CHAPTER TWELVE

Comparison of Sex Differences in Gregariousness in Fission–Fusion Species

Reducing Bias by Standardizing for Party Size

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INTRODUCTION

Fission–fusion grouping means that individuals leave and join others according to their own decisions. It occurs in all chimpanzee populations as well as many other animals, including primates, cetaceans, carnivores, and ungulates. In chimpanzees, temporary associations ("parties") may last from a few minutes to several days. The individuals who form parties together all come from the same social network ("community" or "unit-group").

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The fission–fusion system is associated with variation in parameters such as the average party size, the average duration of time for a party to be stable, and the amount of time spent alone. The amount of variance in such parameters is also of potential interest. Using such variables, studies have examined how grouping tendencies in chimpanzees vary across seasons, individuals, sexes, ages, communities or populations (Symington, 1990; White, 1992; Chapman *et al.*, 1994a; Sakura, 1994; Doran *et al.*, 2002). Such comparisons are full of potential, but confidence in their conclusions is reduced by various methodological problems. Here we discuss methods for standardizing the comparison of grouping tendencies among chimpanzees.

First, while it is clear that parties must be defined in the same or comparable ways, this is often hard to arrange. For example, in relatively open forest, a definition like "all visible chimpanzees" is appropriate, whereas in thicker forest, observers may be forced to use a distance criterion such as "all individuals seen or thought to be within 50 meters." As a result, different observation conditions can lead observers to use different definitions. However, different forest habitats may also be expected to affect chimpanzee grouping variables such as party spread. This problem will probably never be completely solved, but efforts have been made to ensure standardization (Chapman *et al.*, 1993). In this chapter, we assume that parties have been satisfactorily defined in comparable ways.

Second, to reveal differences in grouping tendency, studies need to take account of differences in demographic factors such as the sex ratio or community size. For example, Boesch (1996b) concluded that variation in party size is partly a consequence of variation in community size. Boesch's approach implies that the appropriate dependent variable is sometimes the residual of party size on community size. Similar approaches could be taken with other independent variables, such as community sex ratio. The Ngogo research team attempted to remove this bias by using a randomization technique to calculate indices of gregariousness for each age–sex class (Pepper *et al.*, 1999; Mitani *et al.*, 2002). However, their results may have been biased by introducing the assumption that all individuals of an age–sex class behave in an equivalent manner.

Third, parties may be formed either because individuals have a general tendency to be gregarious or because they have an affinity for a specific other individual (or individuals). Both tendencies lead to grouping, which means that what appear to be similar results may have different causes. Thus, similar average party sizes between sexes or communities could therefore in theory represent different underlying tendencies. For example, Pepper *et al.* (1999)

concluded that chimpanzee males at Ngogo are more gregarious than females, but that females have higher specific affinities for each other.

The fourth problem is that it is impossible to select parties for observation at random. This is because individual chimpanzees move unpredictably through large areas of thick forest, which means that researchers do not have the luxury of scheduling their observations of individuals within the community according to a predetermined design. Instead, they must accept the opportunities that chimpanzees offer. Unfortunately, some parties are more easily located or observed than others (e.g., larger parties are often found more easily, because they are noisier); some individuals are better habituated than others (e.g., males are usually better habituated than females); and some individuals may be more gregarious than others (e.g., males more than mothers). In addition, some observers may be more concerned to obtain data on one class of individuals than another (e.g., males compared to females). For all these reasons, parties that contribute to monthly or yearly data sets are invariably a nonrandom representation of the community. Attempts to evaluate chimpanzee grouping behavior by simply calculating average party sizes observed are therefore misleading and provide little useful information to understand an inherently dynamic process. However, the extent of the bias and the variation in the bias between studies has not been described.

In order to make meaningful comparisons of grouping tendencies, therefore, we need to understand what the biases are, and how to control them. In this chapter we focus on controlling for party size and community composition.

In many studies, observers obtain data by recording from parties located by search. But this method inadvertently biases toward large parties (because they are more easily found and pursued than small parties). If party composition varies systematically with party size, therefore, grouping parameters will be biased also.

Such bias is well known from several sites. It was analyzed for Kanyawara chimpanzees by Wrangham (2000), who showed that mothers tended to be found in smaller parties than males or nulliparous females. Accordingly, apparent differences in party size or sex differences in gregariousness between sites could be a result entirely of observer differences in the degree of bias toward collecting data on large parties.

This means that comparisons between sites can be improved by controlling for party size. Accordingly, we here compare grouping tendencies between two communities, Kanyawara (Kibale) and Sonso (Budongo), by relating party composition to party size. The communities have similar size and composition, and live in habitats of somewhat similar overall structure (lightly disturbed high forest).

