FEEDING COMPETITION AND PATCH SIZE IN THE CHIMPANZEE SPECIES PAN PANISCUS AND PAN TROGLODYTES

by

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Introduction

The social structure of different organisms can be related to various fac-
tors in the ecology of each species or population. Over the past twenty
years, there have been many theoretical considerations of the relationship
between social structures and ecological parameters for primates (for
example, CROOK, 1970; EISENBERG et al., 1972; ALEXANDER, 1974;
CLUTTON-BROCK & HARVEY, 1977; WRANGHAM, 1980; TERBORGH &
JANSON, 1986; SCHAIK, 1983). The spatial distribution and patterning of
food has often been proposed as an important determinant of primate
social structures. Food may be uniformly distributed or clumped into
patches, and the size and quality of these patches may vary in a predic-
table or unpredictable fashion. When primates feed in groups, there is
often competition between them for access to the available food (ALEX-
ANDER, 1974; SCHAIK, 1983). The relative severity of feeding competition

compared to the possible benefits of sociality will vary with the distribution and abundance of food.

Small food patches tend to engender more intense feeding competition between individuals. If patches are large, there are relatively minor effects of feeding competition; individuals may then benefit from grouping, such as by cooperating to defend such patches and by other benefits of sociality. If food is evenly dispersed, the costs of feeding competition can become trivial. In such situations, individuals may form groups or disperse. Whether or not groups form is expected to depend on the importance of factors such as protection from predators and harassment. Despite these links between competition for food within groups and social organization, it is only recently that studies have examined the costs to the individual of feeding in social groups (WRANGHAM, 1977; JANSON, 1985; WATTS, 1986; this symposium).

The aim of this paper is to compare the effects of feeding competition among individuals in the two chimpanzee species *Pan paniscus* and *Pan troglodytes*, and to relate differences to the social organization of each species. Chimpanzees inhabit a broad range across middle Africa. Of the three subspecies of common chimpanzee, *P. troglodytes schweinfurthii* is the best studied, with long-term work from two major sites in Tanzania: at Gombe (for example, GOODALL, 1986) and Mahale mountains (for example, NISHIDA, 1979). There is only one subspecies of pygmy, or bonobo, chimpanzee, *Pan paniscus*, which is limited in its distribution to the primary and secondary forests of central Zaire. It is only recently that detailed information on the social organization and ecology of this species has become available, from two major field sites: in undisturbed forests in the Lomako (for example, SUSMAN, 1984; WHITE, 1986) and from a provisioned population in more disturbed areas around the village of Wamba (for example, KANO, 1982).

Both species of chimpanzee are highly frugivorous and both display a fission-fusion social organization in which individuals are found in parties that are flexible in size and composition (WRANGHAM, 1977; GOODALL, 1968; BADRIAN & MALENKY, 1984; BADRIAN & BADRIAN, 1984). However, in contrast to what one might expect in these two closely related, and similar sized (JUNGERS & SUSMAN, 1984), chimpanzees, there are major differences in their social structures (WHITE, 1986; WRANGHAM, 1986).

P. troglodytes schweinfurthii females tend to show little affiliation towards each other (BYGOTT, 1979; GOODALL, 1986). These females spend much time alone with their offspring in individually recognizable but exten-

sively overlapping core areas (HALPERIN, 1979; WRANGHAM, 1979a, 1979b; WRANGHAM & SMUTS, 1980). The males, in contrast, are gregarious and cooperate to defend communal ranges that include the feeding areas of several females (GOODALL *et al.*, 1979; NISHIDA, 1979). Males often show such affilative behaviors such as grooming towards each other (GOODALL, 1968).

Pan paniscus, in contrast, is characterized by high levels of affiliation among females, including a mutual homosexual behavior referred to as GG (for genito-genital) rubbing (BADRIAN & BADRIAN, 1984; THOMPSON-HANDLER *et al.*, 1984; KANO, 1980; KURODA, 1980). Parties of *P. paniscus* are based on cores of females that regularly associate (WHITE, 1986). Maintenance of feeding proximity also reflects this strong social bonding among females (*ibid.*). Male *P. paniscus*, in contrast, show little affiliation towards each other (BADRIAN & BADRIAN, 1984; WHITE, 1986) and all male parties are almost totally absent (1.3%, n = 383, THOMPSON-HANDLER *et al.*, 1986).

