

Male–female socio-spatial relationships and reproduction in wild chimpanzees

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Abstract Recent research on primates and other taxa has shown that the relationships individuals form with members of the same sex affect their reproductive success. Evidence showing that intersexual relationships also influence reproduction, however, is more equivocal. Here, we show that male chimpanzees living in an exceptionally large community display long-term tendencies to associate with particular females. These association patterns are likely to arise because individuals of both sexes selectively range in specific areas of the communal territory, with males inheriting the ranging patterns of their mothers. These differentiated male–female socio-spatial relationships involved males of widely varying ranks, and their effect on reproduction is as strong as that of male dominance rank, which in turn is as strong a predictor of reproductive success at Ngogo as in other smaller chimpanzee communities. These results show that male–female socio-spatial relationships can play a large role in chimpanzee male reproductive strategies, although they probably neither weaken nor strengthen the relationship between male dominance rank and reproductive success. Our results linking male–female socio-spatial relationships to reproduction in chimpanzees suggest that the gap between the

social and mating systems of humans and their closest living relatives may not be as large as previously thought.

Keywords Chimpanzees · *Pan troglodytes* · Reproductive success · Dominance rank · Social relationships · Paternity

Behavioral ecological theory predicts that the distribution of females is primarily determined by the risks and resources in the environment, whereas the distribution of males is determined by the spatiotemporal dispersion of females (Emlen and Oring 1977). Whenever females form social units that are small enough to be defended by single males, males should try to monopolize female reproduction via the exclusion of rivals (Kappeler 1999). However, when females are dispersed such that the exclusion of other males is impossible, males compete for mating opportunities with fertile females in multi-male, multi-female groups (Kappeler 1999). This competition manifests itself in the formation of male dominance hierarchies, which, to a large extent, reflect individual differences in fighting abilities (Clutton-Brock 1988). As a result, mating is skewed, with higher-ranking males producing more offspring than lower-ranking males. There is considerable variation among and within species, however, in the extent to which male dominance rank predicts reproductive success, particularly in primates (Dewsbury 1982; Cowlshaw and Dunbar 1991; Ellis 1995; Alberts 2012).

The best-supported source of variation in the relationship between male dominance rank and reproductive success is male density (Alberts 2012). Studies of animals in a wide variety of social and mating systems have shown that the reproductive success of high-ranking male decreases as the number of male competitors increases (e.g., seasonally breeding, polygynandrous common lizards *Lacerta vivipara*: Fitze and Le Galliard 2008; lekking birds and mammals: Kokko et al. 1998; stable, multi-male/multi-female groups of primates: Cowlshaw and Dunbar 1991; Kutsukake and Nunn 2006; Ostner et al. 2008). As would

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be expected if the intensity of sexual selection on male fighting ability is relaxed when high rank results in fewer reproductive benefits, male–male aggression often decreases as the number of male competitors increases (Jirotkul 1999; Mills and Reynolds 2003; Weir et al. 2011). This phenomenon has been attributed to a decrease in the economic defendability of females when many competitors are present, leading to a shift from contest to other forms of male–male mating competition (Brown 1964; Emlen and Oring 1977).

Thus, instead of (or in addition to) fighting with one another, males living alongside a large number of competitors may employ other tactics to gain access to females (e.g., kleptogamy in red deer *Cervus elaphus*: Pemberton et al. 1992; coursing in bighorn sheep *Ovis canadensis*: Hogg 1987). In some mammalian species, including horses, dolphins, elephants, and primates, individuals live in social groups that differ from those in most other mammalian species in their high degree of cohesiveness and long-term stability (Dunbar 2012). In such groups, individuals have the opportunity to develop long-lasting social relationships with individually recognized group members based on repeated interactions (Hinde 1976; Mitani et al. 2012). There is good evidence that social relationships between males can influence male mating or paternity success (Indo-Pacific bottlenose dolphins *Tursiops aduncus*: Wiszniewski et al. 2012), weakening the relationship between male dominance rank and reproduction when social relationships are formed between low-ranking males (baboons *Papio cynocephalus*: Alberts et al. 2003) and strengthening it when they are formed between high-ranking males (chimpanzees *Pan troglodytes*: Watts 1998; Duffy et al. 2007; Assamese macaques *Macaca assamensis*: Schülke et al. 2010). There is less evidence, however, that social relationships between males and females influence reproduction and serve as a source of variation in the relationship between male dominance rank and reproductive success.

Most research linking variation in male–female social relationships and reproduction has focused on affiliative interactions. In many cercopithecine primates, specific pairs of males and females form “friendships” or “peculiar proximate relationships” characterized by elevated rates of close spatial proximity and grooming outside the female’s fertile period (Seyfarth 1978; Altmann 1980; Takahata 1982; Smuts 1985; Chapais 1986; Paul et al. 1996). The mating effort hypothesis proposes that a male forms a friendship with a particular female when she is pregnant or lactating because this makes it more likely that she will choose him as a mating partner in the future (Seyfarth 1978). This hypothesis was supported by early research on baboons which showed that males had higher than expected future mating success with their female friends (Smuts 1985). In contrast, subsequent research that employed paternity analyses rather than observations of mating showed that male–female

friendships reflect past rather than future reproduction. These data suggest that friendships reflect parenting rather than mating effort (Palombit et al. 1997; Moscovice et al. 2009; Nguyen et al. 2009; Huchard et al. 2010, 2013). Observations of wild chimpanzees indicated that females mated more frequently with males who, over a period of 22 months, shared meat with them outside of their estrous periods than with males who did not share meat with them (Gomes and Boesch 2009). Because this study did not examine the temporal relation between sharing and mating, it was not possible to determine whether sharing increased the chances of future mating, mating increased the future chances of sharing, or both. In addition, no data on paternity outcomes were provided. To date, the only study linking affiliative relationships among males and females to future reproduction in a free-ranging population was conducted on rhesus macaques (*Macaca mulatta*) whose group sizes were unusually large due to the provisioning of food (Kulik et al. 2012; see Massen et al. 2012 for a study on captive rhesus).

