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Pygmy Chimpanzee Social Organization: Variation With Party Size and Between Study Sites

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Descriptions of social organization based on interactions are difficult for fission-fusion primates, such as pygmy chimpanzees, as interactions may depend on association in parties. Frequencies of male-male and male-female affiliative and female-male and female-female aggressive interactions among Lomako pygmy chimpanzees occurred in proportion to the presence of each sex in parties. Male-male aggression and female-male affiliation, however, were more frequent than expected on the basis of party membership. Females with small swellings received more grooming and less mating than expected. Patterns of interactions at Lomako also varied with party size. Female-female affiliation predominated in small parties, while male-female affiliation predominated in larger parties. This trend parallels observed differences between the Lomako and Wamba study sites. Male-female affiliation is more frequent at Wamba where party sizes are larger. Differences between study sites may also reflect provisioning, habituation, predator threat, and habitat. Provisioning at Wamba may result in higher frequencies of aggression among males and lower levels of aggression among females. Comparison between earlier and later Lomako studies suggests that increased habituation is associated with greater differences from, rather than more similarity to, results from Wamba. Differences between Lomako and Wamba in habitat, provisioning, and human (but not non-human) predation, by affecting party size and composition, most likely account for the observed differences in social organization between the two sites.

Key words: interactions, mating, provisioning, habituation

INTRODUCTION

Social organizations are often described on the basis of relationships and interactions [Hinde, 1976, 1979]. If interactions vary with observed party membership, then differences in party size or composition could produce differences in perceived social organization. Fission-fusion primates such as pygmy chimpanzees vary their social grouping. Because of flexibility in party membership, individuals

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have a constantly changing array of others with which to interact. In this paper, the relationship between social organization and party size and composition is examined for pygmy chimpanzees.

Social organization of pygmy (bonobo) chimpanzees, *Pan paniscus,* has been studied at two major study sites in Zaire: Lomako Forest [Badrian & Badrian, 1984; Thompson-Handler et al., 1984; White, 1986, 1988, 1989; White & Burgman, 1990] and Wamba [Kano, 1980, 1982; Kuroda, 1979, 1980; Kitamura, 1983; Furuichi, 1987].

Descriptions of social organization of the two study populations are similar but do not completely concur. At Wamba, there is affiliation between males and females in many aspects of social organization, including interactions [Kano, 1980; Kuroda, 1980, 1984] and party composition [Kano, 1982; Kuroda, 1979; Kitamura, 1983]. There is also tolerance, if not affiliation, among females, but this is generally considered to be secondary in importance to affiliation between the sexes [Kano, 1982; Kitamura, 1983]. The Lomako Forest study population shows affiliation between males and females [Badrian & Badrian, 1984]; however, affiliation among females is more apparent, as shown by recent studies of party membership and nearest neighbor distances [White, 1986, 1988, 1989; White & Burgman, 1990]. Study sites, therefore, appear to differ in the relative importance of affiliation between males and females compared to affiliation among females. Affiliation, however, has been examined using different criteria (interactions and party composition at Wamba, nearest neighbors and party composition at Lomako). This paper presents new information on interactions at Lomako that is comparable to that from Wamba.

Differences between sites in party size and composition may also account for the apparent disparity in social organization. Data on party composition and nearest neighbors at Lomako [White & Burgman, 1990] suggest that only in large parties do associations between males and females become more significant than associations among females. Since average party sizes at Wamba were larger than those at Lomako (16.9 for $n = 147$ at Wamba [Kuroda, 1979], and 6.2 for $n = 114$ at Lomako [White, 1988]), differences in social organization may reflect the party sizes observed.

Variation in patterns of association and affiliation may reflect individual costs and benefits of being in particular sized parties [White, 1989; White & Burgman, 1990]. Association and affiliation among females is critical for defense of food patches [White, 1986], especially in small parties. These parties occur in patches where food is limited [White & Wrangham, 1988]. Small parties contain no males or only a single male that excludes others from the party [White & Burgman, 1990]. In the large parties found in superabundant food sources [White & Wrangham, 1988], more males enter and maintain feeding proximity to females [White & Burgman, 1990]. If these patterns of association are also reflected in affiliative interactions, then affiliations among males and females may be more apparent at Wamba simply because parties are larger.

