



General Gregariousness and Specific Social Preferences among Wild Chimpanzees

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Wild chimpanzees form temporary parties that vary in size and composition. Previous studies have revealed considerable intraspecific variation in party compositions. We examined patterns of association among age, sex, and reproductive classes of chimpanzees at Ngogo in the Kibale National Park, Uganda. We employed a class-based association index and a randomization procedure to control for confounding factors and to test for differences between classes. Results indicate that males associated with other males significantly more than expected if all classes behaved equivalently, while females generally associated with individuals of the same sex less than expected. To interpret these patterns we used two additional indices that separate associations into two components: general gregariousness and preference for particular classes of associates. Males and estrous females were more gregarious than other classes, while anestrus females were less so. After controlling for general gregariousness, adult males as a class showed no specific preference for associating with each other. Anestrus females preferred each other as party members, and estrous females avoided each other. These results are consistent with previous findings that adult males are more gregarious than females. They diverge from the standard picture of chimpanzee society, however, by suggesting a mutual affinity among anestrus females, but not among adult males as a class.

KEY WORDS: *Pan troglodytes*; animal sociality; associations; randomization tests.

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INTRODUCTION

Patterns of association are a fundamental aspect of social organization because they reflect preferences for associating with or avoiding particular conspecifics. Using group composition data to describe and to quantify association patterns is therefore a frequent focus of socioecological studies (Ficken *et al.*, 1981; Wilkinson, 1985; Smolker *et al.*, 1992; Robert & Evans, 1993; Parker *et al.*, 1995; Holekamp *et al.*, 1997). Observations of group composition often suggest that association patterns vary as a function of age, sex, and reproductive status. Interpreting differences in association frequency as direct evidence for social affinities or bonds, however, can lead to erroneous conclusions.

Inferring social preferences from association frequencies is complicated by two distinct issues. One is that different individuals or classes can vary consistently in their association levels even if they behave identically. Measures of association reflect not only grouping behavior, but also confounding variables such as the relative frequency of each individual or class within the data set. For example, if males and females appear together more often in one data set than another this could indicate greater attraction between the sexes, or it might simply reflect a more even sex ratio or a larger average group size. Recently developed randomization procedures provide a means to control for confounding variables, and thereby quantify and test for real differences in grouping behavior (Smolker *et al.*, 1992; Pepper, 1996; Bejder *et al.*, 1998).

A second issue is that even when two classes show high levels of association because of their grouping behavior, it does not necessarily follow that there is any specific attraction, bond, or affinity between them. This is because even in the absence of any social preference, members of a more gregarious class will associate with each other more than with members of a more solitary class. Association levels can thus be broken down into two aspects: the tendency to aggregate with conspecifics in general, and the tendency to seek certain potential associates over others (Grassia, 1978). We refer to these two aspects of association as general gregariousness and pairwise affinity, respectively. Most indices used to quantify association levels reflect the combined effects of both, and thus cannot distinguish between them. In particular, this is true of the individual association indices commonly used in animal studies (Cairns and Schwager, 1987).

Chimpanzees (*Pan troglodytes*) have been the subjects of several field studies and provide a model system to investigate association patterns. Wild chimpanzees live in distinct unit-groups (Nishida, 1968) or communities (Goodall, 1973). Individuals within these communities do not generally

aggregate together in a common place at a single time, but instead form temporary subgroups or parties (Sugiyama, 1968) that constantly vary in size and composition. Early field research failed to discern any sex difference in association patterns (Goodall, 1965; Reynolds and Reynolds, 1965). Nishida (1968) was the first to describe consistent variations in chimpanzee grouping behavior. During his initial two-year study at the Mahale Mountains National Park, Tanzania, he noted that dyadic associations between males were more frequent than those between males and females, while associations between females were observed least often. From these observations, Nishida (1968) concluded that strong bonds form between males and that males compose the core of chimpanzee society.