Social relationships between males and females do not necessarily need to be based on affiliative interactions to influence the probability of future reproduction. Scramble competition among males, which selects for traits that allow them to successfully monitor and locate fecundable females, is important in many anurans (Wells 1977), invertebrates (Thornhill and Alcock 1983), and some solitary mammals (Schwagmeyer 1988), but has received little attention in species that live in permanent multi-male/multi-female groups. This is presumably because in most such groups, males are in constant association with females, making the tracking of their reproductive condition a relatively easy task. However, this is not the case in fission–fusion societies, where all group members are rarely, if ever, found in the same place at the same time but instead associate in parties that vary in size, composition, and duration. In fission–fusion societies, a male may spend time with a female not because it allows him more opportunities to perform affiliative behaviors that make it more likely that she chooses him as a mating partner but simply because spending more time with her permits him to effectively monitor her reproductive state and predict when she will become fecundable. Such a mechanism may explain why, among Galapagos sea lions (*Zalophus wollebaeki*), whose breeding seasons are unusually long for pinnipeds, a male’s reproductive success is better predicted by the length of his attendance in the female breeding colony than by his dominance rank/fighting ability despite the fact that males and females do not engage in affiliative behaviors with one another such as allogrooming (Pörschmann et al. 2010).

Male–female relationships can also influence future reproduction through sexual coercion. A growing body of evidence suggests that sexual coercion plays an important role in male mating success (Smuts and Smuts 1993; Muller

and Wrangham 2009). For example, in the fission–fusion societies of chimpanzees, an individual male may attempt to sequester an estrous female in a sexual consortship, where he may maintain exclusive sexual access to her for up to several weeks, thus resulting in a high probability of successful reproduction (Constable et al. 2001). While male–female rates of grooming are elevated during consortships and early observations described females as equally interested in initiating and maintaining them (Tutin 1979), later work revealed that males use aggression to encourage female consort participation (Goodall 1986). In addition, the link between aggression and mating in chimpanzees extends to other contexts in which mating occurs, with males having the highest mating success with those females to whom they direct the most aggression when the females are cycling (Muller et al. 2010). Whether males have higher future mating success with the females that they are the most aggressive to outside of the cycling period (i.e., during pregnancy and lactation), and thus the extent to which aggression in the context of a long-term, differentiated social relationship influences reproduction, has not yet been investigated. This possibility is suggested, however, by the finding that even among lactating and pregnant females, those that are the most sexually attractive (i.e., older, multiparous females) receive the highest levels of male aggression (Muller et al. 2006). Paralleling the combination of affiliative and aggressive behaviors that males direct toward females during consortships, these older, multiparous females also receive the highest levels of grooming (Proctor et al. 2011).

In sum, currently available data suggest that male–female social relationships can influence reproduction because a male is more likely to mate with a female that he (1) is more affiliative toward because she chooses him as a mating partner, (2) spends more time with because of success in scramble competition, (3) is more aggressive toward because she is sexually coerced by him, or through a mixture of all three. Regardless of the details of the process through which male–female relationships influence reproduction, the pair must spend time together so that successive interactions can occur. In this regard, chimpanzees are an excellent species in which to study the influence of social relationships between the sexes on male reproduction. First, due to strict male philopatry, the absence of secondary transfer by females, and unusually long life spans, a male can live in the same group as a female for her entire reproductive career, which can span up to ≈ 35 years (Langergraber et al. 2012). Second, because their fission–fusion social system allows individuals to make decisions about who to spend time with and who to avoid, the variation among male–female dyads in how much time they spend together should be much higher in chimpanzees than in other species with less flexible social systems (van Schaik and Aureli 2000; Machanda 2009).

While male chimpanzees are well known for their tendencies to associate with certain males over others, recent research suggests that some pairs of males and females also frequently associate (Machanda 2009). Additional research suggests that this tendency for certain male–female dyads to frequently associate may arise, in part, because chimpanzees, especially females, disproportionately concentrate their activities in relatively small fractions of their community's territory (Newton-Fisher 2002; Emery Thompson et al. 2007; Murray et al. 2007a, b; Gilby and Wrangham 2008; Langergraber et al. 2009; Machanda 2009). Previous research in one chimpanzee community showed that when alone during food-poor times, adult male chimpanzees tended to range mostly in the area of their territory where they lived with their mother when immature and suggested that, similar to females, this selective ranging probably occurred because greater long-term familiarity with the distribution of food in a smaller area resulted in greater foraging efficiency (Murray et al. 2007a). Nonrandom patterns of movement can have important consequences for mating and reproduction, for if males selectively range in the same area of the territory as their mothers do (or did), then they may frequently associate in parties, and potentially reproduce, with unrelated females who also selectively use these same areas (Wakefield 2008; Langergraber et al. 2009).