The social organization of *P. troglodytes schweinfurthii* has been interpreted by WRANGHAM (1979a) as reflecting the importance of feeding competition for female strategies. The major part of the diet of this species at Gombe is made up of small scattered food patches (WRANGHAM, 1975, 1977, 1979a). The chimpanzees feed for less than ten minutes at 50 per cent of their food sources (RODMAN, 1984). Such patches seldom contain many feeding sites (WRANGHAM, 1979a, 1979b, 1980). It has been shown that the semi-solitary behavior of females enables them to maintain a relatively high percentage of time spent feeding (WRANGHAM & SMUTS, 1980). This presumably minimizes the effects of feeding competition, and allows females to maintain a high reproductive rate through effects on fertility or the survival and growth of offspring. Males, by contrast, cooperate to maintain large territories which include the ranges of several females. Their aggressive cooperation is reflected in other social relationships also, such as a high incidence of grooming. Conversely, cooperative aggression among females is rare, as is the frequency of grooming among females.

The social system of *Pan paniscus* has been interpreted with respect to two different aspects of its ecology. First, parallels have been drawn with the ecology of the mountain gorilla, *Gorilla gorilla berengei* (BADRIAN & BADRIAN, 1984; WRANGHAM, 1986). Feeding competition among mountain gorillas appears to be mild because of the relatively uniform distribution of their food. It has been proposed that, since *P. paniscus* feeds partly on the pith of dispersed ground vines, feeding competition in this species

is also mild, thereby allowing the larger party sizes that are observed (WRANGHAM, 1986).

Gorilla females, however, appear to have less highly differentiated relationships than *P. paniscus* females (HARCOURT, 1979a; WHITE, 1986). Female gorillas, instead of dispersing as one might expect in such a habitat, are clumped into social groups that are focused on a dominant male (HARCOURT, 1979b; FOSSEY, 1983). This may function to protect females from predators or from harassment by other males (WRANGHAM, 1979a; STEWART & HARCOURT, 1987). Associations among female *P. paniscus* are also relatively stable, but these associations are not dependent on the presence of males and, therefore, can not be functioning in the same way (WHITE, 1986). This is in contrast to the situation in gorillas, where groups that lose their males rapidly disperse (FOSSEY, 1983). Female associations in the gorilla are produced by their mutual attraction to the dominant males rather than to each other (HARCOURT, 1979a, 1979b).

A second interpretation of *P. paniscus* social organization has been proposed by WHITE (1986) as reflecting the importance of large, predictable and abundant food patches for female strategies. The use of large fruit trees by *P. paniscus* in the Lomako Forest has been previously noted, as well as feeding on dispersed *Haumania* vine (BADRIAN & MALENKY, 1984; BADRIAN & BADRIAN, 1984). If *P. paniscus* does feed in predominantly larger patches, then feeding competition will be lower. The ultimate benefits for female-female association could be concerned with the patchy distribution of food, such as defense of food patches, or they could be unconnected with the food distribution.

In this paper we contrast the types of food patches used by the two chimpanzee populations, and examine the relative effects of feeding competition across a range of party sizes and patch sizes. In addition to discussing the species differences in costs of feeding, we consider the possible benefits of association among female *P. paniscus*.

Methods

Data for *P. paniscus* were from a two year study of the behavioral ecology of this species at the Lomako Forest Pygmy Chimpanzee study site in central Zaire. The study site covers a mosaic of forest types, with predominantly undisturbed polyspecific evergreen climax forest as well as some areas of slope and swamp forest (WHITE, 1986). The data used for this comparison span 10 months from October 1984 to July 1985. There is little apparent seasonality in rainfall, although rains may be somewhat reduced from June to August and from December to February. This study, therefore, encompasses five months of reduced rainfall and five months of heavier rainfall.