Frequencies of male-female affiliation also may reflect reproductive strategies in that males interact more with certain females in order to increase chances of mating. Differences in the distribution of potentially reproductive females in a study population, therefore, may produce differences in male-female affiliation. This paper presents data on the relationship between both grooming and mating and the size of the sexual swelling of the female.

This paper also examines the relationship between social organization and party size. Four hypotheses are developed to account for differences in party size and social organization between the two study sites. These hypotheses are that

the differences result from variation with (1) habitat, (2) provisioning, (3) habituation, and (4) predation.

METHODS

Social interactions of non-provisioned pygmy chimpanzees in the Lomako Forest were recorded opportunistically [Altmann, 1974] between October 1984 and July 1985. The Lomako Forest study site covers 40 square kilometers of mainly climax evergreen, polyspecific forest in the Equateur province of central Zaire [White, 1986]. Observations were made on recognizable individuals from two separate communities and a splinter group, and on unknown individuals (see Badrian & Badrian [1984], Thompson-Handler et al. [1984, 1986] and White [1986] for descriptions of the study population). Interactions were classified according to age and sex of the individuals involved. Party size (excluding infants) at the time of the interaction was recorded. Parties were classified as small (2 to 6 individuals), medium (7 to 10 individuals), and large (11 to 15 individuals) parties. Only dyadic interactions among adults and subadults were included in this analysis.

Categories of Behavior

Interactions were classified as affiliative or aggressive using categories similar to those previously employed in studies at Wamba. Affiliative interactions included affiliative approaches, grooming, genito-genital (GG) rubbing [Kano, 1980; Kuroda, 1980; Thompson-Handler et al., 1984], and play. Aggressive interactions included chases and fights.

These interactions involved two active participants. The number of male-female interactions was, therefore, the same as the number of female-male interactions, except for chases and approaches which were classified according to the initiating sex.

Age and Sex Classes

The age and sex of each individual (and the size of the sexual swelling for females) were recorded. The major age classes used were similar to those described by Thompson-Handler et al. [1984] for pygmy chimpanzees at the Lomako Forest study site, and by Goodall [1986] for common chimpanzees. Female sexual swellings were categorized according to their shape and size [White & Thompson-Handler, in review; Table I].

Statistical Analyses

The probability of observing an interaction in each party was calculated from the number of individuals of each sex present. The probabilities of mating and of male-female grooming were calculated only for parties comprised of at least one male and one female. Expected frequencies of interactions were then calculated from these probabilities, taking into account the length of time each party composition remained constant and the frequency with which each sex interacted. Observed and expected frequencies were compared using goodness of fit G-tests [Sokal & Rohlf, 1981].

RESULTS

The observations totaled 241 dyadic interactions between adults, subadults, and adolescents. The sex of both partners was not observed for 8 interactions. The 37 observed matings were analyzed separately. Of the remaining 196 interactions, there were 24 affiliative or aggressive interactions between males, 88 between females, and 84 between a male and a female (total of 392 interacting individuals

TABLE I. Size Classes of Female Sexual Swellings

Size	Description
0	completely flat circumanal and labial regions
I	the circumanal region was flat, but the labial regions showed very slight tumescence
II	the circumanal region was flat and the size of the labial region was moderate
III	both the circumanal region and the labial region were mildly swollen
IV	the circumanal region showed slight tumescence and the labial region was of medium size
V	both the circumanal region and the labial region were of medium size
VI	both the circumanal region and the labial region were of large size
VII	at maximal tumescence

(excluding matings); Table II). The probability of observing an interaction involving a female was higher than one involving a male since parties contained more females than males. Expected frequencies are based on the observed party compositions so that statistical differences will show interactions that do not reflect the amount of time spent together.

Males interacted affiliatively with others in proportion to the presence of each sex in parties (Table II). Males interacted aggressively significantly more frequently with other males, and less frequently with females, than expected. Females interacted aggressively with others in proportion to the presence of each sex in parties, but interacted affiliatively more with males, and less with females, than expected. Aggressive interactions made up a small proportion of all interactions by females (16%). This category accounted for a larger proportion of the total observed interactions by males (28%).

Size of Sexual Swelling

The frequency of grooming between males and a female was dependent on the size of the female's sexual swelling (Fig. 1a). The major departures from expected were more grooming of females with class I and less with class II swellings. These differences may reflect age differences since class I females were young adult or adolescent females whereas females with class II swellings were older adult females.

