

4 • Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups

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Chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*, differ greatly in their social relationships and psychology, as many chapters in this book show (e.g. Takahata *et al.*, Chapter 11; de Waal, Chapter 12). Why they do so is not understood. Yet since these are the two closest relatives of humans, and since each species has a different set of similarities with humans, the question is especially important by virtue of its relevance to human behavior. Why, for instance, do humans and chimpanzees have similarly violent intergroup aggression? The answer will likely depend on understanding why bonobos do not.

In general, bonobos have more relaxed relationships than chimpanzees, with a more pervasive web of alliances or friendships linking community members, especially adult females. This set of differences is thought to depend crucially on the ecological costs of grouping. Thus, friendly social relationships among female bonobos are thought to be possible because their parties are relatively stable, with individuals rarely forced to be solitary. Equivalently friendly relationships among female chimpanzees, on the other hand, are prohibited because parties are regularly forced to fragment, as a result of feeding competition when fruits are scarce (Chapman *et al.*, 1994). Over evolutionary time, such differences have led to differences in species psychology (e.g. Wrangham, 1993).

Resource-based sociality is the only framework so far proposed to explain the ultimate sources of behavioral differences between the two species. To explore one component of it, this chapter examines feeding competition. We begin by considering general principles of grouping in the great apes.

GROUP SIZE AND FEEDING COMPETITION IN THE GREAT APES

Tree-fruit patches are generally distributed in discrete food patches (trees, or small groups of trees). Individuals feeding in groups share these resources. When a patch has fewer meals than the number of individuals in the group, the result is 'within-group scramble competition' (WGS), realized as reduced food intake or increased travel distance (to reach extra food sources). All frugivorous primates, such as the great apes, experience WGS. The question is, what affects its intensity?

Janson & Goldsmith (1995) found that group size in frugivorous primates is well predicted by the cost of additional travel imposed by extra companions, i.e. by the steepness of the curve relating extra travel to group size. If the slope of the curve relating extra travel to group size is shallow, groups are large; if it is steep, groups are small. The relative shallowness or steepness of this curve is determined both by the nature of the food supply and by the costs of locomotion. There are therefore two kinds of explanation for differences in the intensity of WGS among frugivores: type of food or costs of locomotion (Wrangham *et al.*, 1993).

Both principles can be seen in fission-fusion societies. First, food abundance varies between seasons. Increased fruit abundance means that the amount of additional travel imposed by extra companions is reduced. Thus, groups can be large when fruit is abundant.

Second, the energetic cost of extra travel differs between the sexes. Interestingly, the variation occurs in different directions in different species. In orangutans, *Pongo pygmaeus*, travel is costlier for adult (large) males than for (smaller) females and female-sized males: the

large males cannot travel as fast as females or their smaller rivals (van Schaik & van Hooff, Chapter 1). As expected, therefore, the more social individuals are the females and female-sized males. In less sexually dimorphic chimpanzees, by contrast, travel is costlier for mothers than for males: the burden of carrying an infant may be responsible for the lower velocity of females than males (2.3 vs. 2.8 feet per second, Hunt, 1989). Again, as expected, the more social sex is the one with cheaper locomotion, which in the case of chimpanzees is males. In support of this explanation, females without infants are as social as adult males (Goodall, 1986). Thus, sex differences in the cost of locomotion may explain why male-bonding is possible in chimpanzees, without resort to other factors such as differential benefits to males and females.

THE CHIMPANZEE-BONOBO PROBLEM

Differences in both locomotion and food are therefore candidates for explaining differences in social ecology. However, relevant locomotor aspects have barely been studied. Bonobo and chimpanzee locomotor behavior is detectably different, with bonobos traveling in trees more often and using more agile movements (Doran, Chapter 16). Possibly, bonobos have a lower cost of locomotion than chimpanzees (that is, less time or energy to travel a given distance). If so, this could explain differences in the intensity of WGS, and therefore in group size and stability, between bonobos and chimpanzees. This hypothesis, which has not previously been considered, needs to be tested by appropriate study of the costs of locomotion and their relation to group size.

Attention to date, however, has focused on the food supply, which presents an obvious point of comparison because the forests inhabited by chimpanzees and bonobos are similar and geographically close, especially in the equatorial regions. The two species are allopatric, separated merely by the Zaïre River, a boundary which curls across the equator in such a way that the latitudinal (as well as longitudinal) distribution of bonobos (latitudes 2° N to 4° S) is entirely overlapped by that of chimpanzees (latitudes 13° N to 7° S). As a result, the range of climates and habitats experienced by bonobos is merely a subset of those experienced by chimpanzees. Two kinds of ecological influence have been proposed.

First are habitat differences resulting from plant structure and dynamics. For example, fruit trees used by bonobos could be larger, as proposed by White (1989). However, the only study of tree measurements found the size and density of fruit trees used by the two species to be essentially identical (Kibale vs. Lomako; Chapman *et al.*, 1994). Alternatively, Malenky (1990) suggested that seasonal variance in fruit production may be less for bonobos. But seasonality in lowland forest is strongly related to latitude (van Schaik *et al.*, 1993), so fruiting seasonality is unlikely to differ consistently between the two species. There is currently no evidence of any consistent differences in plant structure and dynamics between the forests occupied by chimpanzees and bonobos.