In this paper, we investigate male–female socio-spatial relationships and reproduction in the unusually large Ngogo community of chimpanzees in Kibale National Park, Uganda. In the first stage of our analysis, we examine party associations within and between the sexes and how variations in association between males and females may develop out of male inheritance of maternal ranging patterns. We then ask whether males and females who preferentially associate in the same areas of the territory also frequently reproduce. In our first “time-insensitive” analysis, we examine male–female socio-spatial relationships and reproduction over the whole 13-year time period for which we have data on conceptions. In a second “mating effort” analysis, we investigate male–female socio-spatial relationships and future reproduction. In a third “potential parenting effort” analysis, we examine male–female socio-spatial relationships and past reproduction. To determine the relative importance of male–female socio-spatial relationships on reproduction, we simultaneously analyze the effects of male dominance rank at time of conception on the probability of paternity and compare the strength of the relationship between dominance rank and paternity success at Ngogo with previous reports in other smaller chimpanzee communities. We conclude by discussing the implications of our results for understanding the evolution of pair bonding in humans.

Materials and methods

Study site and behavioral observations

The Ngogo study site in Kibale National Park, Uganda, lies at an interface between lowland and montane rainforest. It consists of old growth tropical forest, younger forest at varying stages of regeneration, and *Pennisetum purpureum* grassland created by past human disturbance (Struhsaker 1997). The large size of the Ngogo community ($N \approx 150$ members during the period of this study), both in terms of the number of reproductively aged individuals and the number of offspring, permits a powerful test of the relationship between male–female socio-spatial relationships and reproduction. This large community size also makes it difficult to collect sufficient data to reliably characterize the frequency of comparatively rare interactions, such as close spatial proximity and grooming, among a large number of dyads. We have also noticed slow but large changes in the amount of time females spend grooming and in close spatial proximity with males as the level of habituation of females has improved since they became the focus of intensive study in 2001. For these reasons, in most of the following analyses of male–female relationships, we employ party association and space use. Data on these variables can be relatively easily collected on a large number of individuals, even when they are not completely habituated to human presence. We thus mostly leave the precise content and quality of male–female social relationships, and the precise mechanisms through which they might influence reproduction, as subjects for future study.

Analyses of party associations, ranging behavior, spatial proximity, and grooming of male–male and male–female dyads are based on focal follows (duration, 1–13 h) of chimpanzees conducted by K.L. Only individuals of reproductive age were included in our analyses (adolescent and adult males ≥ 10 years: $N=52$, adult females ≥ 14 years: $N=45$). Females with sexual swellings, whether full or only partial, were not included. At half-hour intervals, K.L. recorded the identity of individuals who were associating in the same party (i.e., within ≈ 50 m) and in close proximity (5 m) to the focal subject, as well as their location on a map of the Ngogo territory overlaid with 500×500 -m grid cells. Observations were conducted during two separate sampling periods (period 1: October 2003–September 2004, $N=4,174$ point records; period 2: October 2007–March 2008, $N=1,028$ point records). Analyses of male dominance ranks at time of conception were based on both focal and ad libitum observations of “pant-grunts,” a formal signal of submission given by lower-ranking to higher-ranking individuals, and decided aggressive interactions (i.e., those in which aggression by one individual led to a submissive response by another) made by D.W. and the long-term Ngogo field assistants over the 13-year period in which conceptions occurred.

Calculating dyadic indices of party association, space use similarity, grooming, and spatial proximity

For each male–male and male–female dyad, we calculated pairwise affinity indices of party association and spatial proximity (PAI; Pepper et al. 1999). Numerically, this index is

$$\frac{I_{ab} \times \sum Si(Si - 1)}{\sum ai(Si - 1) \times \sum bi(Si - 1)}$$

where I_{ab} is the number of instantaneous point records where individuals a and b are in the same group, ai is the total number of instantaneous point records of a , bi is the total number of instantaneous point records of b , Si the size of group i , and a “group” is defined as the individuals associating in the same party or within close spatial proximity. Before using these observed indices, we normalized them by dividing by their expected values under the null hypothesis that social behaviors were generic rather than dyad-specific. We produced these expected values using a randomization technique. This procedure repeatedly reshuffled the membership of observed groups while retaining both the observed number of appearances of each individual and the observed distribution of group sizes. After each of 10,000 randomizations, the PAI was calculated for each dyad, and these randomized values were averaged to generate an expected value for each pair. We log-transformed the observed/expected ratios to ensure that dyadic interactions above and below expected levels would have equal weight. To avoid undefined values resulting from observed or expected values of zero, we truncated the range of the log-transformed values to those lying between -2 and 2 , corresponding to a floor of 0.01 and a ceiling of 100 for observed/expected ratios.

To assess similarity in the ranging patterns of male–female dyads, we summed how often each individual used each 500×500 -m grid cell and calculated Spearman's rank correlation coefficients of grid cell usage frequency (Doncaster 1990). This “Doncaster Index” (DI) varies from 1 (the ranks of grid cell usage frequency for two individuals are identical) to -1 (the two individuals never use the same grid cell). Before averaging these two dyadic measures to create a socio-spatial index to analyze factors influencing paternity outcomes, we rescaled the DI to match that of the PAI by multiplying it by 2.

