significantly preferred association and grooming partners; bold lines indicate long-term preferences (as defined in the text).

preference (Silk et al. 2006a, b). In our study, preferred grooming and association partners were not correlated and grooming preferences explained less than 1% of the variation in association preferences in chimpanzee females, suggesting that these two behaviours serve different social strategies: while association preferences seem to guarantee more tolerance and coalition partners (as also shown by Boesch & Boesch-Achermann 2000), grooming preferences, which are much more flexible and shorter lived, may reflect shorter-term goals (see Barrett & Henzi 2002 for a similar finding in baboons). Grooming in chimpanzees may also be used to repair relationships after conflicts (Judge et al. 2006) or to re-establish bonds after periods of absence, so that overall group cohesion can be maintained (Dunbar 1991; Lehmann et al. 2007). However, while grooming interactions appear to reflect true partner choice, association preferences are more difficult to interpret as they can also arise through passive means, such as preferences for particular locations (Wolf & Trillmich 2008). In some chimpanzee populations, females have been reported to occupy specific core areas, thereby forming so-called spatial neighbourhoods (Thompson et al. 2007), which in turn could lead to environmentally driven association preferences. However, in Taï all females use the entire home range evenly and do not form distinct spatial neighbourhoods (Lehmann & Boesch 2005). In addition, because of the fluidity of the chimpanzee social system, in which party size and composition change frequently, females have ample opportunities to choose association partners and male ranging patterns are unlikely to determine female association preferences, especially as there were very few males in this particular group. Thus, we are confident that association preferences as found in this study do indeed reflect social preferences, rather than being a mere by-product of ranging patterns, and are different from grooming preferences.

Possible Benefits of Social Bonds

Although alliances and strong social bonds between females occur in many mammalian species (e.g. Moss & Poole 1983; Smuts 1987; Perry 1996; Holekamp et al. 1997; Weckerly 1999; Newton-Fisher 2006), it often remains unclear exactly what benefits females gain from such relationships, especially when bonds are formed between unrelated individuals. For chimpanzees, having a stable social network that helps to reduce competition might be especially important because they live in a fission–fusion social system where most association partners change frequently and the potential for conflicts is high (Aureli & Schaffner 2007). Our results on reduced aggression rates between preferred association partners suggest that social preferences may be used to reduce conflicts, although cause and effect remain unclear in our study, that is, it may also be the case that females chose to associate with partners with whom conflict was minimal. Some females were the preferred partner of several others (Figs 1, 2) and it could be that these preferences are driven by the fact that particular females are generally less aggressive than others and hence are highly 'valuable' partners. However, in such a scenario one would expect that these females

Table 4
Female preference network parameters for a large (1994) and a small (2001) chimpanzee group

	Association		Grooming	
	1994	2001	1994	2001
Network density				
All preferences	0.125	0.24	0.138	0.14
Long-term only	0.05	0.14	0.016	0
Centrality degree	25.7	63.3	33.3	53.3
Clustering coefficient	0.52	0	0.15	0

Networks are based on preferences (as described in the text). Directional grooming networks were transformed into symmetric matrices for the calculation of centrality degree (so that one value rather than separate values for grooming given and grooming received was obtained). The clustering coefficient was weighted to allow comparison between years.

should be preferred by all other females, which is in contrast to the biased distribution of preferences we found here.

Chimpanzee females may further benefit from stable association networks by an enhanced chance of offspring survival if they die (e.g. through adoption; most of the observed cases of adoption in Taï chimpanzees by adult group members occurred between highly preferred association partners; C. Boesch, personal observation). In addition, the availability of close friends may help individuals to reduce stress levels during periods of instability, as observed in baboons, *Papio hamadryas ursinus* (Engh et al. 2006). Undoubtedly, the ultimate measure of the benefits of social bonds would be reproductive success, as used by Silk et al. (2003) for baboons, *Papio cynocephalus*. However, our results do not allow us to classify females as more or less social (because almost all females had preferred partners over the course of the study); therefore, we cannot compare individual reproductive success with sociality in this case. More detailed analyses of females' social preferences are needed to be able to deduct what quality (number and duration of bonds, intensity, overlap between grooming and association) of social bonds it is that makes a female more or less reproductively successful.

In many species the sexes differ in the extent to which social bonds are formed, reflecting sex-specific priorities: for males, gaining access to mates, for females, access to food resources. Chimpanzee females live in a relatively stable social environment (with regard to same-sex partners), so that establishing long-term alliances may actually be beneficial. On the other hand, males live in a less stable social environment (with respect to same-sex social partners), as males' hierarchies change every couple of years, and hence males may have to adjust their alliances accordingly to the new situation. Thus, sex differences in sociality may reflect this and may be a consequence of the stability of the social environment.

Female Bonds and Competition

Previous studies on female chimpanzee sociality have indicated that at some sites female chimpanzees are rather asocial and do not interact frequently (Kawanaka 1984; Goodall 1986; Wrangham et al. 1992; Williams et al. 2002). Our results, on the other hand, indicate that chimpanzee females have distinct and sometimes long-lasting social bonds. This discrepancy between findings from various sites may be caused by a variety of factors. First, female social relationships have rarely been studied at any length, as most studies have concentrated on the behaviour of the philopatric males. Second, the extent to which social bonds are expected to occur depends on the competitive regime within the group, so that competition rather than kin relationships is the main predictor of female social bonds. Unfortunately, no quantitative data on female competition for different study sites are available, so we do not know to what extent differences in competitive regimes are responsible for the observed differences in female sociality. However, several lines of evidence suggest that Tai chimpanzee females experience relatively strong contest competition (Wittig & Boesch 2003): they have a strictly linear dominance hierarchy (Wittig & Boesch 2003; Lehmann & Boesch 2005) and dominance is a reliable predictor of the outcome of contest competition (Wittig & Boesch 2003). Although stable female dominance hierarchies have now been reported from most other sites (e.g. Goodall 1986; Nishida 1989; Wrangham et al. 1992; Pusey et al. 1997; Fawcett 2000), they were not always found to be linear, which might suggest lower levels of competition than in Taï. Competition between females in Taï may be further increased by the comparatively high levels of predation pressure, forcing females to spend most of their time in parties with other females (Boesch 1991; Lehmann & Boesch 2008), while at other sites females have been described as relatively solitary (Kawanaka 1984; Goodall 1986; Wrangham et al. 1992; Williams et al. 2002). Thus, social alliances and coalitions may be relatively more important for Tai chimpanzee females than for females at sites with less competition.

