

**Do females have friends? The nature of social bonds among female
chimpanzees (*Pan troglodytes schweinfurthii*) at Gombe National Park,
Tanzania**

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Abstract

Chimpanzee (*Pan troglodytes schweinfurthii*) females have traditionally been viewed as asocial and solitary, but recent evidence suggests that they are more social than previously believed and may develop differentiated social bonds like their more gregarious male counterparts. Here we use 38 years of long-term behavioral and spatial data from Gombe National Park, Tanzania to test whether chimpanzee females have differentiated social bonds and whether these bonds are primarily explained by spatial or social factors. We found that female association and grooming relationships were well differentiated. Kin dyads associated, ranged, and groomed preferentially, regardless of rank. Non-kin dyads associated at consistently lower rates than kin dyads, with rank difference likely playing a mediating role between spatial overlap and association preferences. These results demonstrate that strong social bonds do exist among female chimpanzees, but that these bonds are primarily among kin dyads.

Introduction

In many social species, individuals preferentially associate with certain partners rather than distributing social behaviors evenly. These non-random social biases can either reflect true social bonds or simply be a by-product of physical constraints, such as resource distribution (Wolf & Trillmich, 2008). Male chimpanzees (*Pan troglodytes*) demonstrate differentiated social bonds and frequently cooperate, reflecting true social affinities (Mitani et al., 2000; Muller & Mitani, 2005). Female chimpanzees are generally regarded as mostly solitary

(Goodall, 1986), but recent studies suggest that female social relationships may exist. The present study addresses the existence of differentiated social bonds among female chimpanzees (*P. t. schweinfurthii*) at Gombe National Park, Tanzania and subsequently asks whether these bonds can be primarily explained by spatial or social factors.

Social Bonds

Social bonds have been shown to be important indicators of fitness for both sexes in many primate species (Silk, 2007). For example, strong bonds among female baboons improve offspring survival, mediate stress, and resemble human friendships in adaptive, emotional, and psychological functions (Silk, 2003). In male chimpanzees, bonds are correlated with coalition formation (Mitani, 2009), which in turn is linked to increased fitness (Gilby et al., 2013).

Typically, one sex forms stronger bonds than the other. In primates, it has been hypothesized that dispersal patterns predict the strength of intra-sexual bonds. The philopatric sex is assumed to have stronger bonds than the dispersing sex (Lehmann & Boesch, 2008) due to kin selection (Hamilton, 1964) and because they spend their whole lives together. This pattern has been shown to hold true in nearly all primate species. Relationships among philopatric female baboons (Genus *Papio*) have been particularly well studied. For example, Chacma baboon (*P. ursinus*) females have been shown to have enduring and strong social bonds between both kin and non-kin (Silk et al., 2010). Not only are bonds between adult female baboons stronger than those between adult male baboons, as predicted by the dispersal

model, but the strength of these bonds have been demonstrated to correlate positively with certain fitness measures. For example, infant survival is positively associated with sociality of their mother in adult Savannah baboons (Silk et al., 2003). Consistent with this pattern, in species where males are philopatric, such as in red colobus (*Procolobus rufomitratu*s) monkeys, males show stronger bonds while the dispersing females exhibit weaker bonds (Struhsaker & Leland, 1979).

Chimpanzee Social Structure

Chimpanzees (*Pan troglodytes*) fit this dispersal model of sociality, with the dispersing sex being less social than the non-dispersing sex. Male chimpanzees are philopatric while females typically disperse at adolescence (Goodall, 1986; Mitani et al., 2002), suggesting that males, not females, should have the stronger social bonds. Chimpanzee social groups are characterized by fission-fusion dynamics, where individuals spend time in subgroups of the larger community, termed “parties”, that vary in composition, size, and duration (Goodall, 1986; Mitani et al., 2002; Nishida, 1968). This social fluidity allows individuals considerable freedom to choose whom to associate with. Males are more gregarious, associating with males more than females associate with other females (Goodall, 1986; Nishida, 1968). Anestrus females tend to spend time alone or with dependent offspring, with the mother-daughter bond the strongest among adult females (Goodall, 1986). Males have strong, enduring bonds with other adult males while social bonds among females have been traditionally viewed as weak (Goodall, 1986; Wrangham et al., 1992).

However, as more information is accumulated, the assumption that female chimpanzees are weakly social, or do not benefit from sociality, is being challenged.

Chimpanzee Females

Traditionally, scramble feeding competition, and the subsequent ranging patterns that occur due to this competition, is often treated as the determining factor in female social distribution (Wrangham & Smuts, 1979). Indeed, there is evidence that females do have differentiated social bonds that are connected to ranging patterns. While the more gregarious male chimpanzees range over the entire community's territory (Goodall, 1986), females concentrate their space use into small, overlapping core areas (Wrangham & Smuts, 1979). Concentrating space use in these core areas maximizes feeding efficiency and reduces competition for food resources among females (Wrangham & Smuts, 1979). Higher-ranking females have smaller core areas and higher site fidelity, especially in times of food scarcity, suggesting that dominant females outcompete subordinates for the highest quality habitat (Murray et al., 2007). Subordinate females have larger core areas and lower site fidelity, while immigrant females tend to range in areas far from those of the highest-ranking females (Murray et al., 2007; Williams et al., 2002). At Gombe National Park, Tanzania, females center their space use around abundant food resources, resulting in "neighborhoods" of clustered core areas (Williams et al., 2002). Competition over core areas is one of the few instances in which female aggression is observed. In the Kanyawara community in Kibale National Park, Uganda, female aggression increased significantly in response to new immigrant

females, with some female coalitionary aggression occurring (Kahlenberg et al., 2008). Females compete strongly over these core areas as space use is directly linked to fitness, with higher-ranking females having better reproductive success than lower ranking females (Pusey et al., 1997).