The data used for *P. troglodytes schweinfurthii* were from field work in Gombe National Park, Tanzania, and cover the period May 1972 to January 1973, the three missing months being in the late wet season. The habitat of Gombe is a mosaic of semievergreen forests, deciduous forests, and grasslands (GOODALL, 1986). The two data sets, therefore, cover an equivalent period of time (10 *versus* 9 months). However, the study of *P. paniscus* involved more detailed measurements of patch use. Results for the relationship between party size and patch size are restricted to this species.

Both studies employed focal animal sampling, although the data from Gombe are only from male focal animals. The *P. troglodytes* data were from ten-minute sampling, extracted from five-minute sampling, whereas the sampling of *P. paniscus* was from two-minute sampling. We originally intended to use ten-minute time points for both species in this comparison. However, when the *P. paniscus* data were reanalysed using only the data that fell on the ten-minute time point, it was found that sampling of individuals feeding on the ground on *Haumania* vine pith did not fall exactly on any ten-minute time points, and consequently did not appear in the reanalyzed data set. Ten-minute sampling increased the magnitude of those differences between the two species that were already apparent from the two-minute sampling, but otherwise made no extra contribution to this comparison. As ground feeding vine is an important factor in one of the hypotheses relating the ecology of *P. paniscus* to its social structure, the original results from two-minute sampling of *P. paniscus* are presented here.

A food patch was defined as a discrete area within which individuals were able to collect food continuously as they moved within them. An isolated fruit tree or two adjacent trees in contact were considered as one patch. A patch could contain more than one type of food and it was possible for a focal animal to feed at more than one height, at different times, within the same patch. Feeding height for *P. troglodytes* was recorded as being on the ground, with the focal animal's feet between 0 and 2 meters height, or with the feet above 2 meters. Data for *P. paniscus* were recorded as being on the ground, or in one of a series of height classes, each spanning 5 meters up to 45 meters.

The following information was recorded for each time point once the focal animal arrived in a patch: party size (the number of individuals excluding dependent juveniles), number of individuals feeding (the effective feeding party size), food species and food type, and feeding height. The amount of food removed from a patch could, therefore, be estimated by summing the number of feeding animals for the length of time spent in each patch. This total was converted into "chimp-minutes" by multiplying by the appropriate factor for each data set. This was used as the measure of patch size available for both species. In addition, a number of other measurements of patch size were available for *P. paniscus*. The radius of the patch, the diameter at breast height (DBH) if the patch was a single tree, and the amount of time that there were any chimpanzees feeding in the patch (from when first individual entered to when the last left, where observed) were recorded for all patches where possible.

Food patch types were divided into ground patches (either leaves and pith or insects), vines, and food trees (either fruit, leaves, or flowers). Detailed measurements of tree sizes were not recorded for *P. troglodytes*, although the size of the tree species could be generally characterized as either large or small. A small tree species had a DBH of approximately less than 50 cm, and was less than 5 meters in height, and a large tree species generally had a DBH greater than 30 cm and was more than 5 meters in height. As specific data were recorded for trees fed in by *P. paniscus*, trees could be classed along similar criteria to allow comparison between the two studies. 50 cm DBH was used as the dividing point for small and large trees for *P. paniscus*, as all small trees used by this species were more than 5 meters in height.

Observation conditions differed greatly between the two study sites. The high density of tall trees and dense folliage that is characteristic of evergreen climax forest in the Lomako study site made detecting and observing *P. paniscus* difficult. The number of

animals feeding could not always be accurately determined, although inferences could be made from feeding movements of individuals not in open view. The animals spent a large proportion of their time high in the canopy (above 30 m) where visibility was relatively good. They also spent time on the ground where visibility was poorer, such that individuals could only be accurately observed if they were between 5 to 15 meters away. Members of a less tolerant community would flee if approached on the ground, although members of a more tolerant community would remain undisturbed if the observer was 10 to 15 meters away. There is, therefore, a bias in the *P. paniscus* data set towards samples in the trees.