Second is a difference in food availability resulting from feeding competition with gorillas (*Gorilla gorilla*). Like chimpanzees, gorillas live only north of the Zaïre River. They are therefore sympatric with chimpanzees throughout most of their range, but never with bonobos. The relevant food is the leaves and stems of terrestrial herb vegetation (THV), a component of the diet of all three species of African ape.

Gorillas, restricted to a diet of THV, experience very low levels of within-group feeding competition (Watts, 1994; Janson & Goldsmith, 1995). Their only other major dietary component is fruits, similar to those eaten by chimpanzees. Since gorillas live in stable groups, their dependence on THV is presumably the critical difference reducing feeding competition for gorillas compared with chimpanzees.

Because THV is invariably prominent in gorilla diets, gorilla foraging has been hypothesized to reduce the availability of THV for sympatric chimpanzees as compared with bonobos (Wrangham, 1986). Accordingly, the reason why bonobos have more stable groups than chimpanzees may be their ability to eat more THV than chimpanzees.

Two kinds of evidence support this THV hypothesis. The only direct comparison between chimpanzee and bonobo diets suggests that Lomako bonobos eat significantly more THV than do Kibale chimpanzees (Malenky & Wrangham, 1994). At some bonobo and chimpanzee sites, THV is known to be eaten more when arboreal fruit is scarce (Wamba: Kano & Mulavwa, 1984; Ndoki: Kuroda *et al.*, Chapter 6; Lopé: Tutin *et al.*,

1991; Kibale: Wrangham *et al.*, 1991; Kahuzi-Biega: Yamagiwa *et al.*, Chapter 7). Thus, there is preliminary evidence that bonobos eat more THV than do chimpanzees and that it can be a fallback food when competition is relaxed. Whether THV provides enough food to be important for bonobo social ecology, however, is still uncertain (Malenky & Stiles, 1991; Malenky *et al.*, 1994).

WHY DON'T KANYAWARA FEMALES TRAVEL IN PARTIES?

If THV is indeed responsible for allowing bonobo parties to be more stable and larger than those of chimpanzees, it can be expected to have similar effects when different populations of chimpanzees are compared. For example, the most stable chimpanzee parties reported from the wild appear to be those at Bossou, where there are no gorillas, and where THV seems particularly abundant and important in the chimpanzee diet (Sugiyama & Koman, 1992). However, recent comparisons of Gombe and Kanyawara chimpanzees indicate that although the two populations differ in the availability of THV, they do not show the expected differences in grouping patterns.

Comparison of these two populations is instructive because their social organization is generally similar, despite ecological differences. For example, in a preliminary description of social relationships in Kanyawara, chimpanzees were found to be similar to Gombe in having strong male–male friendships and relatively anti-social females (Wrangham *et al.*, 1992). These patterns have been robustly confirmed by subsequent observations. Additional similarities include systematic intercommunity migration by adolescent females, long-term intracommunity alliances used in dominance struggles between males and territories defended through calls and violence, including lethal aggression (Wrangham *et al.*, in prep.).

Gombe chimpanzees, on the one hand, conform to expectation. During fruit-poor seasons in Gombe, chimpanzees have very little THV and no consistent fall-back foods (personal observation). Consistent with the lack of fall-back foods, fruit scarcity leads to relatively intense seasonal food stress (apparently responsible for weight loss, ill health, increased mortality and reduced reproductive effort; Goodall, 1986; Wallis, 1992, 1995). During periods of apparent fruit scarcity, Gombe chim-

panzees travel in small parties and females especially spend much time alone (Wrangham, 1977).

Kanyawara chimpanzees, on the other hand, have relatively abundant THV compared with Gombe and they eat it when fruit is scarce (Wrangham *et al.*, 1991). According to the THV hypothesis, this means that Kanyawara chimpanzees should be able to maintain relatively large parties during periods of fruit scarcity, including having females that commonly travel together, as happens at other chimpanzee sites (whether or not it is THV that allows them to do so, e.g. Bossou, Mahale, Tai; Boesch, Chapter 8). However, Kanyawara's females do not do so. Instead, Kanyawara party size is consistently correlated with phenological measures of fruit availability (1988–89: Wrangham *et al.*, 1992; 1989–92: Chapman *et al.*, 1995); and parties become small during fruit-poor seasons, with the result that mean party size is very similar in Kanyawara and Gombe (Kanyawara: 5.6 (1984–85), 6.1 (1988–89), 5.1 (1989–1992); Wrangham *et al.*, 1992; Chapman *et al.*, 1995; Gombe: 4–5, Goodall 1986; numbers exclude dependent offspring). Furthermore, adult females in Kanyawara spend about as much time alone (with their dependent offspring) as do their Gombe counterparts (70% in Kanyawara vs. 65% in Gombe; Wrangham *et al.*, 1992). Thus, the presence of THV in Kibale does not cause parties to be large or relatively stable and therefore does not have the social effects expected of it.

TOWARD A SOLUTION

Kanyawara chimpanzees accordingly present a problem for the THV hypothesis. Below, we examine data relevant to finding a solution. We ask whether seasonal variation in fruit availability is ecologically and demographically significant, and what drives variation in party size. We conclude that Kanyawara chimpanzees search for fruits even when they are scarce, so that THV is never an important influence on feeding and grouping.