METHODOLOGY

Study Sites

This chapter compares party compositions in two communities of chimpanzees in Western Uganda: the Sonso community of Budongo Forest Reserve and the Kanyawara community of Kibale National Park. Individuals of both communities are well habituated, having been subject to continuous research for more than 10 years. Kanyawara is predominantly moist evergreen forest, with small segments of swamp, grassland, and colonizing forest (Chapman *et al.*, 1994a,b). Although the Budongo Forest Reserve is predominantly a moist, semideciduous forest, the home range of Sonso chimpanzees is a mosaic of forest types owing to a history of managed logging (Reynolds, 1992; Newton-Fisher, 1997). At Kanyawara, major chimpanzee food species include figs *Ficus sansibarica* and *Ficus natalensis*, as well as the drupe fruits *Mimusops bagshawei* and *Uvariopsis congensis*, which can comprise up to 75% of the diet during their short fruiting seasons; Kanyawara chimpanzees also spend an average of 20% (ranging up to 50%) of their monthly feeding time consuming piths. Sonso chimpanzees favor a variety of figs, particularly the abundant *Ficus sur* (*capensis*) and *Ficus mucuso*, as well as the fruits of *Celtis durandii* and *Broussonetia papyrifera*. Piths are rarely eaten at Sonso, while a variety of leaves (e.g., *B. papyrifera*, *Celtis mildbraedii*), flowers (*B. papyrifera*), and seeds (*Cynometra alexandri*) make up more than 20% of the diet (Newton-Fisher, 1999b).

Party composition data from the Sonso community were collected from September 2001 to November 2002; the data set consists of 4021 15-min scan samples (~1005 h). During this study period, the Sonso community comprised 51–58 individuals, including 12–13 males (8 adult, 4–5 subadult), 15–18 adult females, and 1–3 subadult females.

Data from the Kanyawara community were collected from January to December 2000; this data set consists of 8586 fifteen-minute scan samples (~2150 h). Community composition during this period was comparable to that of the Sonso community. The Kanyawara study community contained approximately 50 individuals, including 13 males (11 adult, 2 subadult), 15 adult females, and 2 subadult females.

Observation Methods

The same observation method was used to monitor party composition in each community. At 15-min intervals, observers recorded the number and identity of all individuals present in the party during that period. In both cases, observations were conducted primarily by senior field assistants with the assistance of students and other researchers. For the purposes of this analysis, we consider only nondependent individuals in our calculation of party size, as juveniles and infants can be easily missed or confused in counts.

Party composition analyses were performed by calculating the average number of individuals of each age–sex class present in scans of party size X. This was repeated for all party sizes. To control for the community's composition, numbers of chimpanzees were converted to the percentage of available members of the age–sex class that they represent. For instance, such data would state that an average of 20% of the community's adult females were present in a party size of 10, while at a party size of 20, 55% of the community's adult females were present.

Our analysis began by comparing three methods of quantifying party composition. First, all scan observations were used. Second, to control for any tendency by different observers to stay with certain types of parties longer, we recalculated these results using only the first observation of each party. In this case, we used the strict definition that scans after fissions and fusions were not included if individuals from the initial party were present. Third, to control for any bias in observation times, we performed the same analyses using only one observation per day, that occurring closest to 9:00 AM.

This comparison was instructive in that there was very little difference between plots produced using any of these three methods, and thus little evidence that minor biases affect this method of party analysis. Figure 1 gives an example of such a comparison, here illustrating the number of Kanyawara mothers present at each party size using the three different methods. As a compromise between maximizing data and minimizing potential bias, the results presented in this chapter use the first observation of each party (*n* = 507, Sonso; *n* = 499, Kanyawara).

In a separate analysis, we examined the composition of parties containing at least one fully swollen female. Since party size and the number of swollen females should be expected to vary over the year with food availability (Wrangham, 1977; Wrangham *et al.*, 1992, 1996; Chapman *et al.*, 1994a; Wallis, 1995, 1997; Doran, 1997; Isabirye-Basuta, 1998; Matsumoto-Oda, 1999a,b; but

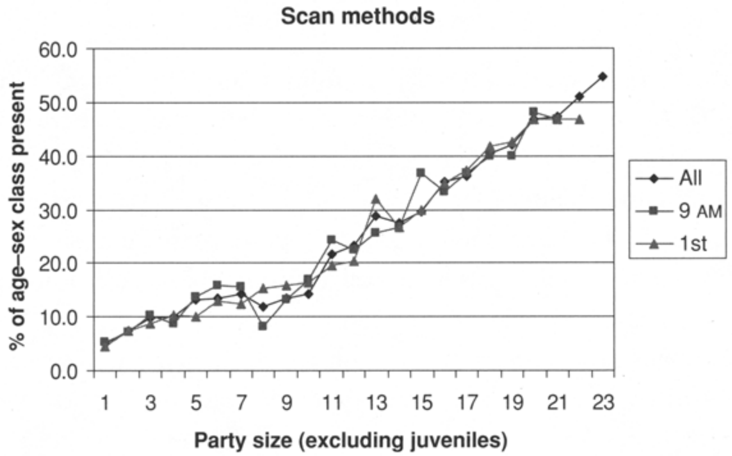

Figure 1. Three methods for evaluating party composition. Example data from Kanyawara adult females.

see Newton-Fisher *et al.*, 2000; Hashimoto *et al.*, 2001, 2003; Anderson *et al.*, 2002), we calculated average numbers for each month of adult and subadult males and nonestrous females in parties containing 0, 1, 2, etc., swollen females. Kanyawara data on estrous parties were collected from January 1999 to April 2001, and Sonso data from September 2001 to November 2002.