This bias was examined by comparing the results from long follows (six hours or more) with shorter follows. As discussed elsewhere (WHITE, 1986), shorter follows do underestimate the amount of time that the chimpanzees spend on the ground, with 5 per cent of all two-minute samples being on the ground compared with about 8 per cent of samples from long follows. Therefore, data from long follows indicate that approximately a tenth of the day, or less, is spent on the ground. Length of observation did not appear to effect results of feeding and resting activities (WHITE, 1986).

Mean length of observation of *P. paniscus* was 112 minutes. Most follows encompassed at least one fission or fusion. Focal animals included both males and females, and were from a wide range of party sizes. Parties were located from patrols along established trials, vigils of both small and large known food trees, and follows from night-nests.

At Gombe, observation conditions were much better than in the Lomako, and the date for *P. troglodytes* were from all-day follows of male focal animals. To minimize effects due to seasonal biases at Gombe, two all-day observations were selected from each month of observation. To maximize the number of focal individuals that contributed to the data set, no month used all-day observations from the same individual. Data were selected from one community only (Kasekela community) in order to maintain demographic consistency. All-day observations began and ended at the sleeping-nest site, and showed no bias in favor of large or conspicuous parties.

The relationship between patch measures and party size, and party size and mean effective feeding party size were examined using regression analysis. Distributions of patch type and height for the two species of chimpanzee were compared using G tests of goodness of fit, and a Kruskal-Wallis test was used to examine the differences in patch size distribution. The slopes and intercepts of the regression lines for the two species were compared and tested for equality. All tests were carried out using the BIOM package of statistical programs that accompany the text ''Biometry'' (SOKAL & ROHLF, 1981; ROHLF, 1986).

Results

1. *P. paniscus*.

The mean DBH of trees fed in by *P. paniscus* was 94.2 cm (median 86.4 cm, s.d. 50.2, n = 72) and the mean radius of all food patches was 12.1 meters (median 12.0 m, s.d. 6.5, n = 101). The mean time that a party spent in a food patch (measured from the when the first individual arrived to when the last individual left) was 1.049 hours (s.d. 1.243, n = 92, range 0.017 to 4.80 hours).

The third measure of patch size, that of the amount of food that a party of chimpanzees removed from a patch (chimp-minutes) as estimated from the total feeding time, may not be an accurate measure of the patch

size if, feeding rates were not constant throughout a feeding bout, or if large parties removed more food than small parties from a patch of the same size. Constant feeding rates would imply that there was a linear relationship between the total feeding time ("chimp-minutes") and the amount of food removed. Feeding rates have been found to decrease during some feeding bouts, but this effect is slight (MALENKY, pers. comm.). However, even if feeding rates did decrease during every bout, the total amount of food removed would be positively (but not linearly) related to the total amount of "chimp-minutes" for each patch.

If the chimpanzees did feed in the patch until there was a significant reduction in the food present, and this occurred in all patches and for all party sizes, then large parties should remove equivalent amounts of food from patches of the same size. As shown by JANSON (this volume), food may be limited in some, but not all, patch sizes. That is, although the total amount of feeding time in small patches may be limited by the amount of food available, large patches may represent superabundant food sources where the total amount of food consumed may be limited by other constraints such as stomach capacity.

In order to examine this question, patches were classed as either small or large, using several criteria, and multiple regressions were performed separately for small and large patches for each criteria on the log-transformed data. The three criteria used for small patches were less than 50 cm DBH, less than 90 cm DBH, and less than 10 meters radius. The results (Table 1) demonstrated that, for the last two criteria, tree radius was a much better predictor of the total chimp-minutes than was party size for small trees, with the opposite result for large trees. That is, the total amount of food removed by a party from a small patch was determined more by the physical size of the patch than by the size of the party, thus implying that food is limited and there was competition for the available food.