STUDY SITE AND METHODS

Kanyawara's chimpanzees have been studied irregularly since 1979, when they were observed briefly (Ghiglieri, 1984). From 1983 to 1985 they were studied by Isabirye-Basuta (1988, 1989) for 30 months. Since 1987, attempts

at observation have been continuous. Habituation has increased steadily. For example, by 1988 parties could be watched on the ground and by 1990 they tolerated observers walking about 15 m behind.

Chapman & Wrangham (1993) described the study site and population. Here we note aspects relevant to understanding some of the more important constraints and biases on observation. Briefly, Kanyawara contains medium-altitude forest (1470–1750 m) bordered by subsistence agriculture. The forest has a history of substantial disturbance, so that only about 30% of the Kanyawara community's range is relatively undisturbed. Other sectors include forest that was logged in the 1960s either lightly (*c.* 20% of the community range, depending on total area measured) or heavily (*c.* 20%), and plantations of exotic trees such as pine (*Pinus caribbaea*) established on hill-top grasslands in the 1960s (*c.* 15%). The balance of the Kanyawara community's range is composed of undisturbed papyrus (*Cyperus papyrus*) swamps (*c.* 3%) and occupied villages, composed mostly of farm bush and fields in various states of regeneration. The population has never been deliberately provisioned, but during periods of fruit scarcity Kanyawara chimpanzees regularly raid village crops such as banana stems. Observation of crop-raiding is difficult.

Since December 1987 attempts to contact and follow chimpanzees have been made about six days per week, normally by one or two teams, each with two observers. Despite the rather constant search effort, the number of observation hours per month has varied widely (mean hours per month 83.6, standard deviation 53.7, range 4.7–219.7, $N = 41$ months, January 1991–May 1994).

Behavioral data analyzed in this paper come from two sources. First, party composition data were compiled by ourselves, Ugandan field assistants or other observers. They consist of records every 15 minutes of: all individuals present or believed to be present (i.e. if seen before and after that 15-minute point without any sign of having left in the interval); map location; and the food being eaten by most of the party. Second, RWW collected 10-minute focal data from February to June 1993. These consisted of 5 scans at 2 minute intervals of a focal individual, recording activity, nearest neighbors and party composition. To reduce dependence in the data, no individual was scanned more frequently than every 30 minutes.

Phenological data were recorded every two weeks from a 12 km trail (starting December 1987). Fecal analysis was done on 1696 dung samples over 78 months, December 1987–May 1994 (mean per month = 21.7, $SD = 18.7$). For phenological and dung analysis methods, see Wrangham *et al.* (1991).

THV is defined by its distribution, rather than in terms of its floral composition or its plant parts. The two key features are its terrestriality and the fact that it occurs in patches sufficiently large to allow individuals to co-feed with minimal within-group competition. Although this definition is frustratingly vague as far as patch size is concerned, THV is a useful concept because it describes a terrestrial component of the diet that is important for all the African apes (e.g. Kuroda, 1979). The particular foods that constitute THV vary widely and routinely include several types during the same feeding bout. Four plant families are especially prominent: Marantaceae, Zingiberaceae, Gramineae and Acanthaceae. The parts eaten include pith (especially of monocotyledonous stems), leaf-shoots, leaves and fruits (especially Zingiberaceae). THV is not strictly 'herbaceous,' because chimpanzees eat items from some woody plants that are found in combination with herbs, such as a shrub-fig (*Ficus asperifolia (urcelolaris)*; Wrangham *et al.*, 1991). This means that THV is not an ideal term, but we use it here in acknowledgement of current practice.

Party size refers to total number of chimpanzees present, excluding dependent offspring (see Wrangham *et al.*, 1992). Computer data entry has not yet been finalized for some years, so different periods are used for different analyses. Statistical tests are 2-tailed throughout.

SOCIAL ECOLOGY IN KANYAWARA

Were fruit shortages important in Kanyawara?

Major fruits were produced irregularly. As in all other wild chimpanzee and bonobo populations, arboreal fruits dominated the diet of Kanyawara chimpanzees (monthly average of 79% of feeding time from 1991 to 1993; see Table 4.1). The potential importance of food scarcity was therefore expected to depend on the availability of arboreal fruits.

Table 4.1. Monthly feeding time on major food types

	1991	1992	1993	1991-93
<i>Ficus natalensis</i>	28.4	10.4	11.7	16.8
<i>Mimusops bagshawei</i>	13.6	15.1	10.4	13.0
<i>Ficus exasperata</i>	5.7	11.9	15.7	11.1
<i>Pseudospondias microcarpa</i>	11.4	12.4	0.6	8.2
<i>Ficus sansibarica</i>	3.4	5.7	12.7	7.3
<i>Uvariopsis congensis</i>	12.3	0.1	8.3	6.9
<i>Ficus saussureana</i>	5.3	4.7	4.4	4.8
7 top fruit species (total of the above)	80.1	60.4	63.8	68.1
24 other arboreal fruit species	5.4	16.6	10.7	10.9
Total arboreal fruit	85.5	77.0	74.5	79.0
THV	12.3	19.9	18.4	16.9
Arboreal leaf	1.3	1.1	5.3	2.6
Meat	0.8	1.2	0.7	0.9
Other (wood, seed, flower, bark, honey, etc.)	0.1	0.8	1.1	0.6
<i>N</i> (15-minute points observed)	3109.0	3242.0	5459.0	
Mean % time feeding per month	59.2	53.9	49.8	54.3

Note: Cells show mean monthly percentage of feeding records for each food type. Each year represents 12 months of observation.