Copulations were observed on 37 occasions. The frequency of mating was dependent on the size of sexual swelling of the female (Fig. 1b). Females with swellings of size classes V and VI mated more frequently than expected. Mating did, however, occur at all stages of the sexual swelling.

Interactions and Party Size

Both affiliative (Fig. 2a) and aggressive interactions (Fig. 2b) among males were mostly observed in large parties (50.0% of affiliative and 71.4% of aggressive). In contrast, most affiliative and aggressive interactions among females were observed in small parties (43.7% of affiliative and 46.2% of aggressive). Most affiliative interactions between males and females were observed in medium and large parties (45.5% in medium parties and 36.4% in large parties), and most aggressive interactions were observed in medium sized parties (47.4%).

Comparison Between Study Sites

At Lomako, both females and males interacted affiliatively more with females than with males. There were slightly more affiliative interactions among females

TABLE II. Observed and Expected Distribution of Interactions*

	All interactions		Affiliative		Aggressive		Groom		Approach		Chase	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Male-male	48	41	24	28	24	11	20	16	1	2	11	6
Male-female	84	91	67	63	13	26	33	37	6	5	9	14
G-test	1.685		0.984		19.427		1.372		0.802		5.382	
P	ns		ns		<0.001		ns		ns		<0.05	
Female-male	84	60	67	48	13	9	33	22	15	9	9	5
Female-female	176	200	142	161	28	32	62	73	24	30	12	16
G-test	11.520		9.024		2.083		6.508		4.614		3.676	
P	<0.001		<0.01		ns		<0.05		<0.05		ns	

*Values are numbers of individuals involved in combination. Matings are not included.

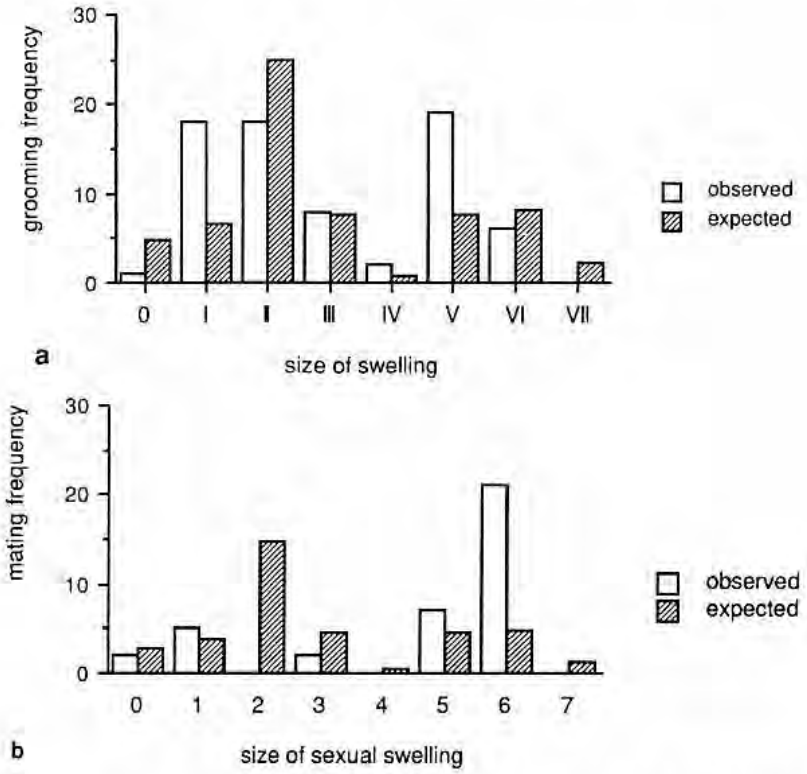

Fig. 1. Distribution of interactions with size of female sexual swelling (see Table I). Expected frequencies were based on the probabilities of observing each interaction, the length of observation, the observed party sizes and composition, and the observed rates of interaction. **a:** Frequency of male-female grooming. Expected distribution as calculated from observations of parties with at least one male and one female. Observed and expected distributions were significantly different (goodness of fit G-test, $G = 37.27$, $P < 0.001$). **b:** Frequency of mating. Expected distribution was calculated from observations of parties with at least one male and one female. Observed and expected distributions were significantly different (goodness of fit G-test, $G = 63.36$, $P < 0.001$).

than between males and females, but slightly more grooming between male-female pairs than between female-female pairs. At Wamba, grooming between males and females was more frequent than grooming between females (Fig. 3a).