Subsequent field work by Halperin (1979) and Wrangham and Smuts (1980) at the Gombe National Park, Tanzania, and Wrangham and colleagues in the Kibale National Park, Uganda (Wrangham *et al.*, 1992), helped to refine Nishida's (1968) picture of chimpanzee society. All of these investigators found that females spent large amounts of time alone compared with males, which were significantly more gregarious. At Kibale, Wrangham and colleagues (Wrangham *et al.*, 1992) also confirmed Nishida's earlier observation that associations among males occurred more often than those between females. The conventional view of chimpanzee society derived from these preceding studies was aptly summarized by Goodall (1986, p. 149) who noted: "The most deep-seated principles underlying chimpanzee community structure are those concerned with sex differences in sociability and in the choice of companions. Males are more gregarious than females and prefer each other's company, except when females are in estrus. Females are less sociable and spend most of their time with their own offspring - except when cycling, at which time they become very sociable." Although Goodall's (1986) qualification regarding the gregarious nature of estrous females has been recognized by several researchers (Kortlandt, 1962; Reynolds and Reynolds, 1965; Riss and Busse, 1977; Sugiyama and Koman, 1979; Furuichi and Ihobe, 1994), the degree to which female reproductive state affects chimpanzee sociability has seldom been investigated systematically (Sakura, 1994; Stanford *et al.*, 1994; Matsumoto-Oda, 1999).

Additional field research on chimpanzees at other sites throughout Africa suggests that sex differences in association patterns might vary substantially within this species. Sugiyama and Koman (1979) noted that males and females spent considerable time together resulting in a high degree of overall cohesiveness in a small, isolated community at Bossou, Guinea. Ghiglieri (1984) found no evidence of a sex bias in grouping tendencies in the unprovisioned and largely unhabituated Ngogo community in the Kibale Forest, Uganda; females associated with each other slightly more often

than males did with each other. These observations led Ghiglieri (1984) to conclude that strong bonds existed both between females and between males. Finally, recent observations by Boesch (1996) in the Tai National Park, Ivory Coast, led him to characterize chimpanzees as bisexually bonded. In this population unisexual parties consisting either of males or of females were rare; most associations involved mixed parties containing adults of both sexes.

Methodological problems impede the interpretation of these intraspecific differences in chimpanzee association patterns. First, prior studies have not properly controlled for confounding variables unrelated to grouping behavior that can affect observed association levels. For example, to examine associations some students have used the proportion of mixed-sex groups or groups containing particular combinations of age-sex classes (e.g., Goodall, 1965; Reynolds and Reynolds, 1965; Halperin, 1979; Tutin *et al.*, 1983; Boesch, 1996; Doran, 1997). These data are difficult to interpret because they reflect not only association preferences but also the frequencies of each class and average group sizes. A partial solution is to calculate a dyadic association index for every pair of individuals, and use the mean of all dyadic values as a measure of association between two classes (Nishida, 1968; Ghiglieri, 1984; Wrangham *et al.*, 1992). This procedure controls for the frequency of each class, allowing valid comparisons within a given data set. Comparisons between data sets, however, are still confounded by differences in average group size, the number of individuals in the community, and the relative frequency with which each is observed (Pepper 1996; Bejder *et al.*, 1998).

A second problem with interpreting differences in grouping behavior concerns the attribution of social bonds or affinities to particular classes of individuals. Differences in grouping behavior, both within and between populations, are often uncritically attributed to differing social preferences. Such assumptions are unwarranted, without considering the alternative explanation that classes differ only in general gregariousness, without discriminating among potential associates.

We examined grouping behavior in a newly habituated community of chimpanzees in the Kibale National Park, Uganda. We first examine overall levels of association among classes based on age, sex, and reproductive states. We then decompose these association levels into two components, general gregariousness and pairwise affinity. This procedure permits us to quantify how each factor contributes to the observed association patterns, and in particular whether males show a stronger preference for same-sex associates than females do. Our results provide evidence of social preferences in chimpanzee grouping behavior, but in ways that diverge from previous interpretations.