Definitions

"Party size" is the number of nondependent individuals considered to be traveling as a group, associating together, or feeding in the same patch of food. Subadult males are those whose testes have descended and who sometimes travel independently from their mothers. Males are adults when their testes have grown to adult size; their faces typically darken at this time as well. Subadult females in this analysis are those who have begun sexual cycling, while adult females are those who have given birth.(Goodall, 1986). A female is considered "fully swollen" when genital tissues are tumescent enough to form a tight slit and there is swelling in both the vaginal and circum-anal tissues (Dahl *et al.*, 1991). "Peripheral" or rare females (7 of 15 at Kanyawara; 6–8 of 15–17 at Sonso) are those who are observed in fewer than 15% of party scans; at Kanyawara these females have been shown to be spatially peripheral in their ranges, maintaining core areas to the north or the south of central females.

Statistics

Linear regression analyses were performed to calculate slopes of best-fit lines through the average party composition data points. The difference between regression slopes was tested using *t* statistics. To test if regression lines were significantly separated, an adjustment was made to a common slope and the difference between mean *y* values calculated using *t* statistics.

RESULTS

Sex Differences in Gregariousness

Both communities showed a significant difference in the gregariousness of males and females. A greater percentage of community adult males than adult females were present in all but the smallest parties and this effect was exaggerated as party sizes grew larger (Figure 2). The sex difference was more pronounced at Kanyawara, with a mean difference of 31% versus 16% at Sonso. This is consistent with previous reports of greater male general gregariousness in wild chimpanzees (Pusey, 1980; Wrangham *et al.*, 1992; Doran, 1997; Pepper *et al.*, 1999; Wrangham, 2000; but not Boesch, 1996b; Boesch & Boesch-Achermann, 2000).

Intercommunity Differences

We compared the two communities for differences in the representation of each age–sex class at various party sizes. These regressions revealed some interesting population differences, while showing, in some cases, striking similarities in patterns of party composition.

Adult males at Kanyawara were more gregarious than those at Sonso (Figure 3). Slopes of these regressions were virtually identical; that is, males were not joining parties at a significantly faster rate in Kanyawara. However, there was a small (9%) but significant difference in the mean *y* for the two communities, so that at any given party size more of the community's males were present at Kanyawara. At a party size of 11, which could contain all of the community's adult males in either case, an average of 63.6% (7) of Kanyawara's adult males were present, while only 43.8% (3.5) of Sonso's males were present.

When all males (adults and subadults) were considered, a significant difference was still detected (Kanyawara: $y = 4.38x + 3.30$; Sonso: $y = 4.20x + 0.60$;