Social factors in the form of dominance hierarchies clearly influence space use, already creating differential association patterns among adult females. However, it is unclear to what extent space use and sociality are linked, or if social relationships exist among females outside shared ranging patterns. In the Kanyawara community in Kibale National Park, Uganda, females show differential association patterns, with some female-female dyads having association indices as high as the strongest male-male dyads (Gilby & Wrangham, 2008). However, association patterns were determined more by shared habitat use and not actual social affinity, as measured by proximity within a party (Gilby & Wrangham, 2008). In the Ngogo community in Kibale National Park, Uganda, females are less gregarious than males, but after controlling for gregariousness, anestrus females preferred associating with other anestrus females above chance (Pepper et al., 1999). However, Pepper et al. (1999) did not analyze the effect of ranging patterns on association. Further studies in the Ngogo community determined that female dyads associated non-randomly, forming associative cliques (Wakefield, 2008) that could not be explained by ranging patterns or kinship alone (Langergraber et al., 2009). These bonds also are associated with potential fitness benefits, with females at Tai Forest, Cote d'Ivoire exhibiting differentiated and long lasting relationships

that correlate with reduced aggression between females with stronger relationships (Lehmann & Boesch, 2009).

In this study, we examined the nature of social relationships among female chimpanzees in the Kasekela community at Gombe National Park, Tanzania. Use of long-term data from the Jane Goodall Institute Research Center data-base allowed for analysis of social bonds over a much longer time span than at any other site. We hypothesized that females would show differential association patterns, as is consistent with data from other East African sites. Furthermore, we investigated whether association patterns are influenced more by spatial or social factors. We predicted that increased similarity in ranging patterns would correspond to higher levels of association. However, if females have true social relationships, we also expected that grooming and rank would influence association patterns. Additionally, Gombe is unique in that nearly half of all females born into the Kasekela community do not disperse at adolescence, resulting in more adult mother-daughter dyads than in other communities (Pusey et al., 1997). This unusual number of adult kin dyads allowed for a better examination of kin vs. non-kin social relationships than has been possible at other sites with fewer adult kin dyads. In line with kin selection theory (Hamilton, 1964), we predicted kin dyads to have stronger associations than non-kin dyads.

Methods

Study site and long-term data collection

Gombe National Park is a 35-km² park on the eastern shore of Lake Tanganyika in Tanzania. The park contains three communities of chimpanzees: Mitumba, Kasekela, and Kalande. The Kasekela community has been studied since the early 1960's and was fully habituated by 1966, with banana provisioning at a feeding station continuing until 2000. Beginning in 1973, Tanzanian field assistants have conducted full day focal follows on members of the Kasekela community. During these focal follows, location of the focal animal and group composition are recorded every 15 minutes on check sheets and a map. Additionally, longhand notes of focal and group behaviors are recorded, including the reproductive state of any females encountered by the focal and group composition based on arrivals and departures of individuals from the party. The data have been compiled in a long-term database and is currently housed at Duke University in partnership with the Jane Goodall Institute.

Time periods & Subjects

We analyzed party association and ranging data from 1974-2011 and grooming data from 1978-2011. These durations were broken down into 19 and 17 2-year periods, respectively.

54 adult females were included across all time periods. Females were included in each period if they were alive, present in the Kasekela community, and

an adult at the beginning and end of each 2-year period. A female was considered an adult if she had experienced a full sexual swelling and had previously mated with an adult male. Males greater than 12 years old were considered adults. Immigrant females were assumed to be adults at time of immigration if their estimated age was 15 or greater.

Ranging patterns

To determine ranging patterns, female core areas were calculated using location data from the 15 minute scans. These core areas are a calculation of the area that a female spends most of her time in while alone or only accompanied by kin or non-adults. Each day, when an individual is encountered for the first time on a focal follow, the individual's location and group composition are recorded. To construct core areas, we used all alone arrival data points. Arrivals into focal parties were used in order to reduce bias against less social females who were the focal in follows less frequently. A female was considered alone if she was only accompanied by kin, which included mothers, daughters, or maternal sisters, and/or a non-adult. Individuals that arrived into a party within 5 minutes of each other were considered to have arrived together.

To map core area boundaries from the first alone arrival locations, we used the adaptive kernel method, which produces a topographic utilization distribution (UD) of the individual's space use (Worton, 1989). We used the 50% UD in order to conservatively capture only the areas in which a female truly ranges. Core areas

were only calculated for females with at least 20 alone arrivals in a given two year period.

Spatial overlap between a dyad was calculated using three distinct methods. First, the percentage of overlap between each dyad's core areas was calculated. This measure was non-symmetrical, producing one value per individual in each dyad, i.e. the proportion of overlap of individual 1's core area on individual 2's, and vice versa. Secondly, we calculated the distance between the centers of mass of each dyad's core areas, a symmetrical measure that produced one value per dyad. Finally, we determined the volume intersection (VI) (Fieberg & Kochanny, 2005) of two individuals' UD's, i.e. the probability of finding both individuals in the area of overlap of their core areas. VI values range from 0, which indicates no overlap, to 1, in which two individuals have identical UD's. We found that both distance between centers and VI values were highly correlated with the basic overlap measure ($r^2=0.63$, $r^2=0.78$). Further analysis continues using only the VI measure, as it captures the most accurate picture of a dyad's spatial overlap and is a symmetrical measure.

Assessment of kinship

Maternal relationships were determined based on genealogical records. Not all relationships were known, specifically for females who were born before data collection began or who immigrated into the community. Some paternal relationships are known from recent DNA testing, but this data set was not complete enough to include in this study. We included only mother-daughter and maternal

sister relationships. In total, there were 18 kin pairs included across all periods: 13 mother-daughter dyads and 5 maternal sister dyads.

Rank

Ranks were derived from single-recipient pant grunts, which were extracted from the longhand notes, and calculated for each period using Modified David's Scores (MDS) (de Vries et al., 2006). From these MDS, categorical ranks were then determined. A female was considered high ranking if her rank was $\geq \frac{1}{2}$ standard deviation above the mean MDS for a given period, low ranking if her rank was $\leq \frac{1}{2}$ standard deviation below the mean MDS for a given period, and medium ranking for all remaining ranks. We then calculated the difference in rank for each dyad for each period. A 0 indicates that individuals were of the same rank category (high-high, medium-medium, or low-low), a 1 indicates that individuals were one rank category apart (high-medium or medium-low), and a score of 2 indicates that individuals were two rank categories apart (high-low).