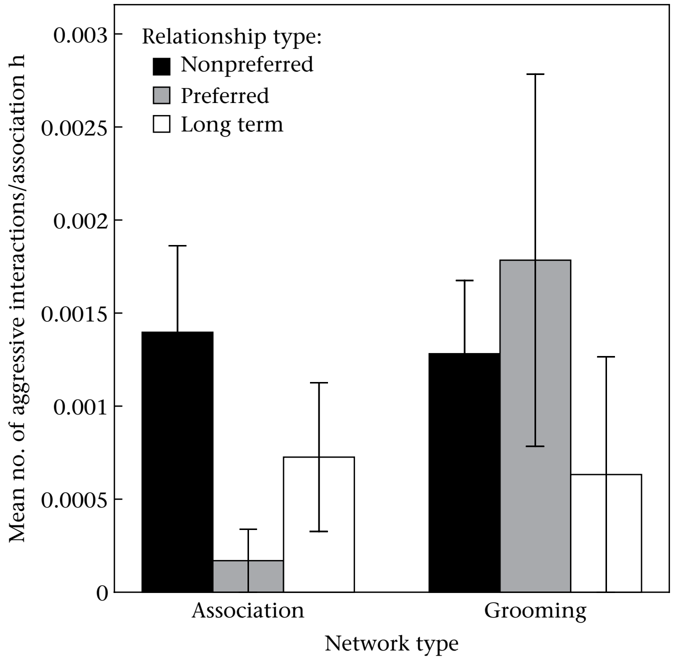

Figure 4. Aggression rates ($\overline{X} \pm \text{SE}$) between nonpreferred, preferred and long-term partners. Classifications of dyadic relationship types are based on association and grooming networks, respectively (see text for details).

Another line of evidence supporting the suggested effect of competition on social relationships comes from our finding that social networks were affected by demographic conditions within the group. In the smaller group, competition was generally expected to be reduced (especially as home range size did not decrease to the expected extent when group size decreased; Lehmann & Boesch 2003), which should result in fewer social interactions, as there is less need for coalitions. In addition, fission–fusion fluidity decreased when the group became smaller (Lehmann & Boesch 2004). Thus, preferences were expected to become less important (or less detectable because all individuals spend more time together in the same party), resulting in a more centralized and less clustered social network in which the existing social relationships are centred around a few individuals without the formation of exclusive subgroups (as most individuals will be together most of the time). This is precisely what we found: chimpanzee females' social interactions were more centralized when the group was small (Table 4), while subgroupings (clusters) only occurred in the large group and were more frequently found in association patterns (see also Fig. 3 where Mys, Bij and Pou form an association subgroup). The finding that small communities showed no clustering in association preferences at all may, however, be an artefact: if group cohesion increases in small communities, we would expect to see most individuals of the group in the same party, so that preferences, even though they may exist, would not be detected by simply looking at party compositions. On the other hand, when competition is low females are expected to show less skew in the distribution of their social interactions (see also Silk et al. 1999). However, our results show that network density (i.e. the percentage of preferred dyads compared to all possible dyads) increased in the small group, indicating that relatively more association preferences existed than when the group was much larger. This might be because such long-lasting preferences are maintained (once established), irrespective of changes in competitive regime. Alternatively, the level of competition (local or global) may be important for the formation of social bonds, as it has been shown in humans that high local resource competition can actually select against cooperation (West et al. 2006). More data on primate social networks and the effects of competition and group size on social interactions are needed to understand fully the dynamics of social investment in primate groups and the effects of demography on social networks.

Conclusion

We found that chimpanzee females form strong and long-lasting social bonds with other females, even in the absence of closely related partners. Furthermore, our results suggest that different kinds of social investment are used to pursue different goals: long-lasting association preferences as found in Taï chimpanzee females may be used to decrease competition by creating tolerance towards certain individuals and may reduce the potential for aggressive interactions. Grooming preferences, on the other hand, may be used in a more flexible way to reach short-term goals and/or as a means to re-establish relations either after long periods of absence of one partner or after conflict situations. We further suggest that such context-specific social investments are not only restricted to chimpanzees but are expected to occur generally in primates, especially in species that are long lived and where dispersal occurs only once in a lifetime. In such species we therefore expect that sex differences in sociality will be much less pronounced than previously hypothesized.

Acknowledgments

We thank the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales and the directors of the Taï National Park of the Côte d'Ivoire for permitting the research in the Taï National Park. We are grateful for the support provided by the Centre Suisse in Abidjan. For financial support we thank the Fonds National Suisse de Recherche Scientifique and the Max Planck Society. We also thank the field assistants Grégoire Kohou Nohon and Honora Néné Kpazahi who collected the data. Finally, we thank Stuart Semple and James Higham for their critical comments on the manuscript.

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