The numbers of grooming partnerships of each sex combination (male-male,

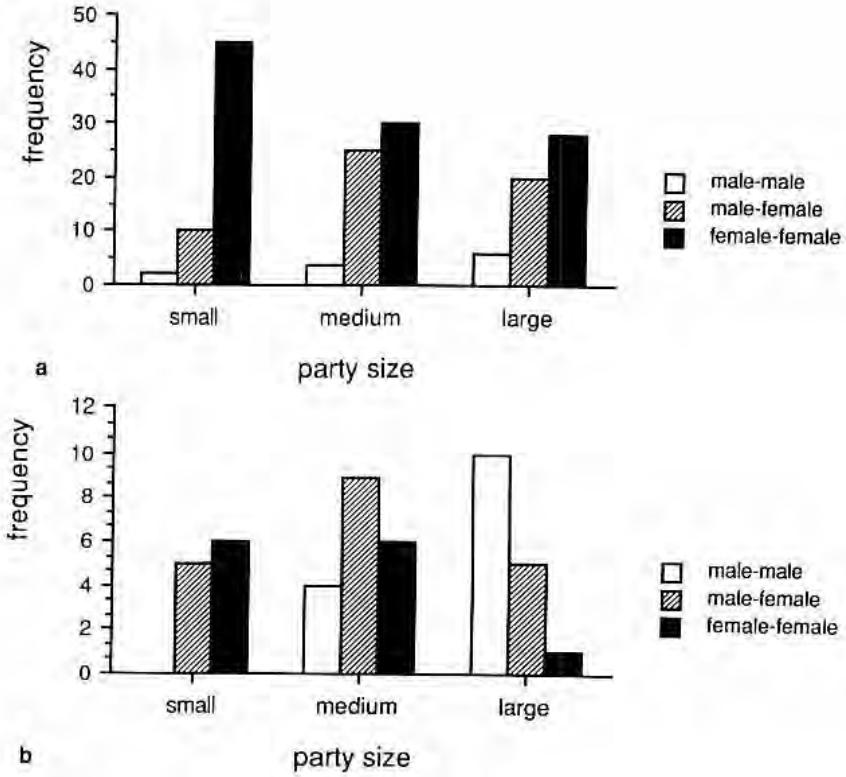

Fig. 2. Differences in observed frequencies of male-male, male-female, and female-female interactions with increasing party size. **a:** affiliative interactions. **b:** aggressive interactions.

female-male, female-female) from the two studies at Wamba [Kano, 1980; Kuroda, 1980] were not significantly different from each other (test of independence, G = 1.033, not significant). The results from two non-overlapping Wamba studies, therefore, were pooled and used to generate an expected distribution of interactions for male-female and female-female grooming partnerships. This expected distribution was compared to the frequencies of male-female and female-female affiliations from an earlier study at Lomako [Badrian & Badrian, 1984] and from this study. There was no significant difference between the results of Badrian and Badrian [1984] and the Wamba expected distribution (goodness of fit test, G = 0.169, not significant). The results from the present study, however, were significantly different from the Wamba expected distribution (goodness of fit test, G = 3.890, $P < 0.05$).

The distributions of aggressive interactions (Fig. 3b) were significantly different between the two study sites (goodness of fit test for this study to an expected distribution based on data from Wamba, G = 77.455, $P < 0.001$). At Wamba, 68.8% of aggressive interactions were between males, 30.0% were between males and females, and 1.2% between females. In contrast, during this study, each partnership accounted for approximately equal numbers of aggressive interactions (30.8% between males, 33.3% between males and females, 35.9% between females).