Association measures

Party association

The first dyadic association measure we used was a party association dyadic association index (DAI), modeled after the Simple Ratio Index (SRI) (Cairns & Schwager, 1987). This measure was used to determine the proportion of time two

individuals spent in the same party, using group composition data from the 15 minute scans, and was calculated as follows:

$$DAI_{PA} = \frac{P_{AB}}{P_A + P_B - P_{AB}}$$

Where P_{AB} = the number of party scans containing both chimpanzee A and chimpanzee B, P_A = the number of party scans containing A, and P_B = the number of party scans containing B.

First arrivals

The second dyadic association measure used was a measure to determine the proportion of instances in which two individuals arrived into a group together. Arrivals and departures from the focal group were recorded ad-libitum; individuals were considered to arrive together if they arrived within 5 minutes of each other. This measure was included in addition to the party association DAI as another measure of dyadic association under the assumption that individuals arriving in close proximity to each other were likely together before they arrived into the focal group. Arrivals of individuals into the focal group were recorded during the all-day follows; only an individual's first arrival of each day was used in this analysis. This measure was modeled after the SRI (Cairns & Schwager, 1987) and was calculated as follows:

$$DAI_{FA} = \frac{Y_{AB}}{Y_A + Y_B - Y_{AB}}$$

Where Y_{AB} = the number of times A and B arrived together, Y_A = the number of times A arrived into a group, Y_B = the number of times B arrived into a group.

We found that the two association measures were highly correlated (Pearson's $r=0.958$). We continue the analysis using the first arrivals DAI.

Grooming association index

The third dyadic association measure used was the grooming association index (GAI), again modeled after the SRI (Cairns & Schwager, 1987). This measure determined the proportion of time two individuals spent grooming each other, controlling for time spent together. This measure was calculated from two different data sets. From 1978 - 1988, 5 minute grooming scans were recorded during the all-day focal follows. Using this data, the GAI was calculated as follows:

$$GAI = \frac{S_{AB}}{S_A + S_B}$$

Where S_{AB} = the number of 5 minute grooming scans where A and B are grooming, S_A = the number of 5 minute scans where A is focal and B is present, S_B = the number of 5 minute scans where B is focal and A is present. Scans were only included when either A or B was the focal.

From 1990 – 2012, grooming durations were extracted from longhand behavior notes.

$$GAI = \frac{D_{AB}}{D_A + D_B}$$

Where D_{AB} = the number of minutes that A and B spent grooming, D_A = the number of minutes A is focal and B is present, D_B = the number of minutes B is focal and A is present. Similar to the GAI calculated using 5 minute scans, grooming durations were only included when either A or B was focal.

Statistical Analysis

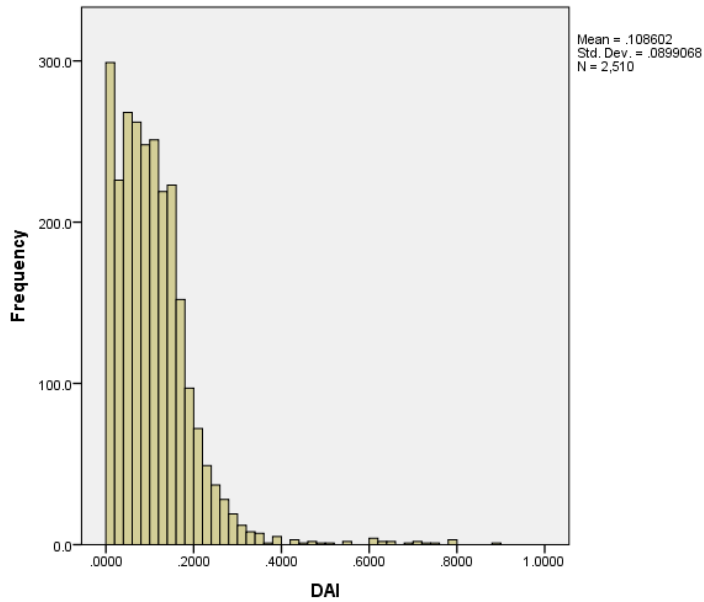
For analysis, we used a subset of the data for which values of GAI, VI, kinship, and rank difference were all present. This subset reduced the data set by 4 years, as GAI data were not available for 1974-1977. Additionally, the number of chimps included was reduced from 54 individuals to 44 individuals. In total, 387 unique dyads were included across all periods for analysis.

In order to determine which factors influenced association and grooming patterns, we ran linear mixed models using the SPSS Statistical software package. Models were run using the heterogeneous autoregressive covariance structure, with individuals treated as crossed random effects and the time period treated as a repeated effect. We determined two models. First, we examined the predictor values of GAI, VI, kin, and rank difference on the dependent variable DAI. Secondly, we examined the predictor variables of DAI, VI, kin, and rank difference on the dependent variable GAI.

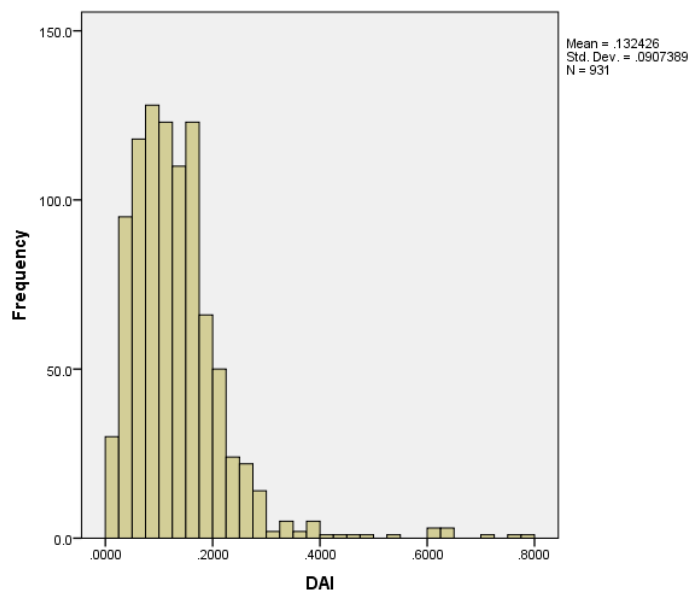
Results

Association patterns

The distribution of DAI values is skewed right, indicating that most dyads associated at low levels, while a smaller set of dyads associated at much higher levels. This is true for both the entire data set (Fig. 1a) and the restricted data set (Fig. 1b) used for statistical analysis. From this point on, all figures and analysis will refer to the restricted data set.



a.



b.