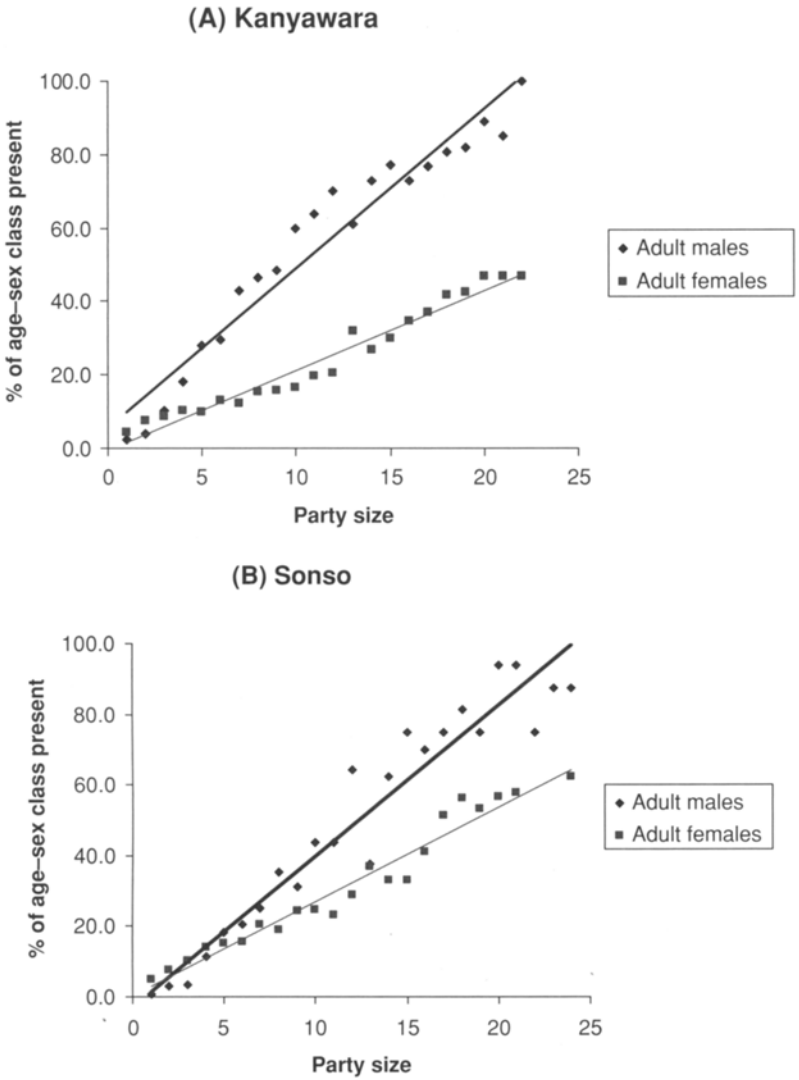

Figure 2. Regressions: sex difference in gregariousness. (A) *Kanyawara chimpanzees.* Males: $y = 4.35x + 5.48$; females: $y = 2.17x - 0.51$; differences between slope $= -2.17$, $t = -8.33$, df $= 40$, $P < 0.0001$; adjusted differences between mean $y = 30.97$, $t = 11.46$, df $= 41$, $P < 0.0001$. (B) *Sonso chimpanzees.* Males: $y = 4.26x - 2.60$; females: $y = 2.66x + 0.50$; differences between slope $= -1.60$, $t = -5.44$, df $= 42$, $P < 0.0001$; adjusted differences between mean $y = 16.04$, $t = 6.31$, df $= 43$, $P < 0.0001$.

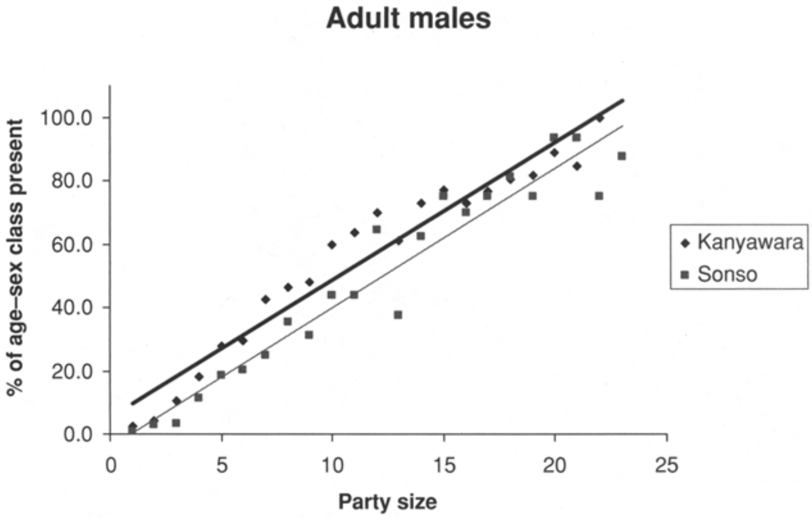

Figure 3. Regressions: intercommunity difference in gregariousness of adult males. Kanyawara: $y = 4.35x + 5.48$; Sonso: $y = 4.26x - 2.60$; differences between slope = -0.09, $t = -0.25$, df = 42, $P = 0.81$; adjusted differences between mean $y = 9.11$, $t = 3.95$, df = 43, $P = 0.0003$.

differences between slope = -0.18, $t = -0.68$, df = 40, $P = 0.50$; adjusted differences between mean $y = 4.80$, $t = 2.82$, df = 41, $P = 0.007$). However, we do not consider subadult males separately here because of a strong potential for individualistic effects given the small size of this age–sex class. Population differences observed for subadults may result from the age of the particular subadults considered and the status of their mothers. For example, the two subadult males in the Kanyawara data for this period still associated frequently with their rarely seen peripheral mothers; the five Sonso males who were subadults during this period were more diverse, including three who were near the transition to adulthood—two without living mothers and one who was the son of the dominant female in the community.

We found the reverse result for adult females. A significantly higher percentage of the parous females at Sonso were present in parties of a given size, and a significant difference in slopes revealed that this effect was greater as party size increased (Figure 4). Further investigation of this phenomenon revealed that the intercommunity difference in female gregariousness was primarily the result of peripheral female behavior. While an analysis of the percentage of central females in parties produced virtually identical regression lines (Figure 5), peripheral females showed much greater gregariousness at Sonso (Figure 6).

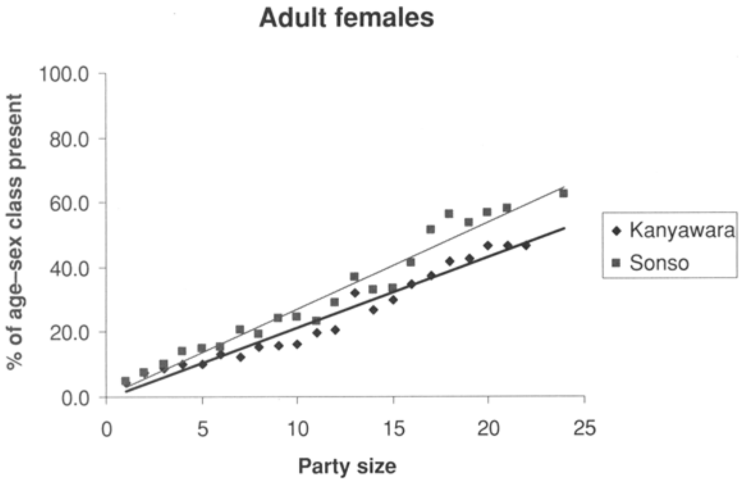

Figure 4. Regressions: intercommunity difference in gregariousness of parous females. Kanyawara: $y = 2.17x - 0.51$; Sonso: $y = 2.66x + 0.50$; differences between slope = 0.49; $t = 3.07$; df = 40, $P = 0.004$; adjusted differences between mean $y = -6.67$, $t = -5.92$, df = 41, $P < 0.0001$.