METHODS

Study Site and Subjects

We observed chimpanzees at Ngogo in the Kibale National Park, Uganda. Kibale lies at an interface between lowland and montane rain forest and is covered primarily with forest interspersed between large blocks of *Pennisetum purpureum* grassland (Struhsaker, 1997). The Ngogo study site includes a trail grid of approximately 12 km². Chimpanzees at Ngogo move over an area of approximately 25 km² that includes the entire study site. The Ngogo chimpanzees range primarily within forested areas, though they sometimes use areas of forest regenerating from past agriculture (Struhsaker, 1997), bush dominated by *Acanthus sp.*, and *Pennisetum purpureum* grassland (Ghiglieri, 1984; Butynski, 1990; Struhsaker, 1997).

Ngogo has been the site of previous behavioral research on chimpanzees by Ghiglieri (1984), who conducted field work during 18 months between 1976 and 1978 and an additional 5 months in 1981. Subsequent observations of chimpanzees were made by Wrangham *et al.* (1992) between 1988 and 1995, Grieser-Johns and field assistants between 1992 and 1993, and Watts from June to August 1993. Chimpanzees at Ngogo have never been provisioned, and the community is exceptionally large. As of June 1998, we have identified 117 individuals, including 26 adult males, 40 adult females, 16 adolescent males, 5 adolescent females, and 30 juveniles and infants. The community size reported here is a minimum estimate and will likely increase as additional subjects continue to be identified.

Behavioral Observations

Observations of chimpanzees were made during four periods by Mitani and Watts in June–December 1995, June–December 1996, June–August 1997, and January–June 1998. Watts conducted field observations between June and August 1996 and the entire 1995 and 1997 study periods. Mitani observed subjects between June and August 1995 and the entire 1996, 1997, and 1998 study periods. By virtue of field work during the previous 20 years, the Ngogo chimpanzees were semihabituated to human presence at the start of our observations in 1995. When feeding together arboreally in large parties, most chimpanzees tolerated human observers. In contrast, subjects fled quickly on the ground when they were alone or in small parties. Rapid progress in habituation has ensued from the beginning of the observations reported here. After one month, some chimpanzees permitted us to follow them within 15 meters along the ground, and after 4

months almost all adult and adolescent males, and a few females, tolerated observers within ≤ 15 meters while in parties; a few males allowed us to follow them when they were alone. Since the inception of field work, we have made near-daily contact with chimpanzees, and by the end of our last observation period, habituation had progressed to the point that all males and some females tolerated our presence to within a few meters.

The fission-fusion society of chimpanzees makes selecting statistically independent observations of parties difficult. Simply defining a party presents problems since chimpanzees sometimes disperse over a wide area yet move together in a single direction in an amoeba-like fashion (Nishida, 1990). Given these two considerations, we defined a party as all individuals present and within visual range when we first contacted chimpanzees, typically at the start of the day (cf. Tutin *et al.*, 1983). Several parties comprised individuals feeding in single trees, or in several nearby trees; in these latter cases, we allowed time to note individuals that were initially obscured by dense vegetation. When we contacted chimpanzees while they were traveling, and we could hear that several were moving in the same direction, we counted all individuals we saw on the ground and in any tree to which they moved to feed. If we re-initiated searches after losing subjects, subsequent sightings counted only if no member of the original party was present. When in the field together, Mitani and Watts frequently split to cover a larger portion of the Ngogo community range; sightings of multiple parties on a single day typically occurred when we two observers were watching subjects in different locations and were separated by hundreds of meters. For each party sighted, we tallied the number of individuals in four age-sex classes as defined by previous researchers (Goodall, 1986; Nishida *et al.*, 1990): adult males, adult females, adolescent males, and adolescent females. We subdivided adult females into 3 classes: estrous, anestrus and lactating, and anestrus and nonlactating (cf. Matsumoto-Oda, 1999). The following analyses are based on 880 observations of parties made during 3 years of study.

Data Analysis

To examine different aspects of grouping behavior we used several class-based association indices, derived largely from Underwood (1981). We first quantified association between two classes using a class association index, defined as the number of individuals of one class accompanying members of the other class on average (Appendix, expression 2). To factor this association level into components corresponding to general gregariousness and pairwise affinity, we used two additional indices. To measure the

overall tendency to associate with conspecifics, we employed a general gregariousness index, defined as the total number of associates accompanying members of a given class on average (Appendix, expression 3). To measure pairwise affinity among classes, we constructed an index that reflects the level of association after accounting for the general gregariousness of each. This pairwise affinity index is derived by dividing the class association index for two classes by the general gregariousness of each (Appendix, expression 4).