DISCUSSION

The social structure of pygmy chimpanzees at Lomako can be described, on the basis of observed social interactions, as one with a high degree of affiliative behavior among females, between males and females, but not among males. Most

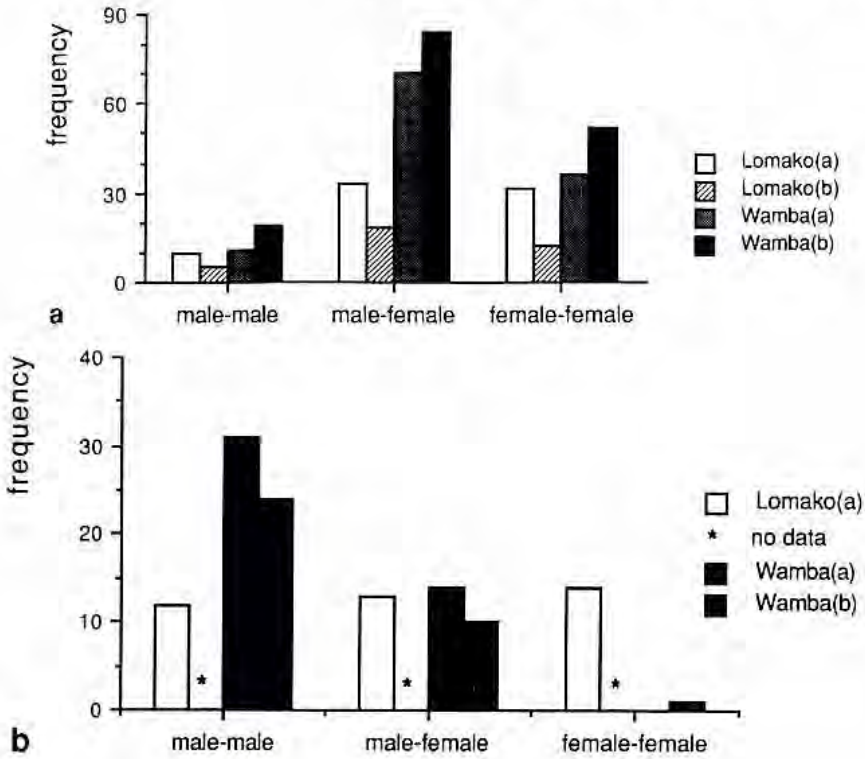

Fig. 3. Observed interactions from behavioral studies at Lomako and Wamba. Data were taken from this study (Lomako, [a], total of 242 hours of observation), from Badrian and Badrian [1984] (Lomako, [b], total hours of observation not reported), from Kuroda [1980] (Wamba [a], total of 210 hours of observation), and from Kano, [1980] (Wamba [b], total hours of observation not reported). Data from Kuroda [1980] were collected before provisioning became successful. Data from Kano [1980] were collected during successful provisioning. **a:** Frequency of grooming dyads. **b:** Frequency of aggressive interactions. No data on aggressive interactions were available for Badrian and Badrian [1984].

interactions reflected the way individuals associated in parties. Party membership was female biased, as lone males frequently left parties whereas females tended to remain together [White, 1988]. Thus, interactions among females were more frequent because females were together more often. Males, when in parties, associated more with females than with other males.

Aggressive behavior by males and affiliative behavior by females, however, did not reflect association patterns. Aggressive behavior by males was directed more often to other males than females, and females showed preferential affiliation towards males. The distribution of aggressive behavior by females and affiliative behavior by males, however, reflected party composition and duration.

Size of Sexual Swelling

The frequency with which females mated with males was dependent on the size of the female's sexual swelling. Pygmy chimpanzees have been observed to copulate at all stages of the sexual cycle [Thompson-Handler et al., 1986; Fig. 1b]. Matings were observed more frequently for females with large sexual swellings during the present study although females with the largest sexual swelling (class VII, maximal tumescence) did not show higher frequencies of mating than expected. This result could be due to the small number of observed females in this swelling class, or may reflect greater selectivity by females near ovulation.

Size of sexual swelling also appeared to influence grooming with males. Un-

like mating, however, most grooming by males was of females with small sexual swellings. This implies that grooming did not reflect a male strategy to affiliate with females close to ovulation. At Wamba, in contrast, males preferentially groomed females with large swellings [Kuroda, 1980]. It is not clear why this particular difference exists, although it may reflect differences in definitions of swellings, differences in analyses of preference, or differences in male strategy between the two sites. If sexual swellings are dependent on the age of a female, differences in grooming frequencies between study sites may reflect differences in age structure of the study populations.

Party Size

For the parties observed during this study, there was a relationship between the size of party and the distribution of affiliative and aggressive interactions. Observations of mostly small parties indicated strong female-female affiliation while observations of medium and large parties showed female-female and male-female affiliation. Aggression between females and between males and females was seen in small and medium party sizes, whereas aggression among males was predominant at large party sizes. These results support the conclusion that the social organization of Lomako pygmy chimpanzees exhibits strong female-female affiliation at small party sizes, with male-female affiliation becoming more important as party size increases.