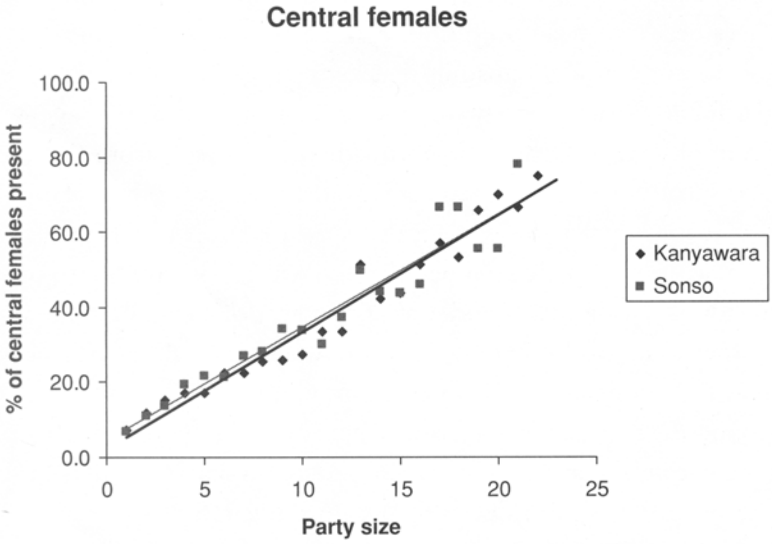

Figure 5. Regressions: intercommunity difference in gregariousness of central parous females. Kanyawara: $y = 3.12x + 2.09$; Sonso: $y = 3.17x + 3.21$; differences between slope = 0.05; $t = 0.22$, df = 40, $P = 0.83$; adjusted differences between mean $y = -1.72$, $t = -1.11$, df = 41, $P = 0.27$.

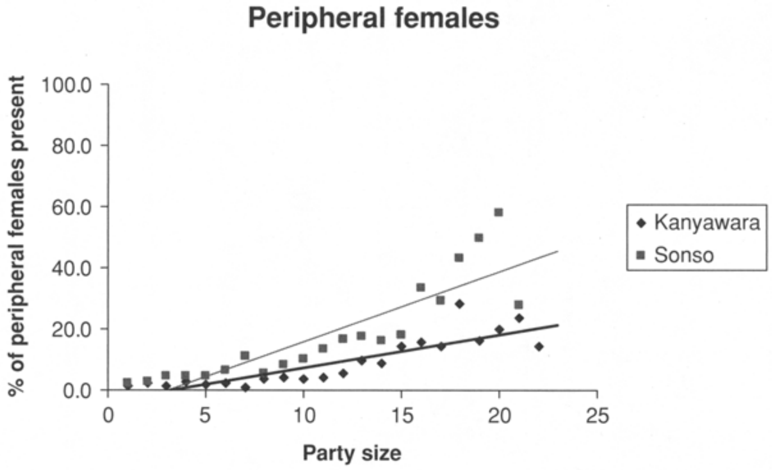

Figure 6. Regressions: intercommunity difference in gregariousness of peripheral parous females. Kanyawara: $y = 1.09x - 3.44$; Sonso: $y = 2.03x - 4.66$; differences between slope = 0.94; $t = 2.91$, df = 40, $P = 0.006$; Adjusted differences between mean $y = -9.59$; $t = -4.26$, df = 41, $P = 0.0001$.

Significant differences were detected in both slope and intercepts for peripheral females, who showed the greatest difference in larger parties. A party size of 20, which could be comprised without any peripheral females in either community, contained an average of nearly 60% (4.2) of the 6–8 peripheral mothers at Sonso but only 20% (1.4) of the 7 peripheral mothers at Kanyawara.

As with males, intercommunity differences in subadult female gregariousness are difficult to describe because of large potential for individualistic differences. In this case, we found interesting evidence of such individual effects when comparing the current Kanyawara data set to a previous analysis of party composition at Kanyawara (Wrangham, 2000). In the examination of 1995–1996 data, using the same method, two nulliparous females seemed to behave more like adult males than like adult females (Figure 7A). This is consistent with the hypothesis that adolescent females suffer fewer costs of grouping than do mothers owing to lack of dependent offspring and decreased travel time (Wrangham, 2000). However, our current examination of 2000 data produced the opposite result: the two nulliparous females in this analysis were more similar in grouping behavior to adult females (Figure 7B). This difference is probably due to the subadults considered. In the 1995–1996 study, the subadult females were both immigrants, while the 2000 subadults were the daughters of central mothers. The Sonso subadults also showed gregariousness more similar to adult females