To generate expected levels of association and to provide statistical tests of the null hypothesis that all individuals behave the same way we used the group randomization method (Smolker *et al.*, 1992; Robert and Evans, 1993; Rowell and Rowell, 1993; Manly, 1997; Pepper, 1996, Bejder *et al.*, 1998). In this procedure the membership of the observed groups is repeatedly reshuffled, while retaining both the observed number of appearances of each class or individual and the observed distribution of group sizes. After each randomization, the selected index is calculated for each pair of classes or individuals. For each pair, the repeated randomizations generate a distribution of values that explicitly model the null hypothesis that all classes are equivalent in their grouping behavior. By incorporating them into this null model, this procedure automatically accounts for potentially confounding variables such as the number and size distribution of groups observed, and the relative frequencies of each class. The mean of the randomized indices for a pair provides an expected value under the null hypothesis that neither differs from the rest of the population in its grouping behavior. The ratio of observed to expected values indicates the magnitude of any deviation from expectation. Comparing the observed level to the 2.5% tails of the distribution of randomized values provides a two-tailed statistical test of the null hypothesis. We implemented the group randomization technique using the GROUPS program (Pepper, 1996), with 10,000 randomizations for each test. All tests were two-tailed. To display graphically deviations from null hypotheses, we present the ratios of observed to expected values minus 1. Positive numbers indicate observed values greater than expected, while negative numbers indicate observed values less than expected.

Our analyses involve multiple comparisons between classes. To correct for the increased probability of committing Type I errors when making these multiple comparisons, we lowered our criteria of significance using a Bonferroni adjustment (Holm, 1979). For k multiple tests, our adjusted significance thresholds were set at:

$$\alpha = a/(1 + k - i) \quad (1)$$

where $a = 0.05$ = the overall experiment-wise error rate and i = the i 'th

sequential test, ordered from smallest to largest p -value. Our analysis of the general gregariousness of each class involved 6 tests, so we set our initial alpha level to 0.008 ($=0.05/6$). The pairwise comparisons of classes involved 21 tests, so our starting criterion of significance was 0.002 ($= 0.05/21$).

RESULTS

Patterns of Association

Table I is a summary of deviations from the null hypothesis that all classes show the same grouping behavior. Association levels between the sexes are higher than expected for estrous females, and lower than expected for anestrus females. Within the sexes, males uniformly associated with each other more than expected, and females associated with each other less than expected. These patterns reflect the effects of both general gregariousness and pairwise affinity. In the following two sections we examine the contributions of each of these factors separately.

Variation in General Gregariousness

Figure 1 shows deviations from the expected number of associates for all six age-sex classes of chimpanzee. Each class formed groups with significantly more or fewer associates than expected by chance ($p <$ sequential Bonferroni criterion for all 6 comparisons). Both adult and adolescent males displayed a tendency to gather with more individuals than chance expectation. Although estrous females occurred in larger parties than expected, all classes of anestrus females associated with significantly fewer individuals than predicted if aggregations formed randomly.

Variation in Specific Social Preferences

To examine preferences for associating with particular classes of conspecifics, we performed a second set of randomization tests using the pairwise affinity index (Table II). Adult males and estrous females associated with each other significantly more than expected given the general gregariousness of each class. In contrast, adult males and anestrus adult females avoided each other. Although adult males and adolescent males were together slightly more than expected, adult males as a class did not show an

Table 1. Biases in association level among chimpanzee age, sex, and reproductive classes^a

	Adult male	Adolescent male	Anestrous nonlactating female	Anestrous lactating female	Estrous female	Adolescent female
Adult male	+0.03					
Adolescent male	+0.11	+0.11				
Anestrous, nonlactating female	-0.16	-0.16	-0.03			
Anestrous, lactating female	-0.33	-0.29	-0.10	-0.29		
Estrous female	+0.28	+0.23	-0.09	-0.23	-0.22	
Adolescent female	-0.22	-0.17	-0.17	-0.19	-0.16	-0.45

^aCell entries are O/E - 1, where O and E are observed and expected values of the class association index (Appendix expression 2). Expected values are means from 10,000 randomizations of the observed data. Positive values indicate greater association than expected, while negative values indicate less than expected.