Major fruit species were defined as those that accounted for > 75% of time spent eating fruit. From 1991 to 1993 there were seven such species (Table 4.1). Three produced succulent drupes (*Mimusops bagshawei* (Sapotaceae), *Uvariopsis congensis* (Annonaceae) and *Pseudospondias microcarpa* (Anacardiaceae)). The remaining four were figs (*Ficus natalensis*, *Ficus exasperata*, *Ficus sansibarica* (*brachylepis*) and *Ficus saussureana* (*dawei*) (Moraceae)). These seven species accounted for between 78% and 94% of total time spent eating fruits (1992 and 1991 respectively), or 60–80% of total feeding time.

Because the diet was dominated by these seven species, their fruiting patterns were critical to overall levels of fruit availability (Fig. 4.1). Fruit production in drupes was tightly synchronized within species, but fruiting was unpredictable. Thus drupe species sometimes failed to fruit at all within a year, whereas figs invariably fruited each year. The result was that drupes were less often available than figs. From December 1987 to September 1993, there were on average 4.5 months per year with none of the drupes fruiting.

By contrast, there were only 1.2 months per year with none of the figs fruiting and only 0.7 months per year with none of the seven major food species in fruit. But figs



Fig. 4.1. Adolescent male chimpanzee eats figs at Mahale. (Photo by T. Nishida)

were eaten less than drupes when drupes were available. Across months, there was a strong negative correlation between drupe-eating and fig-eating (major fruits: Spearman $r_s = -0.75$, $N = 41$, $P < 0.001$; all non-fig vs. fig fruits: $r_s = -0.89$, $N = 41$, $P < 0.001$; data from January

1991–May 1994). Since figs were relatively continuously available, this implies that figs were a fallback food.

Supporting the concept of figs as a fallback food, feeding time was generally more closely related to fruit availability for drupes than figs (percent time being eaten vs. percent trees on the phenology trail with ripe fruit: *M. bagshawei*, Spearman $r_s = 0.84$, $p < 0.001$; *P. microcarpa*, $r_s = 0.42$, $p < 0.05$; *U. congensis*, $r_s = 0.58$, $p < 0.01$; *F. sansibarica*, $r_s = -0.05$, ns; *F. saussureana*, $r_s = 0.35$, ns; *F. exasperata*, $r_s = 0.50$, $p < 0.01$; *F. natalensis*, $r_s = 0.37$, ns; $N = 33$ months, January 1991–September 1993).

Preference for drupes over figs has been found in other studies of apes (Leighton, 1993; Kuroda *et al.*, Chapter 6). Kanyawara's figs tend to have little sugar and therefore generally provide less digestible carbohydrate than do drupes (Conklin & Wrangham, 1994).

In sum, abundance of major drupes varied greatly between months, with chimpanzees relying on figs when drupes were scarce.

Reproductive rate in Kanyawara was low compared with other sites

The ultimate importance of total fruit scarcity is a negative impact on the chimpanzees' reproductive rate. Kanyawara's reproductive rate seems low when compared with other chimpanzee populations: for 11 Kanyawara females for whom minimum interbirth interval has been seen or inferred, the shortest interval between surviving offspring has been 5.5 years. The mean IBI, including minimum IBIs for females who have not yet given birth, was 7.2 years, SD 1.7 years. This is longer than at other sites, especially since data from other sites do not include females waiting to conceive (Bossou 4.4 years, Sugiyama, 1989; Gombe 5.5 years, Goodall, 1986; Mahale 6.0 years, Nishida *et al.*, 1990).

On the other hand, there was no indication that fruit scarcity was associated with ill health or mortality. No widespread bouts of diarrhea occurred. Respiratory infections were rare. Parasitic nematodes and protozoa occurred at low frequency (monitored over five years, Reid & Wrangham, in preparation). One trematode outbreak occurred for a seven-month period, but without any obvious relationship to fruit availability (Wrangham, 1995). No infants died. Kanyawara chimpanzees are relatively large-bodied (*c.* 40–50 kg, Kerbis Peterhans *et al.*, 1993) and, unlike Gombe chimpanzees, visual assessment

did not suggest seasonal weight loss. They never lost their hair sheen. This is in contrast to Gombe, where individuals can look thin and dull-haired during periods of fruit scarcity (personal observation).

We tentatively interpret this pair of results as indicating that the main fallback foods, figs and THV (plus agricultural crops such as banana stems), are adequate for the physiological maintenance of chimpanzees, but provide a poor basis for reproduction. More data are needed to test this conclusion and to establish the demographic and growth parameters of this population. However, the evidence from reproductive rates clearly suggests that the overall level of food abundance was low compared to other chimpanzee sites and that periods of drupe scarcity were ecologically important.