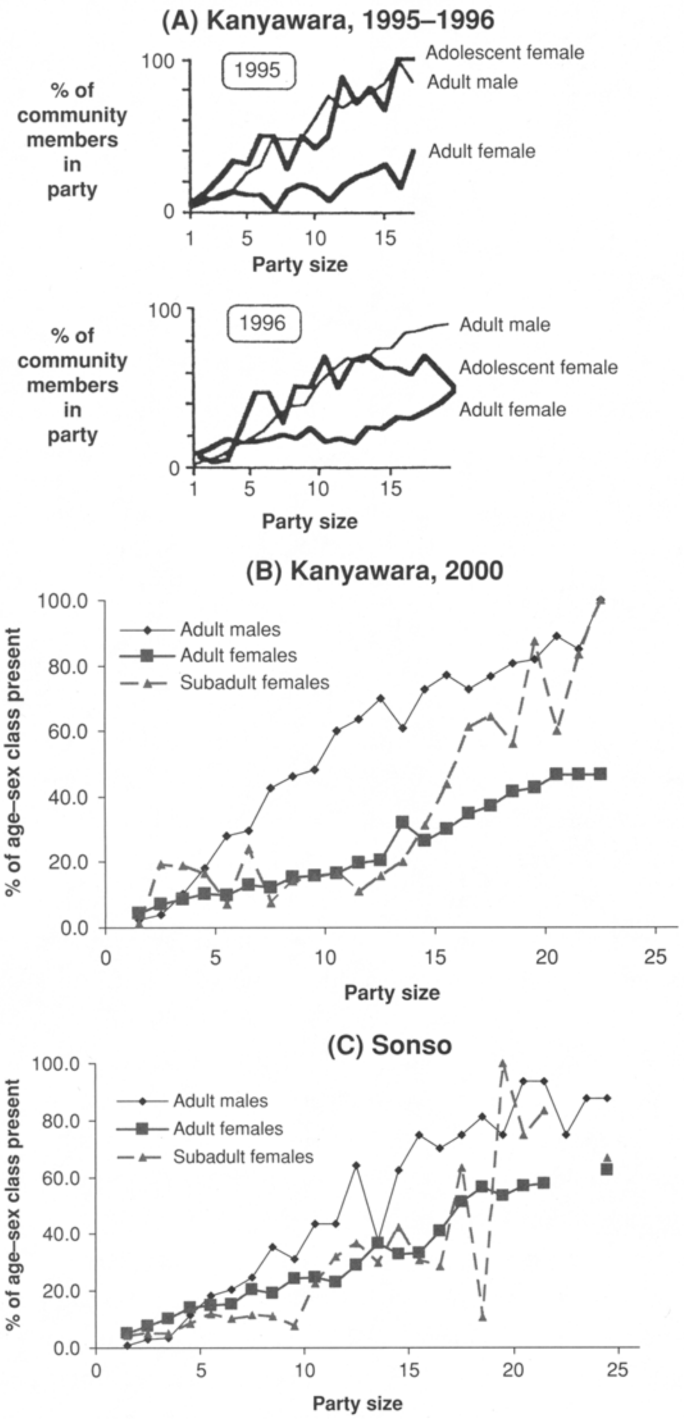

Figure 7. Subadult female grouping behavior in comparison with adult females and adult males: (A) Kanyawara 1995–1996 (Chart from Wrangham, 2000), (B) Kanyawara 2000, (C) Sonso 2001—2002.

(Figure 7C). Only one of the three Sonso females had a mother in the community, while another immigrated 4 years previous, and another with unclear immigration status had been in the community for at least 9 years. Although based on a few individuals, these current data do not support the hypothesis that adolescent females, free from the constraints of offspring, are more gregarious than mothers; subadult females' degree of gregariousness may vary according to the presence of their mother or their length of tenure in the community.

"Estrous" Parties

Next, we examined the grouping behavior of the two communities as the number of fully swollen females increased. There was no discernable difference in the affiliation of nonswollen females with these parties. Kanyawara males, however, associated in greater numbers (average of 2.25 more) with swollen females than did Sonso males, and their numbers rose more rapidly as the number of