Figure 1. Distribution of dyadic association indices. 1a. displays the distribution across the entire data set, while 1b. is the distribution across the smaller subset of data used for analysis.

Our first linear mixed model identified a number of factors that influence DAIs (Table 1).

Kin dyads associated at much higher frequencies ($n=30$, mean DAI=0.4467, std. deviation=0.1684) than non-kin dyads ($n=901$, mean DAI=0.1220, std. deviation=0.0648) (Fig. 2).

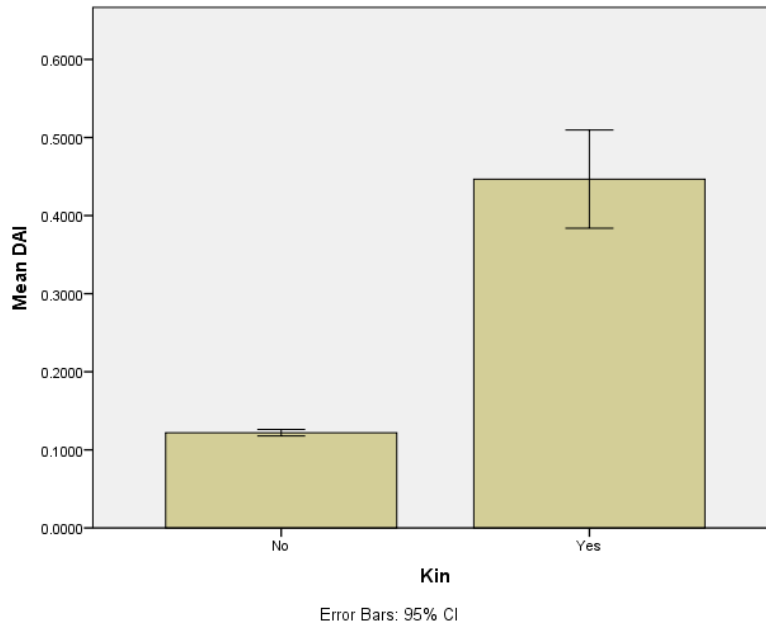


Figure 2. Mean DAI for kin and non-kin dyads.

Dyads with increased spatial overlap interacted significantly more than dyads with lower spatial overlap, with an increase in VI by one unit associated with an increase in DAI by 0.99 ($p<0.001$; Table 1). Examining the significant interaction between kin and VI indicates that the effect of VI on DAI holds only for kin, while non-kin show no effect of VI on DAI (Fig. 3a).

Rank difference also significantly impacts DAI ($p<0.001$; Table 1) and there is a significant interaction between kin and rank difference ($p<0.001$; Fig. 3b). For non-kin, mean DAI values do not significantly vary across rank differences. For kin,

dyads with the same rank have slightly higher DAI values than those with rank differences of 1 or 2.

GAI did not explain variation in DAI after accounting for other factors in the model.

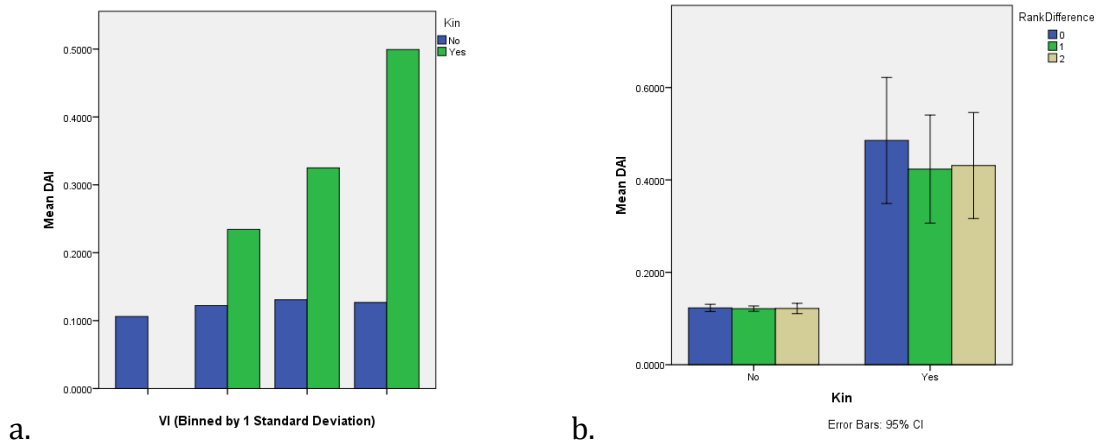


Figure 3. Sources of variation in DAI. a) The effect of VI on DAI. VI values are binned by 1 standard deviation around the mean for visualization purposes. Blue bars indicate non-kin, which show a slight increase in DAI as VI increases. Green bars indicate kin, which show a strong increase in DAI as VI increases. b) The effect of rank difference on DAI. Non-kin dyads have consistently lower DAIs across all rank differences, while kin dyads show higher DAIs at a rank difference of 0 than at rank differences of 1 or 2.

While rank difference and VI did not interact significantly in the model, exploratory analysis indicates that rank difference may impact VI in non-kin, with dyads with larger rank differences having a greater degree of spatial overlap (Fig. 4).