We calculated a simple ratio index of male–female grooming as the number of minutes two individuals spent grooming each other (both giving and receiving) divided by the total sum of the number of minutes that they spent grooming (both giving or receiving) all reproductively aged individuals of the opposite sex. We calculated our dyadic grooming index using ad libitum data and the simple ratio index rather than using instantaneous point sampling of focal subjects and the PAI as we did for party association and close

spatial proximity because of the relative rarity of grooming compared to these other frequently observed behaviors.

Statistical analyses of dyadic indices of party association and space use similarity

We compared average male–male and male–female PAIs of party association with matrix permutation tests. For this test, we created a categorical matrix whose entries consisted of the sex combination of the dyad (i.e., male–male or male–female) and a corresponding matrix of PAIs of party association. We held the categorical matrix constant while randomly permuting the order of individuals in the rows and columns of the PAI matrix, with the order of individuals in columns kept the same as that in rows in order to preserve the diagonal. After each of 10,000 permutations, we calculated the difference between the dyad types in the mean PAI and obtained a *P* value by computing the proportion of permutations in this expected distribution where the mean difference was as large as or larger than that in the observed data. This same procedure was used to compare average PAIs of party association and average DIs of space use similarity in mothers and sons versus unrelated male–female dyads.

We conducted two additional tests to assess whether the patterns of party association were more differentiated in male–female than male–male dyads. First, we used a matrix permutation procedure similar to that described in the previous paragraph to determine whether the standard deviation of male–male and male–female PAIs of party association were significantly different. Second, we used permutation tests to determine whether male–male and male–females dyads differed in the percentage of dyads that were above the 90th percentile (or below the 10th percentile) of these PAI values. In these tests, a categorical sex matrix was held constant and a corresponding PAI matrix of party association was randomly permuted. After each of 10,000 permutations, the difference between the dyad types in the percentage of dyads that had a PAI value above the 90th percentile (or below the 10th percentile) was determined. A *P* value was calculated by computing the proportion of permutations in the expected distribution that was as large as or larger (for the above 90th percentile test) than or as small as or smaller (for the below 10th percentile test) than that of the observed data.

We used Spearman's rank correlations between matrices of PAI of party association in the two study periods, with statistical significance determined by matrix permutation, to evaluate the temporal stability of PAIs between male–male and male–female dyads over the two periods. The 561 male–male and 992 male–female dyads that were present during both study periods were used for these tests.

Calculating male dominance ranks at time of conception

To calculate male dominance ranks for a given year, we first entered data on decided agonistic interactions between each male dyad into an actor–receiver matrix in which “wins” (pant-grunts received plus aggressive acts that induced submission) were above the diagonal. We then used MatMan (de Vries et al. 1993) to order the males in a hierarchy that minimized the number of non-zero entries below the diagonal and to calculate Landau's index of linearity (H'), modified to take empty cells into account. We used MatMan to determine whether the hierarchy was significantly linear by randomly permuting matrix entries 10,000 times to generate a sampling distribution of H' values; the results were highly significant in all cases. In those few cases where individuals had tied rank scores, they were given the same numerical dominance rank. To account for the fact that the number of males varied across years, and thus that the same rank had different meanings in different years (e.g., in a group of 5, a male with the numerical rank of 5 is low ranking, but in a group of 15 that male is high-ranking), we standardized ranks as the proportion of other males that a male dominated. For our analysis comparing the influence of rank on reproduction at Ngogo with that in other chimpanzee communities (Boesch et al. 2006; Inoue et al. 2008; Wroblewski et al. 2009; Newton-Fisher et al. 2010), we calculated the average standardized rank of sires in each community, with 95 % confidence intervals of the mean determined through 10,000 bootstrap replicates. If rank has no influence on reproduction, the expected average standardized rank of sires is 0.5.

The habituation levels of the Ngogo males, as well as the observers' abilities to quickly identify them as individuals and record their dominance-related behaviors, have increased since intensive study began in 1995. Thus, dominance hierarchies for the early years of the study (1995–1997) are probably not as accurate as those of later years (1998–2007). Nevertheless, we judged all dominance hierarchies to be sufficiently reliable and valid for inclusion in this study as Pearson's correlations between the hierarchies of adjacent years had roughly the same magnitude in the early ($r_p=0.97$, range=0.94–1.0, $N=3$ pairs of adjacent years) and later years of the study ($r_p=0.97$, range=0.95–1.0, $N=9$ pairs of adjacent years).

Genetic analyses of maternity and paternity

We genotyped 203 chimpanzees at 44 autosomal microsatellite loci following standard procedures to produce genotypes from noninvasively collected fecal samples (Langergraber et al. 2007). Genotypes were 95 % complete. The sample included 163 Ngogo chimpanzees and 40 chimpanzees from the nearby Kanyawara community. Chimpanzees at Kanyawara

were genotyped to increase the number of unrelated dyads in the sample, thereby minimizing the difficulties in parentage assignment that result when allele frequencies are calculated from the same set of individuals whose relationships are being assessed. Maternity and paternity were determined with likelihood-based parentage analysis (Marshall et al. 1998). See Langergraber et al. (2007, 2009) for further details.