However, in large patches, the total amount of food removed was not determined by the size of the patch. Instead, it was dependent on the party size present in the patch. Therefore, in these large patches, food was presumably not limited, and per-capita feeding time was limited by some other constraint, such as stomach capacity. This division between small patches where food was limited and large patches where it was superabundant has been found for other primate species (see JANSON, this volume).

When dividing food trees into large or small using the 50 cm DBH criterion (a measure also available for *P. troglodytes schweinfurthii* at

TABLE 1. Regression-model analysis relating total chimp-minutes in small and large patches to patch radius and party size of *Pan paniscus*

Patch size	Dependent variable	Common intercept	Independent variables	Regression coefficient	T-value	p
Small	chimp-mins	0.917	radius	1.289	4.801	0.0001
(<or = 50 cm DBH)			party size	0.567	1.866	0.0725
Large	chimp-mins	3.259	radius	0.126	0.410	0.6847
(= 50 cm DBH)			party size	1.211	4.670	0.0001
Small	chimp-mins	1.410	radius	1.147	4.546	0.0001
(<or = 90 cm DBH)			party size	0.406	1.456	0.1532
Large	chimp-mins	4.398	radius	−0.235	−0.310	0.7604
(>90 cm DBH)			party size	1.305	4.282	0.0004
Small	chimp-mins	1.541	radius	1.505	3.580	0.0012
(<or = 10 radius)			party size	0.041	0.134	0.8942
Large	chimp-mins	1.012	radius	0.474	0.887	0.3823
(>10 m radius			party size	1.524	6.651	0.0001

T-value is for a T test of the null hypothesis that the value of the regression coefficient is not significantly different from zero. p denotes the level of significance for the T test value.

Gombe), this distinction between trees with food competition (small trees) and those where feeding competition was absent (large trees) was less clear. Unlike the other criteria, there was some effect of party size on the total amount of food removed in trees less than 50 cm DBH. However, the effect was small and the radius of the patch was still a much better predictor of total chimp-minutes than was party size in small trees. Therefore, the division of trees into small or large appears to reflect a division into trees where competition is present or absent.

Regressions of party size in *P. paniscus* against measures of patch size demonstrate that both party size and mean effective feeding party size are dependent on some measures of patch size (WHITE, 1986). There is no significant regression between either party size or mean effective feeding party size and the DBH of a food tree. Both variables, however, are dependent on both the radius of the patch and the total time that a party spends in a patch. Therefore, more individuals are able to feed in large patches and party size increases in these larger patches that produce more food.

2. Comparison of *P. paniscus* and *P. troglodytes schweinfurthii*.

Physical measures of patch size (DBH, radius) were not recorded for *P. troglodytes*, so the relationships between these variables and party size

TABLE 2. Time spent in food patches of different types and in different habitats by *Pan troglodytes schweinfurthii* at Gombe

	Forest			Woodland			Grassland			All Habitats		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
Ground foods	34.5	40.3	11	27.1	22.3	14	34.0	25.1	5	31.0	29.7	30
Vines	40.0	35.9	10	49.5	67.3	19	20.0	–	1	45.3	57.0	30
Small trees	–	–	0	40.0	39.5	34	47.5	34.4	20	42.8	37.9	54
Large trees	40.0	38.5	27	38.7	23.0	23	–	–	0	39.4	32.0	50
All	38.7	37.6	48	39.7	41.8	90	43.8	32.7	26	40.0	39.1	164

could not be compared for the two populations. Data for a comparable number of patches for each species were examined. A total of 186 *P. troglodytes* food patches were compared with 132 *P. paniscus* food patches.

For *P. troglodytes*, the mean time that a party or combination of parties spent in a food patch (measured from the first ten-minute time-point after the first individual arrived to the last time point before the last individual left) was 4.00 ten-minute time-points (s.d. 3.91), *i.e.* 40.0 minutes, (s.d. 39.1 minutes, n = 164). This is approximately two-thirds of the time spent in food patches by *P. paniscus* (measured from the actual time of entry of the first individual to the actual time of leaving of the last individual). Since *P. paniscus* occurred in larger parties than *P. troglodytes*, this suggests that if feeding competition occurred and was responsible for constraining the amount of time spent in food patches, *P. troglodytes* patches were smaller than those of *P. paniscus*. This issue is discussed further below.