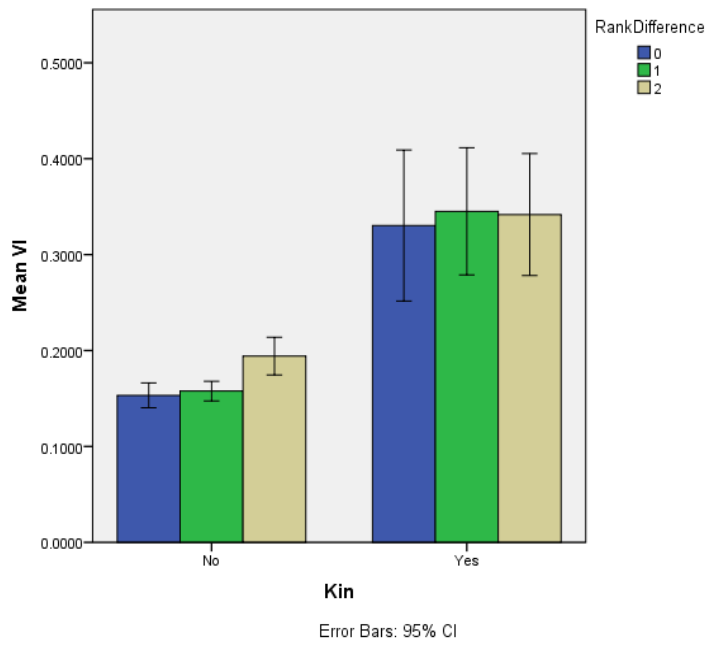


Figure 4. *Effect of rank difference on VI. Non-kin with greater rank differences have increased spatial overlap.*

Table 1. Results of linear mixed modeling using DAI as the dependent variable.

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	221.118	25.902	.000
VI	1	302.100	87.335	.000
Kin	1	221.118	1.055	.305
RankDifference	2	338.292	9.359	.000
Kin * RankDifference	2	338.292	8.725	.000
Kin * VI	1	302.100	71.746	.000

a. Dependent Variable: DAI-100.

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	.142989	.043991	225.797	3.250	.001	.056304	.229674
VI	.990335	.109930	294.183	9.009	.000	.773985	1.206684
[Kin=0]	0 ^b	0					
[RankDifference=0]	.016500	.024404	345.741	.676	.499	-.031499	.064499
[RankDifference=1]	-.063303	.017809	344.388	-3.555	.000	-.098331	-.028276
[RankDifference=2]	0 ^b	0					
[Kin=0] *							
[RankDifference=0]	-.011964	.024844	353.034	-.482	.630	-.060826	.036897
[Kin=0] *							
[RankDifference=1]	.064022	.018278	357.922	3.503	.001	.028077	.099968
[Kin=0] *							
[RankDifference=2]	0 ^b	0					
[Kin=1] *							
[RankDifference=0]	0 ^b	0					
[Kin=1] *							
[RankDifference=1]	0 ^b	0					
[Kin=1] *							
[RankDifference=2]	0 ^b	0					
[Kin=0] * VI	-.941695	.111176	302.100	-8.470	.000	-1.160472	-.722918
[Kin=1] * VI	0 ^b	0					

a. Dependent Variable: DAI-100.

b. This parameter is set to zero because it is redundant.

Grooming patterns

The right-skewed distribution of GAI values indicates that most dyads do not groom, or groom very infrequently, while a few dyads groom at higher rates (Fig. 5).

Kin dyads groom more (n=30, mean GAI=0.01883, std. deviation=0.0098,

range=0.00-0.0360) than non-kin dyads (n=901, mean GAI=0.0010, std. deviation=0.0036, range=0.00-0.0390) overall (Fig. 6), but the range of GAI values for both kin and non-kin are similar.

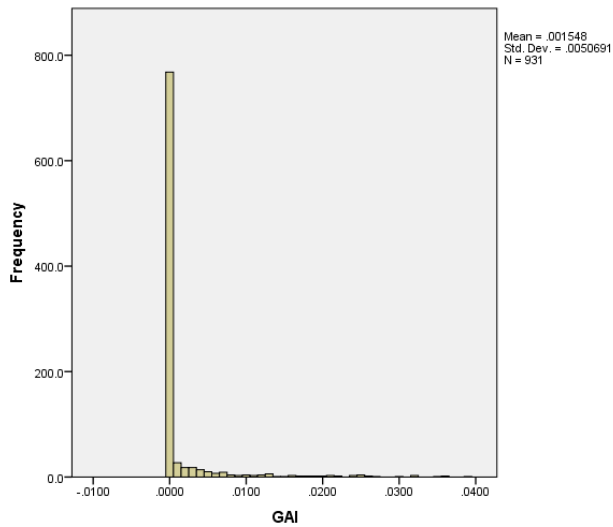


Figure 5. Distribution of GAI values.

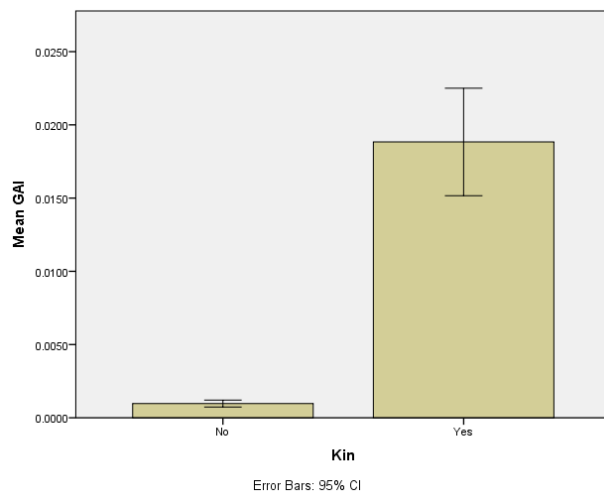


Figure 6. Kin dyads groom more frequently than non-kin.

Our second linear mixed model identified a number of factors that influence GAIs (Table 2).

There is a significant interaction between kin and VI ($p=0.045$, Table 2). Increased VI strongly correlates with increased GAI among kin, but this effect is much weaker, and clouded by many values of zero, among non-kin (Fig. 7).

DAI and rank difference did not explain variation in GAI after accounting for other factors in the model.