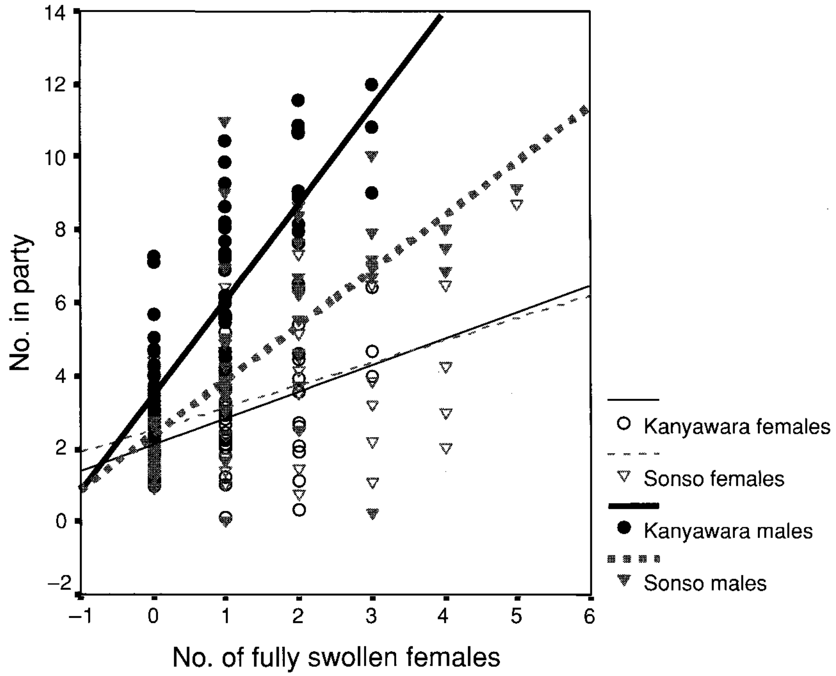

Figure 8. Regressions: intercommunity difference in party affiliation with swollen females. Kanyawara males: $y = 2.63x + 3.51$; Sonso males: $y = 1.51x + 2.45$; differences between slope $= -1.12$, $t = -3.15$, df $= 111$, $P = 0.002$; adjusted differences between mean $y = 2.25$, $t = 5.50$, df $= 112$, $P < 0.0001$. Kanyawara females: $y = 0.73x + 2.10$. Sonso females: $y = 0.61x + 2.52$; difference NS.

swollen females increased (Figure 8). Newton-Fisher (1999a) recorded similar averages for Sonso, with the number of males increasing for parties of one and two swollen females but not increasing significantly with the addition of more swollen females.

Is the Sonso–Kanyawara Difference Due To Behavior of Males or Females?

Our analyses of party composition in these two communities of chimpanzees show differences in the gregariousness of both males and females. In this type of analysis, it is possible, however, that a difference in the social behavior of one sex would make it appear as if the other was behaving differently; that is, if males are more gregarious in one community, then a party of a given size would necessarily contain fewer females. However, these communities show evidence of differences in the behavior of both sexes.

Clearly, peripheral females at Sonso appear less socially isolated than peripheral females at Kanyawara. On the other hand, the analysis of estrous parties illustrated that there was a difference in male gregarious that was demonstrably separate from the effect of female gregariousness. In addition, when we examined the number of bisexual parties containing *x* number of males, regardless of party size, we found that the majority of Kanyawara parties have more males (Figure 9). In particular, parties with seven or more males were more frequent at Kanyawara (38% of all parties, compared with 20% at Sonso).

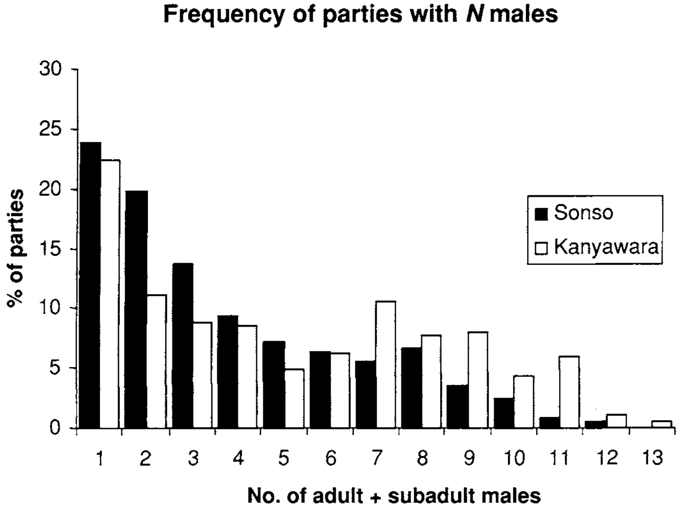

Figure 9. Observation frequency of parties with a given number of males.

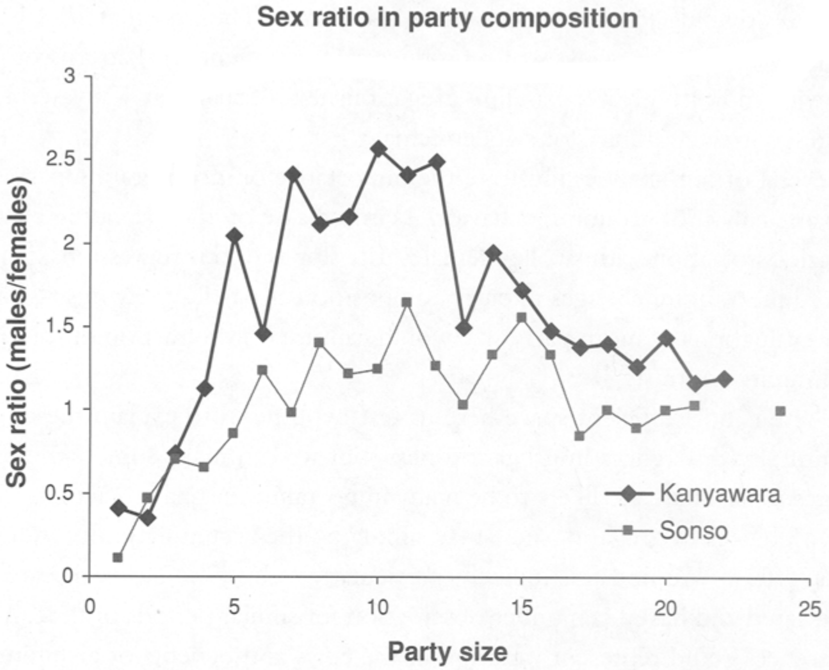

Figure 10. Sex ratio of parties. Males = adult + subadult. Ratios expected by community composition: Kanyawara = 0.76; Sonso = 0.68.