Differences Between Lomako and Wamba Study Sites

The results illustrate why the major conclusion from studies at Wamba has been that affiliation between the sexes is the most important aspect of pygmy chimpanzee social organization, whereas studies at the Lomako site underscore the importance of affiliation among females. The hypothesis that differences between study sites reflect relative party sizes is supported by the data from Lomako. If affiliation at Wamba follows the same pattern as at Lomako, then higher frequencies of male-female affiliation should be observed at Wamba than at Lomako, since large party sizes are more frequent at Wamba. This line of reasoning, however, begs an important question: why should party sizes be so different at the two sites?

Differences in social organization and party size in common chimpanzees, *Pan troglodytes*, can be related to habitat, provisioning, habituation, and predators. Common chimpanzees have been studied in a variety of locations and habitats [McGrew et al., 1981]. Although some aspects of common chimpanzee social organization, including average party size, do not appear to vary greatly, there is a suggestion that the relative proportion of party types does vary with different habitats [Tutin et al., 1983]. Within any one study population, however, variations in party size, party type, or ranging patterns can be related to seasonal differences in food, water, or shade availability [Wrangham, 1977; Baldwin et al., 1982; Tutin et al., 1983]. Providing large artificial sources of food may affect aspects of social organization including ranging patterns, frequency of interaction, and party size [Tutin et al., 1983]. Studies have shown that provisioning increases the frequency of aggressive behaviors [Wrangham, 1974] and number of individuals that aggregate at the artificial feeding site [Wrangham, 1974; Tutin et al., 1983]. Habituation may affect observed social organization because of differences in observability of different party types [Tutin et al., 1983]. Higher levels of predation pressure in open types of habitat in the same area have been related to larger party sizes and fewer vulnerable party types, such as lone animals or mothers with offspring [Tutin et al., 1981].

Given these relationships, it is hypothesized that habitat, provisioning, habituation, and predation may be responsible for observed differences in pygmy chimpanzee social organization between study sites, either directly or indirectly through their effect on party size.

Habitat. Differences in seasons and habitat may produce differences in the abundance, availability, and distribution of food. Seasonal variation in both food availability and party size have been observed at both Wamba and Lomako [Kuroda, 1979; Badrian & Malenky, 1984]. Party size at Lomako increases as food patch size increases [White, 1986; White & Wrangham, 1988]. Despite monthly variation in patch size, however, parties at Wamba remain consistently larger [Kuroda, 1979]. Differences between this study and Kuroda's [1979, 1980] studies at Wamba cannot be explained by seasonal variation, since both studies included parts of all four seasons (October to July for this study, October to August for Kuroda [1979], and November to August for Kuroda [1980]). There may, however, be larger parties at Wamba because food patches are, on average, larger. Greater human impact at Wamba could affect the availability of food by altering the abundance of food patches.

Provisioning. Provisioning at Wamba, although originally unsuccessful [Kuroda, 1979], has provided the study population with supplemental food since November 1, 1976 [Kano, 1980] at the artificial feeding site and wherever animals are encountered in the forests (Doran, personal communication). Larger party sizes at Wamba may result from this artificial feeding. The higher relative frequencies of male-male aggression may reflect these larger parties, or be a direct consequence of increased feeding. Female-female aggression is relatively infrequent at Wamba, which may be a response to relaxed feeding competition due to the availability of provisioned food. Most female-female aggression at Lomako was associated with disputes over feeding sites. Since Kuroda's [1979, 1980] studies were conducted before provisioning became fully successful, however, provisioning cannot be the sole cause of differences between study sites.

Habituation. Differing levels of habituation could result in altered frequencies of behavior due to the presence of observers, or produce differing results because of differential observability of party types. Provisioning at Wamba has facilitated habituation. Early studies at Lomako frequently reported aggressive behaviors towards observers that were associated with low levels of habituation [Badrian & Badrian, 1984]. During the process of habituation, these behaviors have become infrequent. During the present study aggression toward observers was observed only when contacting new individuals [White, 1988]. The habituation process at Lomako, however, is by no means complete, and there is a notable difference in tolerance of observers between the most habituated and frequently observed community (Hedons) and the least habituated and less frequently observed community (Rangers). The Rangers are more difficult to observe in small parties [White, 1986, 1988; White & Burgman, 1990; see Thompson-Handler et al. [1986] and White [1986] for descriptions of the different Lomako communities].