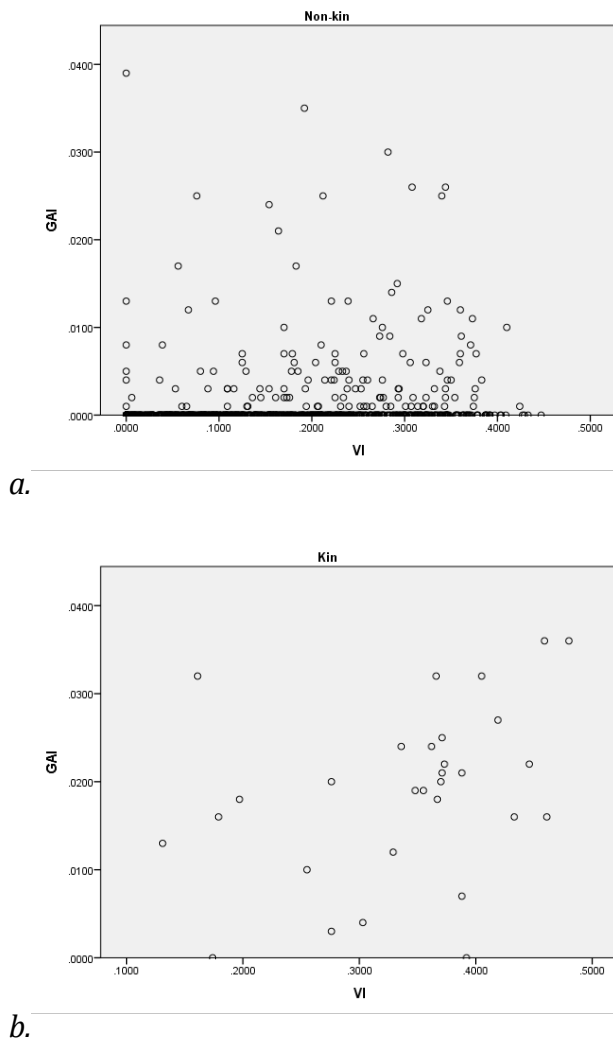


Figure 7. The effect of VI on GAI for a. non-kin and b. kin dyads.

Table 2. Results of linear mixed modeling using GAI as the dependent variable.**Type III Tests of Fixed Effects^a**

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	204.632	43.512	.000
VI	1	215.320	11.532	.001
Kin	1	204.632	43.162	.000
Kin * VI	1	215.320	4.053	.045

a. Dependent Variable: GAI_Combined.

Estimates of Fixed Effects^a

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	.012766	.001931	202.899	6.610	.000	.008958	.016575
VI	.014598	.005320	209.019	2.744	.007	.004111	.025085
[Kin=0]	-.012741	.001939	204.632	-6.570	.000	-.016564	-.008917
[Kin=1]	0 ^b	0
[Kin=0] * VI	-.010866	.005398	215.320	-2.013	.045	-.021505	-.000227
[Kin=1] * VI	0 ^b	0

a. Dependent Variable: GAI_Combined.

b. This parameter is set to zero because it is redundant.

Discussion

This study provides two main results. First, female chimpanzees at Gombe showed differentiated association patterns, supporting our hypothesis. Most dyads exhibited weak associations, while fewer pairs showed stronger associations, a pattern consistent among female chimpanzees at other sites (Gilby & Wrangham, 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009; Wakefield, 2008) and among female Chacma baboons (Silk et al., 2010). Secondly, association patterns were mediated by both spatial and social factors, supporting the idea that female relationships are not purely spatial in nature. However, our results point to very

different patterns of sociality among kin and non-kin. Below, we discuss these findings and their implications for understanding female chimpanzee sociality.

Kin

Chimpanzees are a female-dispersing species (Mitani et al., 2002), so there are typically very few, if any, adult female kin pairs in any given community. On the rare occasions that adult female kin pairs reside in the same community, kin selection theory (Hamilton, 1964) predicts that these bonds should be stronger than between non-relatives. This is the case among female chimpanzees at Kanyawara, where the only mother-daughter dyad associated as strongly as the strongest male dyad (Gilby & Wrangham, 2008), and at Ngogo, where the few kin dyads present formed strong social bonds (Langergraber et al., 2009). Consistent with these sites, kin pairs at Gombe associated more on average than non-kin pairs. However, Gombe is unique in that nearly half of Kasekela females eschew emigration and remain in their natal group to reproduce (Pusey et al., 1997), resulting in many more adult kin pairs than at any other site previously studied. The presence of a greater number of kin dyads allows for a more detailed look at the factors underlying these stronger social bonds than previous studies have achieved.

Scramble feeding competition theory (Wrangham & Smuts, 1979) predicts that shared ranging patterns, driven by resource distribution, should explain female social association in male philopatric species. At Gombe, female distribution is influenced by foraging competition, as females form “neighborhoods” of clustered core areas around preferential resources (Williams et al., 2002). Females and their

dependent offspring often range selectively in the same “neighborhood” (Williams et al., 2002). Our results provide evidence that this preference for ranging in the same “neighborhood” continues beyond offspring dependency into adulthood, as increased spatial overlap significantly predicted increased association. Additionally, rank difference was not correlated with spatial overlap. While there was a significant interaction between kin and rank, kin dyads of all rank differences still associated at high levels. These results suggest that the influence of kinship is much greater than that of rank, with kin pairs ranging and associating preferentially together.

Grooming and first arrival association patterns (i.e. GAI and DAI) were not significant explanatory factors for each other among kin dyads. While grooming and association preferences are often assumed to measure similar aspects of social relationships in primates (Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006), our results are consistent with the alternative hypothesis that grooming and association serve different social functions. This is demonstrated among chimpanzee females at Tai Forest, where grooming and association partners are not correlated, and grooming explains less than 1% of the variation in association patterns (Lehmann & Boesch, 2009). However, even though grooming and association may reflect different social strategies, kin still prefer each other as partners, grooming more on average than non-kin dyads.