The food patches at Gombe are found in a more diverse range of habitats than the predominantly polyspecific climax evergreen forest at Lomako: *P. troglodytes* spent considerable amounts of time also in woodland (defined as having a single canopy of tree crowns) and grassland (where grasses dominate the ground layer and trees may or maynot be present). This raises the possibility that the reason for the smaller lengths of time spent by *P. troglodytes* than *P. paniscus* in food patches is the *P. troglodytes* spent particularly short periods in food patches in woodland and grassland, where patches may be smaller than in forests. Table 2 shows, however, that there were no discernable differences in the time spent in patches in forest, woodland, or grassland. Nor is there any evidence that different types of food (ground food, vine, small tree, large tree) contributed disproportionately to the effect.

TABLE 3. Comparison of *P. paniscus* and *P. troglodytes* feeding heights

Distribution of feeding heights (per cent of all patches)

Height class	Pan paniscus	Pan troglodytes
on ground	13.6	36.5
low (0 to 2 meters)	–	6.5
(0 to 5 meters)	0.0	–
high (above 2 meters)	–	57.0
(above 5 meters)	86.6	–

TABLE 4. Comparison of *P. paniscus* and *P. troglodytes* food patch types

Food patch type (per cent of all patches)

Path type	Pan paniscus	Pan troglodytes
Ground (leaves + pith)	14.8	16.2
Ground (insects)	0.0	2.7
Vines	4.9	17.3
Small trees	15.6	24.9
Large trees	64.8	38.9

G test value = 28.36, p < 0.005.

Table 3 shows the distribution of feeding heights for the two populations. *P. paniscus* and *P. troglodytes* feeding heights had very different distributions. *P. paniscus* fed more frequently at greater heights than did *P. troglodytes*. The modal height class from two-minute sampling of *P. paniscus* was 30 to 35 meters (WHITE, 1986). As shown in the distribution of patch types (Table 4), *P. paniscus* and *P. troglodytes* fed at different frequencies in the various types of patches. *P. paniscus* was observed to feed less frequently in patches consisting of insects, vines and small trees. Ground feeding on leaves and pith is approximately equal for the two species of chimpanzee. *P. paniscus* fed more frequently in large trees, where there is presumably little or no competition for food, than did *P. troglodytes*.

As discussed previously, the amount of food removed from a patch by *P. paniscus* was a useful measure of patch size for small patches. In small patches used by *P. paniscus*, there was competition for a limited amount of food food, but in large patches food was abundant and there was little or no feeding competition. A comparison of the amount of food removed from patches by two populations of chimpanzees (Table 5) shows some

TABLE 5. Comparison of *P. paniscus* and *P. troglodytes* food patch sizes

Frequency distribution of patch sizes (per cent of all patches)

Patch size estimate (number of chimp-minutes)	Pan paniscus	Pan troglodytes
1 to 50	38.8	59.1
50 to 100	14.7	19.4
100 to 150	5.4	10.8
150 to 200	7.0	4.3
200 to 250	6.2	2.7
above 250	27.9	3.7

Kruskal-Wallis H value = 15.19, p < 0.005.

interesting differences. Small patches made up a larger proportion of all patches visited by *P. troglodytes* compared to *P. paniscus*. The distributions for the two populations were significantly different.

The most striking difference between the two distributions was for patches larger than 250 chimp-minutes. These made up 3.2 per cent of the patches visited by *P. troglodytes* compared with 27.9 per cent of patches visited by *P. paniscus*. Therefore, it does appear that *P. paniscus* fed more frequently in larger food patches than *P. troglodytes*. If there was a similar relationship between patch size and the degree of feeding competition in both species, *P. paniscus* presumably experienced less feeding competition than *P. troglodytes*.