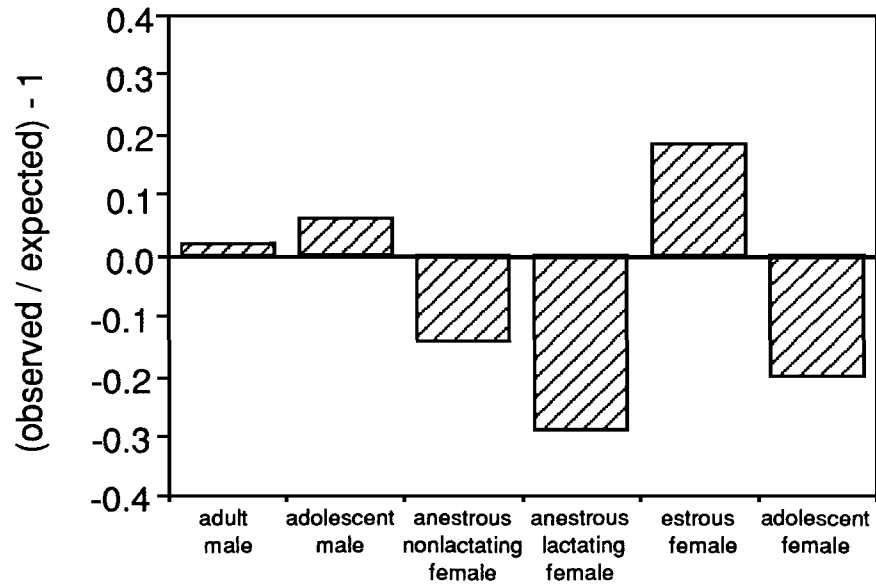


Fig. 1. General gregariousness of age, sex and reproductive classes as measured by the ratio of observed to expected number of associates minus 1 ($n = 880$ parties with 7,199 members). Observed and randomized values were calculated from Appendix expression 3, and expected values are the means from 10,000 randomizations. Values >0 indicate association with more individuals than expected, while values <0 indicate fewer associates than expected. All age-sex classes had significantly more or fewer associates than expected ($p < \text{sequential Bonferroni criterion for all six tests}$).

affinity for each other. Instead, the strongest affinities among classes involved anestrus females. Females displayed strikingly different preferences when in estrus, showing an affinity with adult males rather than other females, and a marked avoidance of other estrus females. Some entries in Table II that deviated sharply from the expected value of 0 did not reach statistical significance due to small sample sizes for the relevant classes.

DISCUSSION

The associations we observed between classes (Table I) are qualitatively similar to those reported in previous studies of chimpanzees. In particular, they display the typical patterns of high levels of male-male association and low levels of female-female association. Our interpretation, however, differs from those of previous authors. The two additional indices

Table II. Social preferences among chimpanzee age, sex, and reproductive classes^a

	Adult male	Adolescent male	Anestrous nonlactating female	Anestrous lactating female	Estrous female	Adolescent female
Adult male	-0.01					
Adolescent male	+0.02*	-0.02				
Anestrous, nonlactating female	-0.03*	-0.08*	+0.32*			
Anestrous, lactating female	-0.06*	-0.06*	+0.50*	+0.43*		
Estrous female	+0.06*	-0.02	-0.11	-0.08	-0.43*	
Adolescent female	-0.03	-0.02	+0.21*	+0.43*	-0.11	-0.13

^aCell entries are O/E - 1, where O and E are observed and expected values of pairwise affinity index (Appendix expression 5). Expected values are means from 10,000 randomizations of the observed data. Positive values indicate affinity, while negative values indicate avoidance. Entries marked with asterisks indicate pairs of classes that showed a significant level of affinity or avoidance.

we used help to clarify whether classes varied in their association levels because of differences in general gregariousness or specific pairwise affinities.