Statistical analyses of the effects of male dominance rank at time of conception and the composite socio-spatial index on paternity outcomes

We used general linear mixed models (GLMMs; Baayen 2008) fit with the Laplace approximation to examine the effects of the composite socio-spatial index and male dominance rank at time of conception on paternity outcomes. For each conception, we included the identity of the offspring's mother and the identities of the reproductive age males present in the community at the time of the conception as random factors, as each value of these variables appeared multiple times in the model. Males were not considered as candidate sires for their mothers' offspring. We included standardized male dominance ranks at the time of the conception and the relevant composite socio-spatial index between each of the candidate males and the offspring's mother as predictor variables with fixed effects for each of three models (see below for details). The response variable was each male's status as father of the offspring (0=no, 1=yes). Statistical significance was determined by comparing the observed effects with those obtained when the identity of the father was randomly assigned to one of the candidate sire males present for the conception of each offspring through permutation (Adams and Anthony 1996). We used the absolute estimates derived for the fixed effects as test statistics and determined *P* values as the proportions of permutations revealing an estimate at least as large as that of the original data. We performed 1,000 permutations, with the original data included as one permutation. We calculated the GLMMs using the function "lmer" provided by the package "lme4" (Bates and Maechler 2010) for R (version 2.10.1).

The three models included a "time-insensitive" model as well as two temporally explicit models: a "mating effort" model, which examined the relationship between male–female socio-spatial behavior and future reproduction, and a "potential parenting effort" model, which examined the relationship between male–female socio-spatial behavior and past reproduction. The time-insensitive model examined the relationship between the male–female socio-spatial index, calculated from combined dyadic behavioral data of the 2003–2004 and 2007–2008 study periods, and the paternity of the entire

set of 62 offspring who were conceived over the 13-year period (1995–2007). This model has the advantage of having the largest sample size in terms of individuals, paternities, and behavioral data on which the socio-spatial index is based. However, it has the disadvantage, like the Gomes and Boesch (2009) analysis of meat-sharing and mating, of not being able to distinguish among whether socio-spatial behavior predicts conceptions, conceptions predict socio-spatial behavior, or a combination of both. It is also important to note that while in this model dominance ranks were calculated on a yearly basis, the socio-spatial index was calculated from male–female behavior that in some cases occurred several years from when the conceptions actually occurred. This latter feature of the time-insensitive model makes it difficult to rule out type II error if we were to find no relationship between male–female socio-spatial index and paternity. However, if we find that socio-spatial indices do predict paternities despite the fact potentially large time gap from when the conception occurred, this would provide further evidence for the long-term stability of patterns of male–female association and ranging. The mating effort model examined the relationship between male–female socio-spatial behavior in 2003–2004 and male dominance rank at time of conception on paternity outcomes for 22 offspring conceived after this time period, in 2005–2007. The potential parenting effort model examined the relationship between male–female socio-spatial behavior in 2003–2004 and paternity of 37 offspring conceived before this time period, in 1995–2003, and the relationship between male–female socio-spatial behavior in 2007–2008 and paternity of 24 offspring conceived before this, in 2004–2007.

We used the composite socio-spatial index of the behavior of male–female dyads, rather than the two dyadic predictor variables independently, because their high intercorrelation could lead to competition in variance explanation and failure of model convergence. We obtained results similar to those presented in the text in three variations of the time-insensitive model, where in conjunction with dominance rank at time of conception, we entered as predictor variables DI of space use similarity, PAI of party association, or PAI of party association outside individual core areas (i.e., the minimum set of grid cells where 50 % of an individual's party association scans occurred; data not shown).

Results

Patterns of party association among male–female dyads

We found that the average PAIs of party association were significantly higher for male–male (0.01) than male–female

dyads (-0.19 ; matrix permutation test, $P < 0.0001$; Fig. 1). However, the standard deviation of PAIs was significantly higher for male–female (0.44) than male–male (0.21) dyads (matrix permutation test, $P = 0.0001$). Similarly, the percentage of dyads with very high PAIs (> 0.26 , the 90th percentile of male–male and male–female PAI values) did not differ (matrix permutation chi-squared test, $P = 0.4433$) between male–male (28/561 = 5.0 %) and male–female (70/1088 = 6.4 %) dyads, while the percentage of dyads with very low PAIs (less than -0.75 , the 10th percentile of male–male and male–female PAI values) was significantly higher in male–female (78/1,088 = 7.2 %) than male–male (3/561 = 0.5 %) dyads (matrix permutation chi-squared test, $P = 0.0020$). These results indicate that although males generally preferred to associate more strongly with each other than with females, the patterns of party association of male–female dyads were more differentiated than those of male–male dyads in that the strongest association indices were as common, and the weakest more common, in male–female than male–male dyads. Correlations of PAIs between the two study periods were significant and of approximately equal magnitude for male–male ($r_s = 0.39$, $P = 0.0001$) and male–female ($r_s = 0.37$, $P = 0.0001$) dyads, indicating that associations within and between the sexes did not differ in their temporal stability.