Increased habituation at Lomako, however, has not produced greater similarity in pygmy chimpanzee social organization between the two study sites. As shown in Figure 3a, earlier studies at Lomako found that grooming affiliations between males and females were more frequent than among females. These earlier results are more like those from Wamba than are the results from this study. During habituation, biases in results because of changes in normal behavior should decrease. If the differences in results from the two study sites were due to such biases, increased habituation should produce greater similarity in results. Increased habituation at Lomako has instead produced greater differences be-

tween the two study sites. These differences in levels of affiliation through grooming, therefore, do not appear to be a direct result of habituation.

Habituation also does not appear to have an effect on the sizes of parties observed. Increased habituation at Lomako has resulted in more frequent observations of small party sizes [White, 1988]. Study animals at Wamba are better habituated to human observers, yet this is associated with larger rather than smaller parties. Changes in party sizes with habituation within a study site, therefore, do not account for differences in social organization between study sites.

Predation. Larger group sizes are usually associated with increased threat of predation [van Schaik, 1983]. Larger party sizes, however, were more frequently observed at Wamba where large predators are absent. Leopard spoor was often seen at Lomako, although the pygmy chimpanzees at this site showed no visible reaction to nearby leopard calls (personal observation). Non-human predator threat, therefore, appears greater at Lomako where party sizes are smaller. Greater party sizes at Wamba, however, could be a response to possible predation by humans. When unhabituated chimpanzees are contacted by humans for the first few times, they rely on cryptic behavior, presumably to avoid predation. Under such conditions, party sizes are expected to be small. Partially habituated individuals direct defensive and threat displays toward observers. This stage of habituation at Lomako was associated with larger, predominantly male, parties [White, 1988]. Habituated animals at Lomako no longer show defensive behaviors. Observed party sizes at Lomako have decreased as habituation has increased [White, 1988], but it is possible that large parties may persist if there is a threat of human predation. This threat is greater at Wamba, where there are permanent local settlements, than at Lomako, where there are none. Larger party sizes at Wamba, therefore, may be a response to higher threat of human predation.

In conclusion, the larger parties observed at Wamba, as compared to Lomako, may result from differences in available food. Greater threat of non-human predation cannot explain the difference in party size between sites. Human impact, through both direct effects like hunting and indirect effects such as competition for forest resources, also may affect observed party size, which in turn may explain differences in observed social organization of pygmy chimpanzees between the two study sites.

CONCLUSIONS

1. The social organization of the pygmy chimpanzee is characterized by high levels of affiliation among females, between males and females, but not among males.

2. Affiliation varies with party size at Lomako. Female-female affiliation is more apparent at small party sizes, whereas male-female affiliation is more frequent at larger party sizes. This variation parallels differences between study sites.

3. Differences in party size and social organization between Lomako and Wamba may reflect differences in habituation, habitat, provisioning at Wamba, or predation. Of these factors, provisioning, relatively greater degradation of the habitat, and the threat of predation by humans at Wamba most likely account for the observed differences in social organization at the two sites.

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REFERENCES

Altmann, J. Observational study of behavior: Sampling methods. BEHAVIOUR 49: 227–267, 1974.

Badrian, A.J.; Badrian, N.L. Group composition and social structure of *Pan paniscus* in the Lomako Forest. Pp. 325–346 in THE PYGMY CHIMPANZEE: EVOLUTIONARY BIOLOGY AND BEHAVIOR. R.L. Susman, ed. New York, Plenum Press, 1984.

Badrian, N.L.; Malenky, R.K. Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaire. Pp. 275–299 in THE PYGMY CHIMPANZEE: EVOLUTIONARY BIOLOGY AND BEHAVIOR. R. L. Susman, ed. New York, Plenum Press, 1984.

Baldwin, P.J.; McGrew, W.C.; Tutin, C.E.G. Wide-ranging chimpanzees at Mt. Assirik, Senegal. INTERNATIONAL JOURNAL OF PRIMATOLOGY 3:367–385, 1982.

Furuichi, T. Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee females at Wamba, Zaire. PRIMATES 28: 309–318, 1987.