The analysis of general gregariousness revealed that males and estrous females were significantly more gregarious than other classes. In contrast, anestrus females had fewer associates than expected, especially when adolescent or accompanied by a nursing infant (Fig. 1). These findings are consistent with prior observations that adult males are more gregarious than anestrus females, but that females become very sociable during estrus (Goodall, 1986). Because it controls for general gregariousness, the pattern of pairwise affinity among classes (Table II) differs substantially from the pattern of association (Table I). The excess association among adult males compared to other classes was due to greater general gregariousness rather than to a specific pairwise affinity. In contrast, anestrus females showed strong affinities for each other that were masked in the association levels by their relative asociality. These findings depart from the standard model of chimpanzee society, which posits strong social bonds among adult males but not among females (Nishida, 1968; Goodall, 1986; Wrangham *et al.*, 1992).

Several previous studies have noted the regular occurrence of nursery parties consisting of multiple mothers with young (Kortlandt, 1962; Goodall, 1965; Reynolds and Reynolds, 1965; Sugiyama and Koman, 1979; Tutin *et al.*, 1983; Sakura, 1994; Boesch, 1996). These nursery parties and the bonds they appear to suggest between females have received scant attention, especially in contrast to the extensive documentation that exists for all-male parties (Nishida, 1968; Wrangham and Smuts, 1980; Goodall, 1986; Sugiyama, 1988; Takahata, 1990; Furuichi and Ihobe, 1994). When they are noted, nursery parties are sometimes assumed to be passive aggregations (Nishida, 1979). Instead, our results suggest that despite being relatively asocial, anestrus females may actively prefer each other's company. This interpretation diverges from conventional depictions of chimpanzee association patterns but is nevertheless consistent with observations from some prior studies. For example, Halperin (1979) reported that anestrus female chimpanzees consistently formed nursery groups with other females at the Gombe National Park. Similarly, Pusey (1983) found that after weaning her son one female at Gombe frequently associated with other females. Finally, Ghiglieri (1984) noted during his initial field work at Ngogo that adult females associated with each other more than adult males did with each other.

The interpretation presented here differs from that of a previous study at the Kanyawara study site in the Kibale Park. Here too, male chimpanzees associated with each other frequently, while anestrus females were rela-

tively asocial. Wrangham *et al.* (1999) took these observations as evidence that males preferred the company of other males, while females were attracted to males rather than to each other. Our findings also differ from the pattern described among the Taï chimpanzees in West Africa (Boesch, 1996). Levels of associations between Taï males and females are reported to be high, with females described as highly gregarious, resulting in “bisexual bonding” between the sexes (Boesch 1996). The effect of female reproductive state on the association patterns of the Taï chimpanzees cannot be ascertained since estrous and anestrus females were pooled in these analyses. At Ngogo, we found no evidence for male-female bonds among chimpanzees outside of the mating context. Instead, males and anestrus females appeared to avoid each other. This latter result differs from recent observations of chimpanzees at the Mahale Mountains (Matsumoto-Oda, 1999), where cycling females were in relatively large parties irrespective of their estrous state.

It is important to note that previous studies of chimpanzee grouping behavior suffer from two methodological problems. First, they have relied on the direct interpretation of association levels to infer social preferences. Such inferences are problematic because association levels are affected by variables other than grouping behavior, such as the composition of the population and the distribution of party sizes. For example, a low frequency of all-female groups might suggest weak female-female bonds, but could also result simply from small groups or a male-biased sex ratio. The group randomization procedure controls for these confounding variables, while also providing statistical tests for non-random differences in association. A second problem is that prior studies have not measured social preferences independently of general gregariousness. If males are found in larger groups than females, this will result in frequent male-male association and infrequent female-female association, even if males do not prefer male associates. The usual interpretation of high male-male association as evidence for a male preference for associating with males is therefore unfounded. Our use of an index of pairwise affinity circumvents this problem and provides robust evidence for association preferences among chimpanzees.