Non-kin

Kin relationships are clearly very important, but the majority of possible social bonds occur between non-kin, especially at sites other than Gombe. As predicted, non-kin dyads, on average, had lower association rates than kin dyads. Non-kin dyads showed increased association rates as spatial overlap increased, but this positive effect was very weak compared to kin dyads. If both groups were associating in response to spatial overlap in similar ways, we would expect to see similar effect sizes. Instead, non-kin dyads appear to be actively avoiding each other as spatial overlap increases. This effect could be explained by examining interactions between females of different ranks. Average association rates remained constant across all rank difference categories (Fig. 3b), but spatial overlap increased as rank difference increased (Fig. 4). Non-kin dyads with the biggest rank difference (one high ranking individual and one low ranking individual) overlapped the most, yet associated at the same level as the other rank categories. This may suggest that the higher-ranking females, which have smaller core areas and higher site fidelity (Murray et al., 2007), preferentially range far from other high ranking females. The larger core areas of lower ranking females (Murray et al., 2007; Williams et al., 2002) subsequently overlap with high ranking females, but individuals avoid each other to avoid conflict. This is a starkly different picture than the ranging patterns of kin, who appear to preferentially range closely together regardless of rank.

Although rank appears to be particularly influential for non-kin association patterns, the same does not hold for grooming patterns. Grooming rates increased slightly as spatial overlap increased, and neither grooming or association patterns

influenced each other. It appears that, similarly to in kin, grooming and association serve different social functions (Lehmann & Boesch, 2009). However, while all kin dyads groomed, the vast majority of non-kin dyads never groomed. These results suggest that grooming relationships between adult female non-kin dyads are rare, and that dyads that associate preferentially do not necessarily groom preferentially. Adult females without kin may choose grooming partners based more on short term hygienic needs (Henazi & Barrett, 1999) than social preferences.

Conclusions

This study provides a description of female chimpanzee relationships in a population with a large number of adult kin pairs. Kin dyads range, associate, and groom preferentially together. Conversely, non-kin dyads appear to have associations mediated strongly by both shared ranging patterns and rank differences; dyads containing low and high ranking individuals may actively avoid associating even when spatial overlap is high.

However, this study only provides a general picture of sociality, especially in regards to non-kin relationships. Examining patterns on the dyadic level shows that while non-kin associate and groom less frequently on average, there is evidence that some dyads form strong, consistent associations. This is not readily apparent from a modeling approach, as the effect of the few stronger associations are masked by the majority of non-kin dyads, which associate and groom at consistently lower rates than kin dyads. By visualizing the association and grooming patterns for each dyad, it becomes clear that some non-kin dyads also demonstrate social bonds (see

Appendix A). The modeled interaction between spatial overlap and rank does not entirely explain the differential association patterns among non-kin dyads that are apparent in the visualization. It is likely that other factors, such as age of offspring or sterility of females, play an important role for non-kin association choices.

Additionally, while analyzing the consistency of association and grooming patterns was beyond the statistical scope of this study, visualizing the data demonstrates that long lasting bonds do exist among both kin and non-kin. Further research should address the consistency of relationships, the specific factors that mediate non-kin association preferences, and the impacts of social bonds on fitness.

Appendix A

This appendix contains a visualization of DAI and GAI values. Each chart shows all possible dyads that were present for at least one period while the subject chimp was present in the study. Dark grey shading corresponds to the period of time when the subject chimp was present in the study. Medium grey shading corresponds to the periods when other chimps were present in the study at the same time as the subject chimp. Light grey shading corresponds to periods when non-subject chimps were present in the study when the subject chimp was not in order to provide context.

The visualization contains information on DAI and GAI values compared to the population mean for each period as well as to individual means for each chimp for each period (Fig. A1). Two year periods are listed along the top row. Hatched boxes indicate a DAI value at least 1 standard deviation above the population mean

for that period. Borders around a box indicate that that chimp was in the top three DAI values for the subject chimp for that period. Colored shading indicates the presence of a mutual association based on individual means. Green shading indicates the dyad was 1 standard deviation mutual associates (i.e. the DAI value was 1 standard deviation above the individual means for each chimp). Blue shading indicates the dyad was .5 standard deviation mutual associates (i.e. the DAI value was at least .5 standard deviations above the individual means for each chimp). Finally, GAI values are indicated by X's. A single X indicates the dyad was .5 standard deviation mutual grooming associates, while a double XX indicates that the dyad was 1 standard deviation mutual grooming associates.

By visualizing the data in this way, it is possible to examine specific dyadic association and grooming patterns over multiple periods. Below are visualizations for three chimps to provide a snapshot of the variety of association patterns that were present over the study period.

The strength and consistency of kin bonds can be seen by examining the association and grooming patterns between FN and FF, a mother-daughter dyad (Fig. A2). This dyad demonstrates strong and consistent association and grooming patterns across all periods in which both chimps were present in the study population. For each period, the DAI was 1 standard deviation above the population mean, 1 standard deviation above each chimp's individual means, and among the top three DAI values for FN. Additionally, the dyad was 1 standard deviation mutual grooming associates for each possible period. The consistency and strength of this relationship is typical of all mother-daughter dyads within the study.

Some non-kin pairs also have consistent and strong bonds that are similar to those bonds shown among kin pairs. SIF and JF are one non-kin dyad that demonstrate this (Fig. A3). This dyad shows strong association patterns across all five periods, and strong grooming patterns across three of the five periods.

However, there are some females that don't show any strong or consistent bonds with any other females, as demonstrated by NP (Fig. A4).

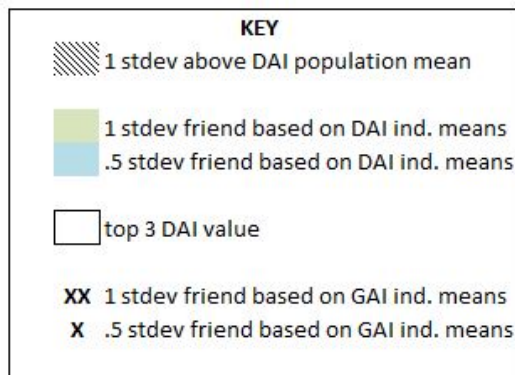


Figure A1: Key for visualizations.