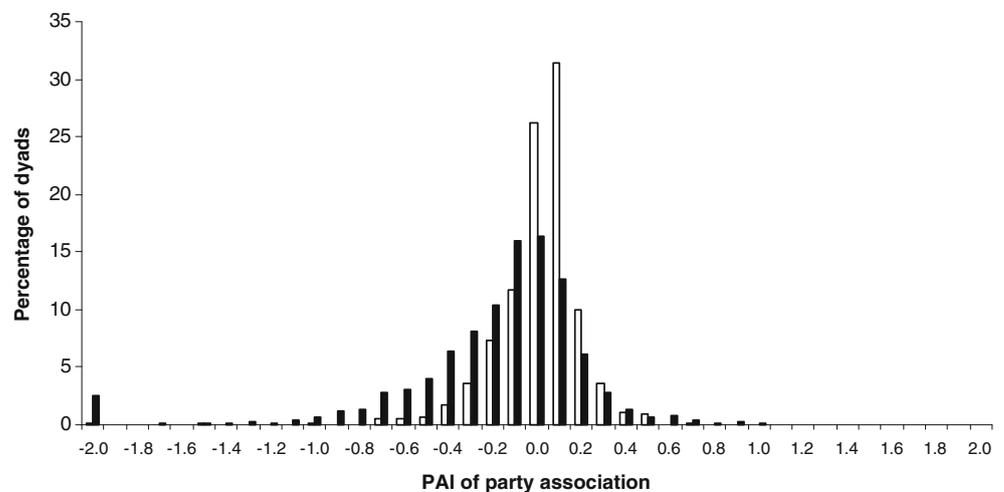
Space use and the ontogeny of differentiated patterns of party association in male–female dyads

Although we lack the long-term data to examine maternal influence on male ranging patterns directly, we found that the average DIs of space use similarity were significantly higher between sexually mature males and their mothers ($\bar{x} = 0.51$, $SD = 0.13$, $N = 13$) than between unrelated male–female dyads ($\bar{x} = 0.26$, $SD = 0.19$, $N = 1075$; matrix permutation test, $P = 0.0004$). The average PAIs of party association were also significantly higher in mother–son ($\bar{x} = 0.21$,

$SD = 0.26$, $N = 13$) than unrelated male–female ($\bar{x} = -0.19$, $SD = 0.44$, $N = 1075$) dyads (matrix permutation test, $P = 0.0026$). We found nearly identical results regarding patterns of association and space use in male–male versus male–female dyads even after we removed all mother–son pairs from the analyses, indicating that our finding of differentiated patterns of association and space use among male–female dyads was not merely an artifact of these related pairs (data not shown). Along with our finding that patterns of dyadic similarity in space use and party association were highly correlated for male–female dyads in general ($r_s = 0.73$, $P = 0.0001$), these results suggest that the highly differentiated patterns of party association in unrelated male–female dyads may arise from a tendency of males to range selectively in the same areas as their mothers do (or did). They then frequently associate in parties with unrelated females who also selectively use these areas.

We also found that all of our results regarding party association in unrelated male–female versus male–male dyads held even after PAIs of association were calculated on a reduced data set in which we removed individuals from all parties located in the areas where they spent most of their time (i.e., the minimum set of grid cells where 50 % of an individual's party association scans occurred). Additional results indicated that as in previous research on male–male dyads at Ngogo (Mitani et al. 2000), pairs of males and females that frequently associated were also more likely than male–female dyads that associated infrequently to maintain close spatial proximity (< 5 m; $r_s = 0.24$, $P = 0.012$) and groom with each other ($r_s = 0.18$, $P = 0.033$). Thus, although high rates of party association among certain unrelated male–female dyads probably initially develop from coincidental similarity among individuals in their preferences to use the same areas of the territory, their maintenance also reflects active choices by one or both individuals that are at least partly based on genuine social affinity

Fig. 1 Pairwise affinity indices (PAIs) of party association in male–male (open bars) and male–female (black bars) chimpanzee dyads. Values shown are rounded to one decimal place



(Newton-Fisher 2002; Wakefield 2008; Langergraber et al. 2009). However, given the limitations of our behavioral data, and previous research indicating that relationships among male and female chimpanzees often exhibit a mix of both affiliative and aggressive interactions, we urge caution in drawing strong conclusions about the specific nature or quality of the relationship of male–female dyads with high socio-spatial indices.

Differentiated socio-spatial behavior and reproduction

We found that both a male’s dominance rank at the time of conception and the strength of the socio-spatial index he had with the offspring’s mother had strong and statistically significant effects on the probability that he was the father (Tables 1 and 2). In the “time-insensitive” model, which involved all 62 offspring and where dyadic socio-spatial behavior was calculated by combining data collected in the two study periods, the influence of the socio-spatial index on reproduction was actually larger than that of dominance rank. This is a surprising result considering that the time frame during which the socio-spatial behavioral data was collected was both very narrow (periods 1 and 2 sum to only 1.5 years) and potentially much more separated in time from when the conceptions actually occurred compared to male dominance rank, which was calculated for each of the 13 years that the conceptions occurred.

We found similar results in our models examining the relationship between male–female socio-spatial behavior and future (“mating effort”) and past (“potential parenting effort”) reproduction (Tables 1 and 2). In both analyses, both predictor variables had a strong positive relationship with reproduction, but unlike the larger “time-insensitive” analysis, the influence of male–female socio-spatial behavior was not stronger than that of dominance rank at time of conception. In sum, male–female chimpanzee dyads that frequently associated and ranged in the same areas of the territory were likely to reproduce together in the future. Moreover, these differentiated patterns of socio-spatial behavior showed enough long-term stability that they persisted well beyond the birth of offspring.