In order to examine the effects of feeding competition within the patches across a range of patch sizes, the relationships between party size and mean effective feeding party size were compared for each species of chimpanzee. There was a significant positive regression for both *P. paniscus* and *P. troglodytes* (F = 75.59, p < 0.001 and F = 190.75, p < 0.001, respectively). The slopes and intercepts of these regression lines were compared using ANCOVA analysis and were found not to differ significantly (F = 2.032, not significant, common regression line $y = 0.71672 + 0.38149 \times$). Therefore, there is no difference in the numerical value of the regression lines for the two study populations. The two species of chimpanzee appear to show similar relationships between the size of the party present and the mean number of animals feeding.

The size of the feeding party was compared between the two species. The data were first transformed by taking the square-root because, as count data, the means and variances were interdependent (SOKAL & ROHLF, 1981). It was found that *P. paniscus* had a significantly larger

mean party size (6.54 *versus* 2.78, F = 128.7, p < 0.001) than *P. troglodytes*. The mean effective feeding party sizes were also compared and found to be similarly larger in *P. paniscus* than in *P. troglodytes* (3.45 *versus* 1.76, F = 68.0, p < 0.001).

Discussion

Party size has been shown to be dependent on the size of the food patch in *P. paniscus* (WHITE, 1986) and *P. troglodytes schweinfurthii* (GHIGLIERI, 1984). The amount of food removed from the patch (total number of chimp-minutes), which was the principal variable recorded for both populations of chimpanzees compared here, was found to be a useful measure of patch size in *P. paniscus*. In *P. paniscus*, feeding competition appears to be important in small trees, but to be low or absent in large trees.

The comparison of patch types show that the major difference between the two species of chimpanzee is the more frequent use of large food trees by *P. paniscus*. At the same time, we found that the relationship between party size and mean effective feeding party size was similar for the two species. This means that the larger parties of *P. paniscus* than *P. troglodytes* can be attributed to the more frequent use of larger patches by *P. paniscus*. Gombe chimpanzees certainly appeared to use the largest trees available to them, and we therefore conclude that the key difference between the Lomako and Gombe feeding behavior is a result of the greater availability of large food tree patches in Lomako.

It is important to remember that this conclusion is based on two particular populations, at Lomako and Gombe. The Lomako habitat is possibly typical for *P. paniscus*, but Gombe is different from many *P. troglodytes* habitats because, instead of including a large proportion of rain forest, its only forest is discontinuous, riverine, and poorly developed. It will be interesting to find out whether forest-living *P. troglodytes*, *e.g.* in Uganda, Zaire, Gabon, Cameroun, *etc.*, have food trees available to them as large as those used regularly by Lomako *P. paniscus*. If so, the prediction from our data is that forest-living *P. troglodytes* will feed in larger parties than *P. troglodytes* living in Gombe and other mixed habitats with poorly developed forest. Preliminary evidence, however, suggests that this is not the case. For example, TUTIN *et al.* (1983) pointed out that *P. troglodytes* party size appears to vary little across habitats varying from forest to savannah. Again, GHIGLIERI (1984) found that *P. troglodytes* living in the Ngogo area of Kibale Forest, Uganda, fed in small

parties despite using large food trees. The relationship between food tree size and party size for chimpanzees in general may, therefore, not always be as simple as is suggested by our comparison of Lomako and Gombe.

While the use of food tree patches clearly differed between Lomako and Gombe, our results suggest that *P. troglodytes* and *P. paniscus* utilize ground feeding with equal frequency. This observation does not support the hypothesis that a major difference between the ecology of the two species is the use of terrestrial vegetation by *P. paniscus*. It must be pointed out, however, that the observations of *P. paniscus* used here were undeniably biased away from observations of ground feeding by *P. paniscus* because of poor visibility and poor tolerance to observation. Therefore, the relative importance of ground feeding by *P. paniscus* cannot be determined unequivocally from the data presented here.