Fruit patches were highly attractive to chimpanzees

The major drupes were produced in groves of locally high density. Figure 4.2(a) gives an example for the eating of *Mimusops bagshawei* fruits during 1993–94, showing that it was consumed in a limited portion of the community range compared with THV (cf. Fig. 4.2(b)). Such fruiting groves occurred in areas that were visited routinely by Kanyawara chimpanzees between peaks of drupe production, because they found other foods there also. Therefore, we have long-term records of which individuals use the areas.

The community had eight resident adult females, compared with a conservative count of 12 peripheral adult females who shifted their core areas for a week or more at a time, sometimes within their own community's range and sometimes to another community's range. During peaks of drupe production, there were more sightings both of familiar-but-rarely-seen females or mother-offspring units, and of completely unfamiliar females. The behavior of males suggested that these stranger females visited from neighboring communities: mothers were the object of great social interest by males and offspring were twice subject to apparent attempts at infanticide (February 1993, February 1994). This suggests that females visited fruiting groves both from distant parts of the Kanyawara community (e.g. mother *EK*, Fig. 4.3(c)), and from other communities (e.g. mother *PU*, Fig. 4.3(b)), in contrast to the even use of the range by central females (e.g. mother *LP*, Fig. 4.3(a)).

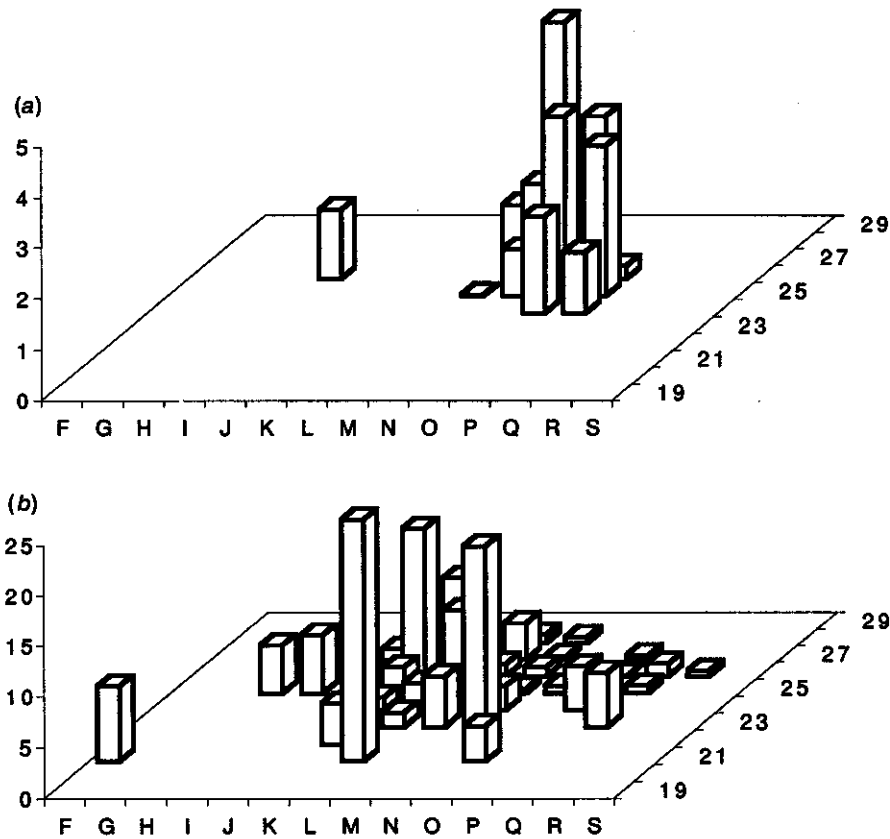


Fig. 4.2. Grid maps of relative use of community range at Kanyawara: feeding sites. Data from January 1993 to May 1994, $N = 7172 \times 15$ -minute points. Grid represents an area of 7 km north-south (F to S), and 5.5 km east-west (19 to 29); each square is 0.25 km². 'Relative use' shows the proportion of observations recorded for a given food, divided by the proportion of observations recorded in that grid square. (a) Relative use

An alternative explanation for the occasional sightings of peripheral females is that they were in the process of migrating between communities, but immigration by adolescent females occurred rapidly. Thus, we recorded six newly arrived adolescent females. After their initial sightings, five of these females were seen as often as central females (70–100% of months, $N = 2$ –41 months, mean 24.8, compared with 44–100% for resident adult females). Only the sixth (*TW*) behaved like a peripheral female by visiting for two days only.

In sum, variation in the spatial and temporal production of fruits seems very important, because it

of range by chimpanzees when eating *Mimusops bagshawei* fruits, showing a patchy distribution centred in the south and east. $N = 547 \times 15$ -minute points. (b) Relative use of range by chimpanzees when eating THV. THV-feeding was more widely spread than when eating *M. bagshawei* fruits, but was still patchy. The western concentration of data occurred near the forest edge. $N = 300 \times 15$ -minute points.

appeared to have a major impact on chimpanzee social relationships and use of space.

Was THV density sufficient to provide food for chimpanzees?