The number of competing males and the relationship between rank and paternity success

Despite the large number of males present at Ngogo throughout our study period, the mean standardized rank of sires at Ngogo was as high as that observed in other smaller chimpanzee communities (Fig. 2). In addition, although the correlation between the standardized rank of sire and the number of competing males across chimpanzee communities was statistically significant, its magnitude was fairly small ($r_s = -0.19$, $P = 0.02$, $N = 153$ conceptions, range in number of males present per conception = 3–42), indicating that in chimpanzees the number of male competitors has only a moderate effect on the ability of high-ranking males to monopolize reproduction. The finding that dominance rank has as much influence on reproduction at Ngogo as in other chimpanzee communities, along with our findings that the influence of male–female socio-spatial relationships on reproduction is as strong as that of male dominance ranks, suggests that socio-spatial relationships are an important source of variance in reproductive success in the Ngogo community.

The prevalence and patterning of highly differentiated socio-spatial/reproductive relationships

Differentiated socio-spatial relationships were fairly widespread among individuals, but proportionally more females (18/38 = 47.4 %) than males (13/50 = 26.0 %) reproduced with a member of the opposite sex with whom they had a high socio-spatial index (i.e. ≥ 90 th percentile of the female’s indices with males). Furthermore, males who reproduced with females with whom they had high socio-spatial indices belonged to a variety of rank classes (proportion of non-sires that the sire dominated at time of conception; $\bar{x} = 0.58$, $SD = 0.21$, range = 0.28–0.97, $N = 22$ conceptions), with a non-statistically significant tendency for higher-ranking males to combine high socio-spatial indices and reproduction with a larger number of females than did lower-ranking males ($r_s = 0.25$, $P = 0.07$, $N = 34$ males who were present for all conceptions). Thus, dominance rank influences reproductive success at Ngogo, as in other chimpanzee communities, but was a poor predictor of the tendency to reproduce in socio-spatial relationships; together, these results imply that the tactical use

Table 1 Summary statistics for GLMM of factors influencing reproduction in male–female chimpanzee dyads

	Time-insensitive			Mating effort			Potential parenting effort		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Intercept	−3.90	0.18	0.001	−4.24	0.35	0.014	−3.75	0.16	0.009
Socio-spatial index	0.83	0.18	0.001	1.09	0.36	0.001	0.54	0.17	0.001
Male dominance rank	0.60	0.15	0.001	0.79	0.27	0.003	0.57	0.15	0.001

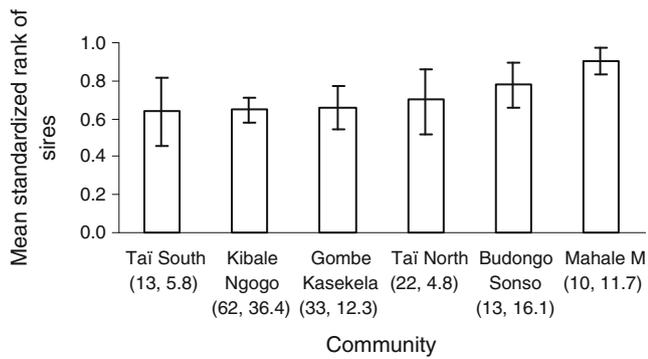


Fig. 2 Mean standardized dominance rank of sires at Ngogo and five other chimpanzee communities. *Error bars* represent 95 % confidence intervals. Also shown in *parentheses* for each community are the number of conceptions on which the mean is based and the average number of competing males per conception

of differential association and reproduction with certain females neither strengthens nor weakens the relationship between dominance rank and male reproductive success.

Discussion

Male chimpanzees at Ngogo display temporally stable tendencies to associate with particular females. These association patterns likely arise out of the tendency of individuals of both

Table 2 Effect size estimates for GLMMS of factors influencing reproduction in male–female chimpanzee dyads

	AIC		
	Time-insensitive	Mating effort	Potential parenting effort
Full model	535.4	195.2	540.7
Socio-spatial index only	551.2	203.1	554.4
Male dominance rank only	559.4	205.0	550.1
Null model	573.0	210.3	563.4
Absolute difference of null versus full	37.5	15.1	22.7
Absolute difference of socio-spatial index only versus rank only	8.1	1.8	4.3

Since standard effect sizes for fixed effects are not available for GLMMs (Nakagawa and Cuthill 2007), we compared values of Aikake’s Information Criterion (AIC; Burnham and Anderson 2002) to ascertain the relative importance of the two fixed effect predictor variables. Specifically, we compared the AIC of the full model (including all fixed and random effects) with those of three reduced models, which included: (1) random effects plus the composite socio-spatial index, (2) random effects plus male dominance rank, and (3) only the random effects (the null model). Models with smaller AIC values have greater relative support, with standard conventions suggesting that a difference between models of an AIC of ≤ 2 indicates a small and >10 a large difference in explanatory power

sexes to selectively range in particular areas of the territory, and their effect on reproduction is as strong as that of male dominance rank. Male dominance rank, in turn, is as strong a predictor of reproductive success at Ngogo as it is in other smaller chimpanzee communities. Males from a wide variety of ranks reproduced with females with whom they had high socio-spatial indices. Together, these results suggest that male–female socio-spatial relationships play a large role in male reproductive success, but they probably neither strongly weaken nor strengthen the relationship between male dominance rank and reproductive success.