When we examine the cumulative effect of male and female differences, the contrast is pronounced. Figure 10 depicts the male-to-female sex ratio at each party size. Across party sizes, this sex ratio averaged 1.6 at Kanyawara and 1.0 at Sonso. All parties of greater than three are predominately male at Kanyawara. At Sonso, males tend to outnumber females in parties of 6–16 and, even then, not to the dramatic degree that they do at Kanyawara.

DISCUSSION

One way to look at data presented in this chapter is to point out the striking similarities in grouping patterns between the two sites. For instance, regression lines for percent central mothers present at each party size were virtually identical between the two communities. While parties of the same size contained a greater percentage of the community's males in Kanyawara, the regression slopes for the two communities were very similar.

On the other hand, the differences are clear and consistent. Kanyawara's central and peripheral females show a much greater contrast in their social strategies than do females at Sonso (see also Emery Thompson *et al.*, Chapter 13, this volume, for analysis of reproductive consequences). Patterns of male behavior indicate greater baseline gregariousness of males at Kanyawara and suggest a greater affinity for swollen females.

Several of our analyses illustrate the importance of incorporating party size into an analysis of grouping behavior. As in the case of understanding changes in male association with swollen females, the slopes of our regressions demonstrated meaningful changes in party composition as parties grew in size. Snapshot evaluations of mean party size would capture only a fraction of this intercommunity contrast.

There is not sufficient space here to test hypotheses to explain these intercommunity differences in gregariousness, but we can make some preliminary suggestions. There are likely to be many important interrelated factors.

Differences in gregariousness may simply be the accumulation of individualistic effects. We find this unlikely, particularly as both communities are well habituated and have been under observation for similar periods of time. These differences could represent variation in the costs and benefits of grouping for male and female chimpanzees at the two sites:

(i) Female cost of grouping at Sonso could be lessened by reduced scramble competition for food (Janson & Goldsmith, 1995; Wrangham, 2000; Williams *et al.*, 2002a), for instance if feeding trees or patches were larger and/or fruit abundance less seasonal, as proposed by Newton-Fisher *et al.* (2000). Increased use of nonfruit items could decrease cost of grouping, but this is unlikely the source of the difference in this case as Kanyawara chimpanzees could do this by utilizing THV. Furthermore, Wrangham *et al.* (1996) report that THV had little effect on feeding competition, as fruit and fig production continued to determine party size.

(ii) Female cost of grouping could be increased as an effect of male coercive behavior (Wrangham, 2002). Severe and prolonged male beatings of females, even with the use of large branches as weapons, can take place at Kanyawara even outside of the context of sexual coercion (Linden, 2002; Muller, 2002). Sonso females experience relatively little severe aggression from males, those few cases typically occurring in the context of failed consort attempts (personal observation, MET; Newton-Fisher, in press).

(iii) Male benefits of grouping could be increased because of (a) more frequent hunting and/or (b) increased intercommunity encounters. Larger parties should be more successful at or more likely to engage in these endeavors, and party membership may promote bonds that are beneficial for these activities (Stanford *et al.*, 1994; Mitani & Watts, 1999; Boesch & Boesch-Achermann, 2000; Wilson *et al.*, 2001, 2002; Watts & Mitani, 2002). Because they typically occur at the borders of the range, intercommunity encounters are so rarely observed that it would be difficult to judge this assertion. However, Newton-Fisher (1999a) suggests alternatively that male alliances may be better fostered in small parties with less interference from competitors.

(iv) Greater reproductive rates could alter benefits of grouping for males, particularly in parties with cycling females, as suggested by operational sex ratio theory (Mitani *et al.*, 1996a). That is, if fecund females are less common, males may be more likely to associate with females or with other competing males to increase their chances of encountering a fecund female.

(v) Differing distribution of fruiting trees (Newton-Fisher *et al.*, 2000) and/or size of home range might affect gregariousness in a chance manner. That is, when major food species are concentrated in a smaller area, individuals may be more likely to encounter one another. Newton-Fisher (2003) estimates the home range for Sonso chimpanzees to be half the size of those of Kanyawara, despite comparable community size. However, this could be expected to have the same effect on gregariousness of both sexes.

This comparison, as with many others, illustrates the further need to document the diversity of behavior in chimpanzees. It is increasingly unproductive to make overly restrictive generalizations about the behavior of chimpanzees as a species. Behavioral diversity in chimpanzees, as in humans, is likely to extend well beyond easily observable differences in material culture and foraging strategies, to more subtle differences in everyday social interactions.

Cost of grouping arguments typically are posed in the context of sex differences in party membership within a single community. These examinations have provided intriguing hypotheses (Wrangham, 2000; Williams *et al.*, 2002), but these data are limited in their hypothesis-testing capacity. We propose that intercommunity comparisons of gregariousness would be useful in testing these hypotheses across a range of ecological and sociosexual circumstances. These data collection and analysis methods provide a simple means to compare study communities; while controlling for varying composition of communities, they provide a dynamic view of party composition changes with increasing party size.

We encourage other chimpanzee researchers to assist us in documenting this variation in male and female gregariousness.

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