THV species were abundant

Stem densities of THV species eaten at Kanyawara have been shown to be significantly lower than at Lomako, and appear to be lower than at Ndoki (Malenky *et al.*, 1994). However, the data on which these figures are

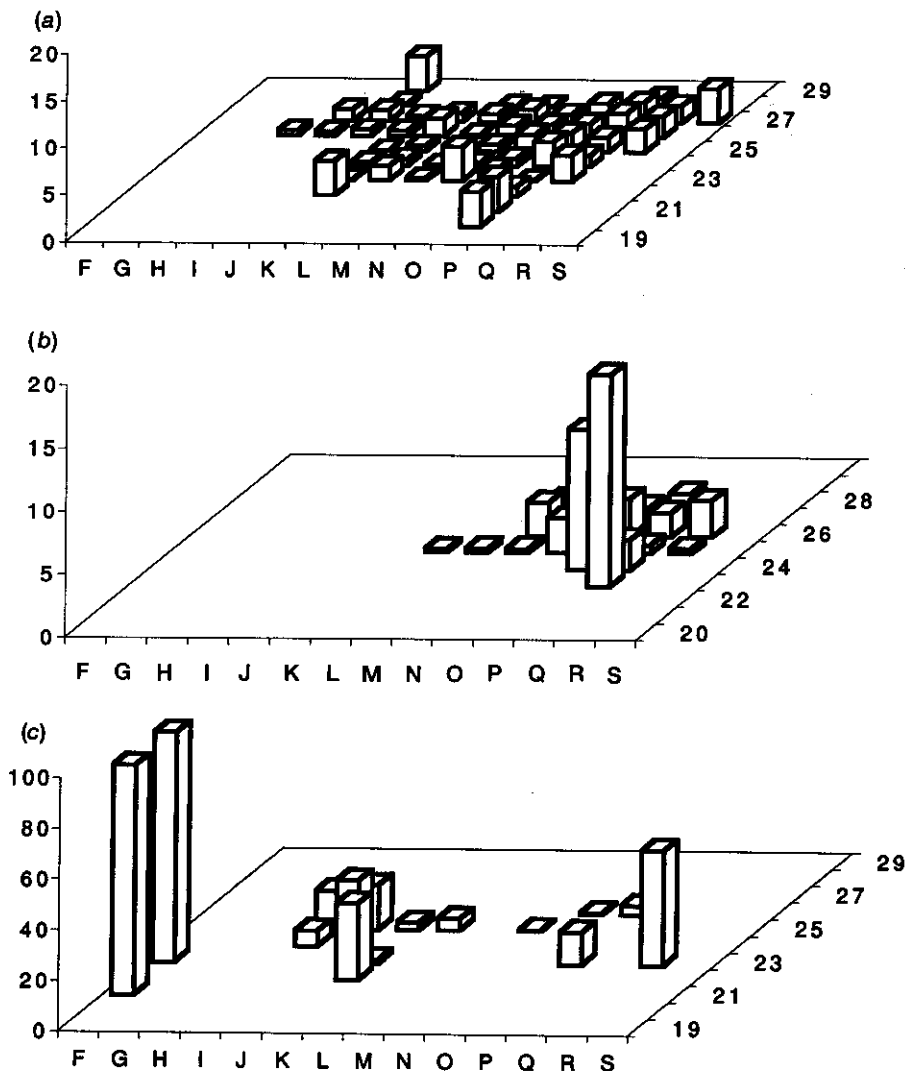


Fig. 4.3. Grid maps of relative use of community range at Kanyawara: individual occupancy. Data source and analysis are as in Fig. 4.2. (a) Relative range use by LP, a resident central mother. Her time was spread evenly over the central and southern part of the range. $N = 1948 \times 15$ -minute points. (b) Relative range use by PU, a peripheral southern mother. Her visits were

restricted to the southern and eastern part of the range. $N = 332 \times 15$ -minute points. (c) Relative range use by EK, a resident northern mother. Map shows that EK made an occasional journey to the southern part of the range. $N = 79 \times 15$ -minute points.

based came from natural forest areas of Kanyawara, and excluded the plantations of exotic trees (such as pines) and the swamps. Both plantations and swamps were highly productive of THV foods. Pine plantations were routinely visited in the late afternoon by chimpanzees

who foraged there for the relatively abundant herbs. Swamps in Kanyawara are dominated by papyrus, a species whose pith is eaten by chimpanzees during periods of extreme food scarcity, which grows all year and has the highest growth rate known for any herb

(Thompson, 1976). Papyrus pith is not a preferred food but it is enormously abundant.

A second type of evidence that THV was abundant came from how easily chimpanzees found it. When drupes were scarce, chimpanzees sometimes visited a particular fig tree daily for a week or more. Typically no other fruits were eaten within several hundred meters of the target fig tree, apparently because none occurred, whereas THV food-patches were found every day at high density within a few minutes' walk from the fig-tree. Even if no THV happened to be nearby, chimpanzees could find THV patches predictably, for example in the ecotone areas between exotic plantations and natural forest, or in large gaps in logged areas.