Our study has two significant limitations, which highlight important areas for future research. First, what is the content and quality of male–female relationships at Ngogo and what are the precise mechanisms that influence the probability of future reproduction? Differentiated patterns of association between male–female dyads held even when using data collected outside areas where both of the individuals typically ranged. This finding accords with our observations that some pairs of males and females were in near constant association as they travelled through large portions of the territory over the course of several days and even weeks. Thus, the strong associations among some male–female dyads apparently represent more than passive aggregations resulting from mutual attraction to the same feeding location in the same part of the territory, such as large fruiting trees (Gilby and Wrangham 2008). A male who actively chooses to associate with a particular lactating female may increase his chances of reproducing with her during her next fertile period simply because his increased knowledge of her reproductive condition allows him to predict when she will become fertile. While our finding that male–female dyads that frequently associated were also more likely to maintain close spatial proximity and groom suggests that affiliation and female choice may also affect the probabilities that males gain paternity, previous research in other chimpanzee communities suggests that the differentiated social and reproductive relationships of male and female chimpanzees at Ngogo may involve male agonism and coercion, as well as—or even instead of—affiliation and female choice (Goodall 1986; Muller et al. 2006, 2007, 2010; Stumpf and Boesch 2006; Gomes and Boesch 2009; Proctor et al. 2011). Collecting the detailed behavioral data necessary to test the relative contributions of these and other factors remains a priority for future research at Ngogo.

A second limitation of our study is that it was only conducted on one unusually large chimpanzee community, which raises questions about the generality of our results. Here, we have demonstrated that some male–female dyads frequently associate with one another over several years because of stable tendencies to range selectively in the same areas. Although previous research in other smaller east African chimpanzee communities has shown selective

ranging behavior on the part of both males and females, whether this phenomenon is as strong as at Ngogo is unknown. Early anecdotal observations of Tai chimpanzees suggested selective ranging behavior by females when community size was large (Boesch and Boesch-Achermann 2000), but later quantitative analyses conducted when community size substantially decreased suggested even use of the territory (Lehmann and Boesch 2005). These results suggest that chimpanzees may show more selective ranging behavior in larger communities and that differentiated male–female relationships consequently may be more common in large communities than in smaller ones. In contrast, additional research from Tai revealed that, even when community size was small and females showed no selective space use, males and females formed differentiated social relationships that may influence reproduction (Wittig and Boesch 2005, 2010; Gomes and Boesch 2009).

A better understanding of the content and quality of male–female relationships, the mechanisms through which they influence reproduction, and their existence and form in other chimpanzee communities may shed light on the evolution of our own social and mating system. Although humans show considerable cross-cultural variation in these respects, in all societies, people live in multi-male, multi-female groups where most reproduction takes place in the context of long-term, monogamous pair bonds (Fox 1967; Rodseth et al. 1991). The evolution of monogamous pair bonds within multi-male/multi-female groups has long been puzzling not only because it is unique among mammals but also because of the strong role phylogenetic inertia plays in the evolution of primate social and mating systems. Here, closely related species are typically very similar (Di Fiore and Rendall 1994; Shultz et al. 2011; Opie et al. 2012). Whether they emerge only under the specific demographic and ecological conditions characterizing Ngogo or are characteristic of *Pan* more generally, differentiated social and reproductive relationships among male–female chimpanzees go some way toward filling in the apparent phylogenetic gulf between the social and mating systems of humans and our closest living relatives. In particular, future research investigating the link between differentiated socio-spatial relationships and reproduction among male–female dyads in smaller chimpanzee communities may shed light on the role of group size in the evolution of pair bonding in humans. Humans are unusual among primates in having a nested hierarchy of social groups, making it impossible to meaningfully characterize them with a single group size estimate. However, the hierarchical level of grouping in hunter-gatherers most directly analogous to the “community” in chimpanzees may be the “community/clan,” the set of individuals sharing access rights to territorial resources (Dunbar 1993; Gowlett et al. 2012). Consisting of an average of 165 members (Hamilton et al. 2007), the

hunter-gatherer community/clan is similar in size to the Ngogo community ($N \approx 150$), but larger than is typical for chimpanzees in general ($\bar{x} = 47.7$; Mitani 2006). If socio-spatial and reproductive relationships only occur in large chimpanzee communities, this would suggest that an increase in group size in human evolution may have played an important role in the evolution of pair bonding in humans. As often occurs in other taxa, a decrease in the economic defensibility of females when many competitors are present may have led to an increase in the importance of alternative or additional male mating strategies of the sort discussed here.

Our results also provide support for Chapais' (2008) recent account of the initial evolution of stable breeding bonds in hominins, which acknowledges that while biparental care may be the most important function of stable breeding bonds now and throughout much of human evolution (Washburn and Lancaster 1968; Lovejoy 1981, 2009; Kaplan et al. 2000), as in other taxa (Brotherton and Komers 2003), pair bonding in humans probably initially originated as a response to selection for male mating rather than parental effort. Indeed, despite the long-term nature of the socio-spatial and reproductive relationships of particular male–female pairs at Ngogo (i.e., in one extreme case, one male fathered three of a female's four offspring born over a ≈ 16 -year period), male chimpanzees at Ngogo and elsewhere show little paternal care (Lehmann et al. 2006; Langergraber et al. 2007; Wroblewski 2010). Like all complex adaptations, the pair bonds of humans likely represent the end product of a multistep evolutionary sequence in which gradually more elaborated forms succeeded one another (Chapais 2008).

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