However, observations on the nature of ground feeding on *Haumania* vine do not support the hypothesis that reduced competition when feeding on this type of food allowed the larger party size of *P. paniscus*. Typically no more than one or two individuals in a party fed on *Haumania* vine at any one time (mean = 1.32 individuals, n = 15), and each feeding bout usually lasted for less than ten minutes (mean = 4.67 minutes, n = 15). If the party remained together on the ground, the other non-feeding members rested in close association. They were not prevented from feeding as the vine was not found in patches but was ubiquitous in its distribution. It was more usual, however, for individuals to disperse when feeding on this type of food rather than to remain in a cohesive unit. Most observations of single individuals of *P. paniscus* adults were of individuals feeding on *Haumania* vine (FJW, personal observation).

Therefore, although this question of what is the major difference between *P. paniscus* and *P. troglodytes* feeding ecology is by no means resolved, there are indications that the size of patches used by the two species may be an important factor. Both of the two hypotheses discussed here propose that food distribution affects the relative importance of feeding competition and, therefore, party size in the two species of chimpanzee. However, they do so in different ways. In the first hypothesis discussed, it was proposed that ground feeding, for example on *Haumania* vine, allows the formation of larger parties. Although *Haumania* vine does occur throughout the Lomako study site, it is not a patchy resource, but is ubiquitous in its distribution. There will, therefore, be little feeding competition when feeding on this food type. However, individual *P. paniscus* dispersed to feed on this food rather than forming larger parties.

The second hypothesis discussed here proposed that the food patches used by *P. paniscus* are larger than those used by *P. troglodytes*. These larger patches will also have reduced feeding competition, but unlike a uniformly distributed resource like *Haumania* vine, will allow female social groups to become a cost-effective strategy.

The relationship between party size and mean effective feeding party size reflects the degree of feeding competition among individual in parties of different sizes. The similarity in the regressions for the two species implies that there may have been a similar effect of feeding competition in the two populations. However, the two species differ in their relative positions on this regression line. In *P. troglodytes*, party sizes, mean effective feeding party sizes were small. The severity of feeding competition per individual is presumably so great that there is no advantage to further sociality between females. In contrast, *P. paniscus* had larger mean effective feeding party sizes and larger sizes. Female *P. paniscus* can, therefore, afford to be more social.

The relationship between party size and patch size in *P. paniscus* appears to support the second hypothesis discussed previously. That is, the social structure of this species reflects an adaptation to feeding in large, predictable, and abundant food patches. In order to examine the question of the importance of feeding competition in determining the social structure of these two chimpanzee populations in greater detail, it will be necessary to compare detailed phenological studies of the two habitats to determine the distribution and abundance of food at each site. Furthermore, the advantage of female sociality in *P. paniscus* has been proposed by WHITE (1986) to be defense of these large food patches. This hypothesis is supported in that this species uses large patches and has larger party sizes and displays highly differentiated female relationships and cores of females in the association patterns (WHITE, 1986), but other factors including actual patch defense have yet to be demonstrated.

The technique, therefore, of comparing two species that were studied in different habitats by using measures of the amount of food removed appears to be useful. However, such estimates assume that feeding rates are equivalent for the two species. This comparison has also only focused on one population of each species, and it would be interesting to compare these results with data from other populations and subspecies from a wide range of habitats when these data become available.

Summary

The relative importance of feeding competition in *Pan paniscus* and *Pan troglodytes schweinfurthii* is examined in an attempt to understand the major differences in social organization of the two species. *P. paniscus* at Lomako is characterized by a stronger tendency for association among females than among female *P. troglodytes* at Gombe. Party size in *P. paniscus* is dependent on patch size. Feeding competition was more important in small patches than in large patches. The total amount of feeding time by a party in a patch (chimp-minutes) was a measure of patch size that was available for both chimpanzee species. *P. paniscus* was found to have larger party sizes and to use larger food patches than *P. troglodytes*. The importance of dispersed ground foods for each species of chimpanzee was compared and, although the results are not conclusive, they indicate that this type of food was equally important in the diets of both populations. Two hypotheses of the ecological basis for differences in social structure are compared in light of this evidence.

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