THV was eaten all year

Previously, we found that the presence of THV remains (fibrous strands) in the dung was predicted by fruit scarcity (when variation in rainfall was statistically controlled, Wrangham *et al.*, 1991). This suggests that the percentage of feeding bouts on THV is negatively correlated with the percentage on fruits. When non-fig and fig fruits were combined into a single 'fruit' category, there was indeed a significant negative correlation between feeding time on THV and feeding time on fruits (Spearman $r_s = -0.94$, $N = 41$ months, $p < 0.001$; January 1991–May 1994). When only non-fig fruit are considered, however, the correlation with THV was not significant ($r_s = -0.31$, $N = 41$ months; partial correlation using log-transformed data showed neither non-figs nor figs were correlated with THV: non-fig fruits, partial $r_s = -0.09$; figs, partial $r_s = 0.02$). This suggests that THV was only a secondary fallback food, after figs.

THV was the most important component of the diet after arboreal fruits, with a monthly average of 17% of feeding points (standard deviation 12%, $N = 41$ months, 1991–94; see Table 4.1). Typically it was eaten late in the day (correlation between hour of day and percentage of feeding time spent eating THV, Spearman $r_s = 0.96$, $N = 14$ hours, $p < 0.01$ ($N = 2213$ feeding points, 1993–94). This was probably partly the result of fruit shortage later in the day. However, even during periods of drupe superabundance, chimpanzees often left fruit-rich trees to eat THV in the evening. THV therefore appeared to have a nutritional role beyond being a fallback food. It is rich in fermentable fiber (Conklin & Wrangham, 1994)

and may provide a more efficient use of overnight inactivity than the more rapidly digested nutrients in fruits.

There was no indication that THV induced feeding competition. Individuals fed close to each other. For example, no aggression was observed while eating THV, even though individuals fed closer to each other when eating THV than when eating non-fig fruits (mean number of other individuals within 5 m = 0.8, $N = 152$ scans for THV, vs. 0.2, $N = 291$ scans for fruits; Wilcoxon $T = 0$, $N = 7$ individuals each with > 5 data-points as focal when eating each food type, $p < 0.05$).

Did THV buffer party size?

Party sizes while eating non-fig fruits, fig fruits and THV tended to rise and fall in parallel, all influenced in the same way by overall monthly changes in the grouping pattern. Thus, inter-monthly correlations between sizes of party when eating each of the three main food types were positive and significant. For THV and figs, Spearman $r_s = 0.68$, $N = 33$, $p < 0.001$; for THV and non-fig fruits, $r_s = 0.64$, $N = 34$ months, $p < 0.001$; for figs and non-fig fruits, $r_s = 0.51$, $N = 30$, $p < 0.05$ (data from 1991–93). This implies that fruit abundance drove party size, regardless of the particular food being eaten at a given time.

Comparisons of party size on days when two food types were recorded support this conclusion. Thus, within days, no differences were found in the size of parties eating non-figs, figs or THV (non-figs, figs and THV compared within days from 1991–92; Wilcoxon $z \leq 0.30$, $N \leq 49$, ns). Similarly, Malenky & Wrangham (1994) found that parties did not increase in size when moving from fruit trees to THV.

The only evidence for THV buffering party size was that mean party size within months was slightly higher when eating THV than when eating figs (7.3 vs. 6.3, Wilcoxon $z = 2.30$, $N = 33$ months, $p = 0.05$; 1991–93).

Arboreal fig fruits were a dominant component of the diet in many months, averaging 42.5% of monthly feeding time over a three-year period (1991–93). In months when more figs were eaten, parties were smaller (mean monthly party size vs. percent feeding records on arboreal fig fruits: Spearman $r_s = -0.39$, $N = 41$ months, $p < 0.05$, 1991–94), whereas when more non-fig fruits were eaten, they were larger ($r_s = 0.35$, $N = 41$, $p < 0.05$).

Correlations between party size and feeding time on arboreal leaves or THV, by contrast, were not significant ($r_s = 0.29$, leaf; 0.22 , THV; $N = 41$, ns). Thus, more fig-eating was associated with smaller parties. This is presumably because fruits were generally scarce at those times.

DISCUSSION

THV did not ameliorate feeding competition for Kanyawara chimpanzees

The Kanyawara population is not representative of chimpanzees in general. For example, no other population of chimpanzees or bonobos has been described with so few fruit species accounting for the majority of feeding time. Similarly, movements by peripheral females into communities with temporarily abundant fruit patches, which indicate the importance in Kanyawara of a heterogeneous fruit supply, appear to be uncommon elsewhere. Furthermore, the relationships between diet and life-history variables in Kanyawara chimpanzees appear unusual. On the one hand, low mortality and good body condition suggest that the population had a good food supply. On the other hand, frequent periods of non-fig fruit shortage and long interbirth intervals suggest that nutrition was poor. Nevertheless, even if Kanyawara has ecological idiosyncracies, the relationships between food supply and grouping should follow general rules. We therefore use these rules to address the THV hypothesis.

The effect of THV as an ecological (and social) buffer was originally expected to depend on its abundance, without regard to quality (Wrangham, 1986). Our data, however, show that although THV was abundant in Kanyawara, drupe scarcity led chimpanzees to forage on figs, though rare, in preference to THV. The result was that parties were small. This contradicts the prediction of the THV hypothesis, by showing that even when THV was present, the fruit component of the diet continued to drive party size. THV thus had little effect on the intensity of feeding competition.