One final and previously undocumented aspect of chimpanzee association patterns revealed here concerns the preferential association between adult and adolescent males. The Ngogo community is extremely large and includes more males than has been documented in any other chimpanzee community. This unusual demographic situation, combined with the female-biased dispersal typical of chimpanzees, makes the coresidence of closely related males likely. In this context, we have noted frequent associations between specific pairs of adults and adolescents and have recently initiated

noninvasive studies sampling the Ngogo community to ascertain the genetic relationships between them (cf. Goldberg and Wrangham, 1997).

While the observations presented here do not accord with the view that association patterns reveal strong bonds among adult male chimpanzees as a class (Nishida, 1968; Goodall, 1986; Wrangham *et al.*, 1992), several limitations apply to our results. First, our analyses examine age, sex, and reproductive classes in the aggregate, and do not reflect individual variation within classes. This is important because differentiated social relationships are characteristic of chimpanzees. For example, the lack of general affinity among males shown by our results does not imply that specific male dyads are not strongly bonded. The class-based indices we used are complementary to individual-based indices and provide different information. Class-based analyses reveal differences between sexes and reproductive classes but obscure individual variation, while individual-based analyses reveal individual variation but obscure differences between reproductive states. The latter consideration is particularly important for females, which may radically change their association patterns with other females as well as males depending on their reproductive status (Matsumoto-Oda, 1999).

We also recognize that social bonds are not defined solely in terms of party composition, and that other aspects of social behavior such as grooming and agonistic support are also important (Wrangham, 1980; Sterck *et al.*, 1997). Researchers have portrayed chimpanzee society as male-bonded for reasons beyond putative association preferences (Nishida, 1968; Goodall, 1986; Wrangham *et al.*, 1992; cf. van Hoof and van Schaik, 1994). For example, male chimpanzees groom one another more often than members of any other age-sex class do apart from mothers and their young, and individual males typically have other males as their preferred grooming partners. In addition, agonistic support between males is common, and pairs of males form alliances over prolonged periods. Males at Ngogo cooperate in aggression both within and between communities, and form differentiated male social networks (Watts and Mitani, unpublished data). For example, 21 of 23 males groomed more with adult males than with members of any other age-sex class, and 20 of them had another male as their most frequent grooming partner. In contrast, grooming between females is uncommon. Thus, our analyses of group composition are insufficient grounds for us to recharacterize chimpanzees as female-bonded. However, they call into question some commonly accepted interpretations of association levels as direct evidence of social bonds.

We close with two final caveats regarding the nature of the data and analysis presented here. First, although we have attempted to collect an independent and unbiased set of observations regarding chimpanzee associations, it is unclear to what extent we have achieved that goal. For instance,

there are more adult females than adult males at Ngogo, but observations of the latter exceed those of the former in our data set. This problem is not unique to our study; given their relatively asocial nature, females have been undersampled in all previous field research on chimpanzees. At Ngogo, the paucity of observations of females may underscore an important sampling bias insofar as they were generally less well-habituated to human presence than males. As a result, we may have inadvertently oversampled females when together than when alone. Our future field efforts will attempt to rectify this potential sampling bias in order to assess its effects on the patterns displayed here. Second, the fact that our interpretations of chimpanzee association patterns differ from those of previous studies does not necessarily mean that the conclusions of those studies are incorrect. At present, there is no way to evaluate this until data from other sites are analyzed using similar methods. In the absence of information on how general gregariousness and pairwise affinity vary across study sites, the generality of the results presented here cannot be assessed. It is therefore crucial that these analytical methods be applied to observations from multiple populations before drawing wider conclusions about the nature of chimpanzee society.

APPENDIX: DERIVATION OF CLASS-BASED ASSOCIATION INDICES

Class Association Index

To measure the level of association between classes, we used the average number of members of class B accompanying each member of class A. This index, labelled as “C₃” by Underwood (1981), is calculated as

$$\frac{\sum a_i b_i}{\sum a_i} \quad (2)$$

wherein a_i = the number of members of class A in group i , b_i = the number of members of class B in group i , and the summations are over all groups. This index is asymmetric because members of class A may be accompanied by more members of class B than vice versa. However, because the group randomization procedure does not alter the total number of sightings of a given class ($\sum a_i$), the denominator of expression (2) cancels out in the ratio of observed to expected values, leaving a symmetric measure of association bias. The p -values based on this index are symmetric for the same reason.