Goodall, J. THE CHIMPANZEES OF GOMBE: PATTERNS OF BEHAVIOR. Cambridge, Massachusetts, Harvard University Press, 1986.

Hinde, R.A. Interactions, relationships and social structure. MAN 11:1–17, 1976.

Hinde, R.A. The nature of social structure. Pp. 294–315 in THE GREAT APES. D.A. Hamburg, E. McCown, eds. Palo Alto, Benjamin Cummings, 1979.

Kano, T. Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. JOURNAL OF HUMAN EVOLUTION 9:243–260, 1980.

Kano, T. The social group of the pygmy chimpanzees *Pan paniscus* of Wamba. PRIMATES 23:171–188, 1982.

Kano, T.; Mulavwa, M. Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. Pp. 233–274 in THE PYGMY CHIMPANZEE: EVOLUTIONARY BIOLOGY AND BEHAVIOR. R.L. Susman, ed. New York, Plenum Press, 1984.

Kitamura, K. Pygmy chimpanzee association patterns in ranging. PRIMATES 24: 1–12, 1983.

Kuroda, S. The social group of the pygmy chimpanzee. PRIMATES20:161–183, 1979.

Kuroda, S. Social behavior of the pygmy chimpanzee. PRIMATES 21:181–197, 1980.

Kuroda, S. Interactions over food among pygmy chimpanzees. Pp. 301–3234 in THE PYGMY CHIMPANZEE: EVOLUTIONARY BIOLOGY AND BEHAVIOR. R.L. Susman, ed. New York, Plenum Press, 1984.

McGrew, W.C.; Baldwin, P.J.; Tutin, C.E.G. Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. JOURNAL OF HUMAN EVOLUTION 10: 227–244, 1981.

Sokal, R.R.; Rohlf, F.J. BIOMETRY, 2nd Ed. New York, Freeman and Company, 1981.

Thompson-Handler, N.; Malenky, R.K.; Badrian, N.L. Sexual behavior of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur, Zaire. Pp. 347–368 in THE PYGMY CHIMPANZEE: EVOLUTIONARY BIOLOGY AND BEHAVIOR. R.L. Susman, ed. New York, Plenum Press, 1984.

Thompson-Handler, N.; Malenky, R.K.; White, F.J.; Lanjouw, A. Reproductive and affiliative behavior and the social organization of pygmy chimpanzees. Paper presented at Understanding Chimpanzees Symposium, Chicago Academy of Sciences, Chicago, 1986.

Tutin, C.E.G.; McGrew, W.C.; Baldwin, P.J. Responses of wild chimpanzees to potential predators. Pp. 136–141 in PRIMATE BEHAVIOUR AND SOCIOBIOLOGY. R.S. Corruccini, A.B. Chiarelli, eds. Heidelberg, Springer, 1981.

Tutin, C.E.G.; McGrew, W.C.; Baldwin, P.J. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus* at Mt. Assirik, Senegal. PRIMATES 24:154–173, 1983.

van Schaik, C.P. Why are diurnal primates living in groups? BEHAVIOUR 87:120–144, 1983.

White, F.J. Behavioral ecology of the pygmy

chimpanzee. State University of New York at Stony Brook, 1986.

White, F.J. Party composition and dynamics in *Pan paniscus*. INTERNATIONAL JOURNAL OF PRIMATOLOGY 9:179–193, 1988.

White, F.J. Ecological correlates of pygmy chimpanzee social structure. Pp. 151–164 in COMPARATIVE SOCIOECOLOGY: THE BEHAVIORAL ECOLOGY OF HUMANS AND OTHER MAMMALS. V. Standen, R.A. Foley, eds. Special publication number 8 of the British Ecological Society. Oxford, Blackwell, 1989.

White, F.J.; Burgman, M.A. Social organization of the pygmy chimpanzee: Multivariate analysis of intracommunity associations. AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 83:193–201, 1990.

White, F.J.; Thompson-Handler, N. Female homosexual behaviour in the pygmy chimpanzee: Ecological and social correlates, in review.

White, F.J.; Wrangham, R.W. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. BEHAVIOUR 105:148–164, 1988.

Wrangham, R.W. Artificial feeding of chimpanzees and baboons in their natural habitat. ANIMAL BEHAVIOUR 22:83–94, 1974.

Wrangham, R.W. Feeding behavior of chimpanzees in Gombe National Park, Tanzania. Pp. 504–538 in PRIMATE ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.