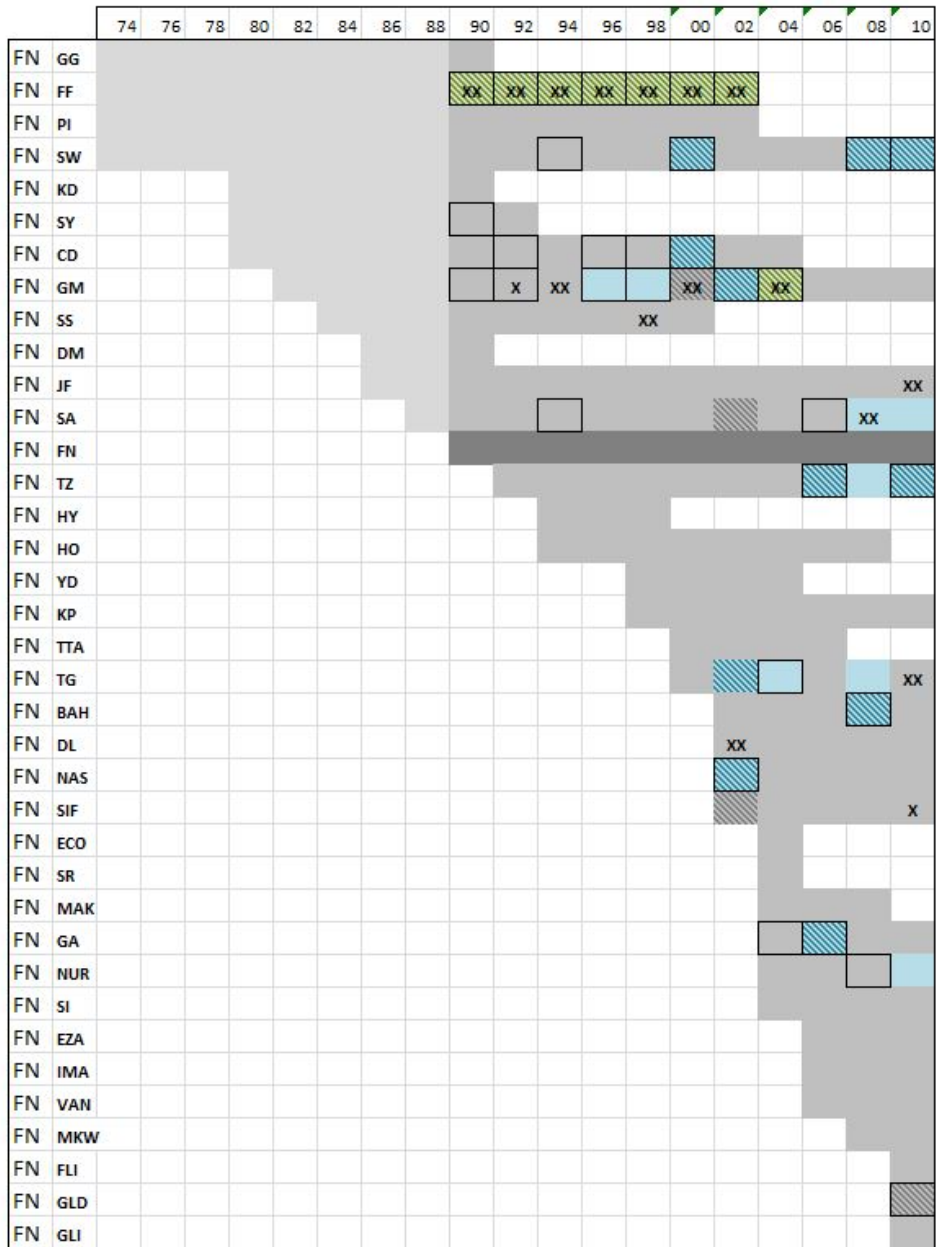


Figure A2: Visualization for FN.

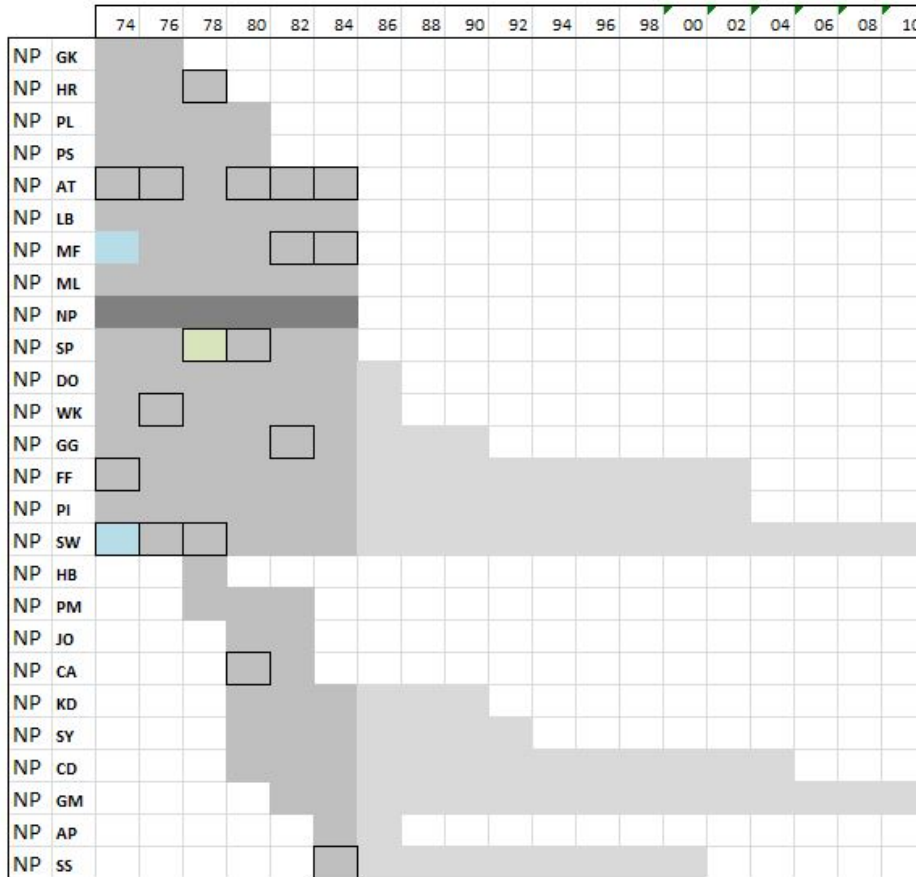


Figure A4: Visualization for NP.

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