There are two reasons why observed class association levels may deviate from those expected under the null hypotheses that all classes behave

the same way. The first is that members of some classes appear in larger groups than others, so that they have more associates overall. This is termed general gregariousness. The second is that two classes make up a disproportionate share of each other's associates, given the general gregariousness of each. These two sources of association bias can be independently quantified using the two indices described below.

General Gregariousness Index

To quantify how gregarious the members of a given class are, we used their number of within-group associates averaged across all appearances. This could be calculated by summing the number of associates of each class, but a simpler formula is:

$$\frac{\sum a_i(s_i - 1)}{\sum a_i} \quad (3)$$

wherein a_i = the number of members of class A in group i , s_i = the size of group i , and $(s_i - 1)$ = the total number of associates for each member of group i . This index was labeled C_4 by Underwood (1981), and is one less than the typical group size of Jarman (1974).

Pairwise Affinity Index

To construct an index that reflects only pairwise affinity, one can modify the class association index (expression 2) to remove the effects of general gregariousness. To accomplish this, Underwood (1981) suggested dividing the association index for classes A and B by class A's general gregariousness (expression 2/expression 3). However, the level of association between two classes is affected by the sociability of each. To completely control for general gregariousness, it is therefore necessary to divide by the general gregariousness of both. The resulting expression can be simplified because the total number of appearances of each class is not altered by group randomization. The summations $\sum a_i$ and $\sum b_i$ can therefore be neglected, because they are constants that cancel out of observed-to-expected ratios and associated p -values. The resulting formula is:

$$\frac{\sum a_i b_i}{\sum a_i(s_i - 1) * \sum b_i(s_i - 1)} \quad (4)$$

Although not necessary, it is convenient to multiply this expression by the correction factor $\sum s_i(s_i - 1)$, which represents the total number of associates

summed across all individual appearances in the data set. This correction factor is fixed under randomization because the number and sizes of groups are held constant, so that it cancels out of observed-to-expected ratios and p -values. However, it has the useful effect of making the index insensitive to the group sizes involved. The resulting pairwise affinity index:

$$\frac{\sum a_i b_i * \sum s_i (s_i - 1)}{\sum a_i (s_i - 1) * \sum b_i (s_i - 1)} \quad (5)$$

measures any tendency to associate that is not accounted for by the general gregariousness of each class, but instead is specific to the interaction of two particular classes.

Within-Class Measures

Both the class association index (2) and the pairwise affinity index (5) can be calculated within as well as between classes. To do so, b_i in the numerator is replaced with $(a_i - 1)$, reflecting the fact that within group i , each member of class A has $a_i - 1$ associates that are members of class A. Thus the within-class version of the class association index (expression 2) becomes:

$$\frac{\sum a_i (a_i - 1)}{\sum a_i} \quad (6)$$

and the within-class version of the pairwise affinity index (expression 5) becomes:

$$\frac{\sum a_i (a_i - 1) * \sum s_i (s_i - 1)}{\sum a_i (s_i - 1) * \sum a_i (s_i - 1)} \quad (7)$$

Relationship between the Indices

We have claimed that all differences in association levels are attributable to a combination of general gregariousness and pairwise affinity. If so, any deviation of the class association index from its expected value should be entirely accounted for by deviations from expected levels of gregariousness and affinity. This can be demonstrated formally by manipulating the above formulas. Randomization analyses of multiple data sets have also confirmed it empirically. The deviation of the association level from its expected value is the product of the deviations of the gregariousness

of each class and of the pairwise affinity between them. In other words, for any two classes, or for any class with itself:

$$R(CA_{AB}) = R(PA_{AB}) * R(GG_A) * R(GG_B) \quad (8)$$

where in $R(x)$ = ratio of observed to expected value of x , CA = class association index (2), PA = pairwise affinity index (5), GG = general gregariousness index (3), and the subscripts A and B denote the classes involved.

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