Importance of THV quality

Our data require that the THV hypothesis be rejected in its original form, because Kanyawara chimpanzees preferred fruit to THV. But preliminary data show that

THV eaten by bonobos has higher nutritional quality than that eaten by Kanyawara chimpanzees (Malenky & Stiles, 1991; Wrangham *et al.*, 1991), so this problem may not apply to bonobos.

Accordingly, and in line with the distinction made by Kuroda *et al.* (Chapter 6), we suggest a classification into high-quality (H-THV) or low-quality (L-THV). H-THV is protein-rich, is of sufficient nutritional value to allow growth and reproduction, is more preferred than typical fig fruits, and typically appears to occur at low density requiring 'feed-as-you-go' foraging: examples include the shoots of *Haumania* spp. and the pith of *Megaphrynium* spp., which occur at low density in Wamba, Lomako and elsewhere (Kano & Mulavwa, 1984; Malenky & Wrangham, 1994; Kuroda, Chapter 6). L-THV, in contrast, is cellulose-rich, is of insufficient quality to allow growth and reproduction by chimpanzees and bonobos, is less preferred than most fig fruits, and may occur in high-density patches: a clear example is papyrus pith, occurring in dense patches in Kanyawara but eaten only *in extremis*. The revised hypothesis substitutes H-THV for THV. Thus, it proposes that the evolution of differences in the social ecology of chimpanzees and bonobos has depended on bonobos having greater access to H-THV, that H-THV is an important fallback food where it occurs in sufficient abundance and that it allows for relatively stable foraging parties by reducing the intensity of WGS.

The revised hypothesis has the merit of distinguishing more clearly between the diets of *Gorilla* and *Pan*. It suggests that L-THV is an adequate diet for *Gorilla* (as seen in high-altitude gorillas, e.g. Yamagiwa *et al.*, Chapter 7) but not for reproduction by *Pan*. It conforms to the observation that H-THV appears important in the diet of bonobos (Kano & Mulavwa, 1984; White, Chapter 3), and that there are important distinctions in the way that gorillas, chimpanzees and bonobos forage according to THV quality (Kuroda *et al.*, Chapter 6).

Two important questions concern differences across species and within species. First, how does the use of H-THV differ between bonobos and those chimpanzees that occur sympatrically with gorillas in bonobo-like habitats, such as in Lopé and Ndoki (Tutin, Chapter 5; Kuroda, Chapter 6). In particular, does competition between gorillas and chimpanzees limit the availability of H-THV for chimpanzees?

Second, to what extent can intraspecific variation be explained by variation in H-THV availability? In the case of Kanyawara, there is essentially no H-THV. We hypothesize that Kanyawara chimpanzees are therefore forced to search for fruits even when few are available, and this leads them to disperse into small parties. This pattern appears likely to explain the fact that Kanyawara chimpanzees conform to the classic type of social organization for *Pan troglodytes schweinfurthii*. Comparisons between Lomako and Wamba, or between Gombe and Mahale, will be helpful because these cases involve sites with similar climate but different party sizes.

Such tests will not explain all differences within a species. For example, Tai chimpanzees form large and relatively stable parties, but eat little THV (C. Boesch, personal communication). This emphasizes that there are several potential sources of explanation for species differences in grouping.

The THV hypothesis has the merit, however, of being the only one to date that also incorporates an explanation for the evolutionary differentiation of bonobos and chimpanzees. By showing that L-THV has little social effect in chimpanzees, our present data have sharpened the search for the origins of the bonobo-chimpanzee differences. The absence of gorillas on the south side of the Zaïre River certainly means that a THV-eating niche has been left vacant, so the question now is: do bonobos eat enough H-THV to account for their reduced feeding competition compared to chimpanzees? If not, a renewed focus on locomotor differences between bonobos and chimpanzees may be required to explain their social differences.

ACKNOWLEDGMENTS

This paper was originally prepared for the Wenner-Gren conference 'The Great Apes Revisited,' held November 12-19, 1994 in Cabo San Lucas, Baja, Mexico. We thank the Government of Uganda, especially the National Research Council, Forestry Department and National Parks Board, for permission to work in the Kibale National Park. Facilities were provided by Makerere University Biological Field Station and the Wildlife Conservation Society. The Department of Zoology, Makerere University, assisted at all times. Acknowledgement for funding is due to the National Science Foun-

ation (BNS-8704458), National Geographic Society (3603-87 and 4348-90), Leakey Foundation, USAID and MacArthur Foundation. Assistance was provided by L. Barrett, J. Basigara, B. Beerlage, A. Berle, J. Byaruhanga, L. Chapman, N. L. Conklin, K. Clement, the late G. Etot, B. Gault, J. Gradowski, M. Hauser, K. Hunt, G. Isabiryé-Basuta, the late G. Kagaba, E. Karwani, C. Muruuli, P. Novelli-Arcadi, the late J. Obua, E. Ross, E. Tinkasimire, P. Tuhairwe, P. Weeks and R. G. Wrangham. RWW thanks T. Kano for his hosting a fascinating and informative visit to Wamba. B. Beerlage and the editors provided helpful comments.

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Reprinted from *Great Ape Societies*
edited by W. C. McGrew, L. F. Marchant and T. Nishida

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Transactions of the Royal Society of London, Series B,
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