PRELIMINARY STUDY OF FEEDING COMPETITION BETWEEN BABOONS AND CHIMPANZEES IN THE MAHALE MOUNTAINS NATIONAL PARK, TANZANIA

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ABSTRACT Of eight primates sympatric to chimpanzees (*Pan troglodytes schweinfurthii*) in the Mahale Mountains National Park, Tanzania, yellow baboons (*Papio cynocephalus cynocephalus*) are the second largest in size after chimpanzees. Baboons in Mahale have invaded the chimpanzee range over the year. Group size, range use, feeding behavior, and diet of baboons and chimpanzees were recorded during the same season to investigate the interspecific relationship. The data indicate feeding competition between the two species. Chimpanzees may be negatively affected by the competition due to their dependence on specific ripe fruits, as their dietary items significantly overlap with those of the baboons.

Key Words: Baboon; Chimpanzee; Sympatric; Feeding competition; Mahale.

INTRODUCTION

Animals do not fix but vary their range according to environmental and climatic change; e.g., glacial changes in the forest line (Vrba, 1985), or human-induced vegetational changes such as deforestation or designation of nature preserve. To clarify how animal ranging affect local fauna and flora offers insights into conservational ecology, feeding ecology and anthropology.

In ecology, according to the competitive exclusion principle (Gause, 1932), two species with the same diet generally cannot live in the same habitat (e.g., Chappell, 1978; Munger & Brown, 1981). Multiple species of primates, however, sometimes live sympatrically. Since many primate species have a large fruit component to their diet, primate species may potentially compete for the same diet or exhibit interspecies dietary segregation (e.g., Janson, 1988; Ungar, 1995). One common pair of sympatric frugivorous primate species is the chimpanzee (*Pan troglodytes*) and baboon (*Papio* spp.). Chimpanzees live along the equatorial zone between Senegal and western Tanzania in Africa. Baboons are very widely distributed in dry areas of Africa and live sympatrically in the East African chimpanzee habitats of Gombe and Mahale, Tanzania (Goodall, 1986; Nishida, 1990), Budongo, Bwhindi, Kalinzu and Kibale, Uganda (Howard, 1991; Wrangham *et al.*, 1991; Mitani & Watts, 1999), and Kahuzi-Biega, Democratic Republic of Congo (Yamagiwa *et al.*, 1988). Do baboons and chimpanzees compete for their diet? Unfortunately, research has been focused on the apes in the above habitats. Many studies have shown the density of co-exis-

tence animals but none has focused on the interspecies relationships. In Kibale, it was simply reported that chimpanzees and baboons ate the some fruits and leaves in their diet (Wrangham *et al.,* 1991). Peters & O'Brien (1981) compared the diet among Eastern and Southern African humans, chimpanzees, and baboons in the literature and found that among 191 dietary items, 76 (39.8%) were eaten only by chimpanzees, 80 (41.9%) only by baboons, and 35 (18.3%) both by chimpanzees and baboons (calculated from Fig. 2 of Peters & O'Brien, 1981). The percentages seem to show that the diet overlap is not large. Data from various sources offer either the baboon or chimpanzee diet. Chimpanzees have been reported to depend on fruits (Hladik, 1977; Wrangham, 1977; Nishida & Uehara, 1983; Sugiyama & Koman, 1987; McGrew *et al.,* 1988), whereas the baboons have a very diverse diet (Norton *et al.,* 1987). At Gombe, Tanzania, where the baboon habitat is one of the most biodiverse, fruits accounted for 31% and leaves and shoots accounted for 28% among the 86 dietary items (calculated from Ranson, 1981). Grass and acacia trees are particularly important in the diet of the Amboseli baboons (Altmann & Altmann, 1970; Altmann, 1998). Those studies point to the importance of data on the diet of baboons and chimpanzees in co-existence areas.

In this study, we investigated the diet of baboons and chimpanzees in the Mahale Mountains National Park, Tanzania. The Mahale Mountains National Park is a well known chimpanzee (*P. t. schweinfurthii*) habitat, but eight other primates live sympatrically (Nishida, 1990): red colobuses (*Colobus badius*), Angolan black-and-white colobuses (*C. angolensis*), blue monkeys (*Cercopithecus mitis*), red-tailed monkeys (*C. ascanius*), vervet monkeys (*C. aethiops*), yellow baboons (*P. cynocephalus cynocephalus*), thick-tailed galagos (*Galago crassicaudatus*), and lesser galagos (*G. senegalensis*). Of these, the yellow baboons are the second largest in size after chimpanzees. Baboons in this area have uniquely invaded the range of the M group chimpanzees over the years. Nishida (1997) reported that there was no baboon sighting in most the M group range in 1965, with the baboon range exclusively along the lakeshore. However, some baboon groups spread deeper into the interior of the M group range in early 1990, while moving 1km inland from the shores of Lake Tanganyika in 1995 (Nishida, 1997). Why the baboons quickly expanded their range is unknown. To estimate how the inland expansion of the baboon range affected the chimpanzees, we investigated the group size, range use, feeding behavior, and diet of both primates during the same season.

METHODS

I. Study Site and Subjects

The Mahale Mountains were designated a National Park in 1987 and vegetation has recovered since then. The vegetation of the park is approximately 70% gallery forest, and the remainder is woodland, some of which is recovering from slash-and-burn agriculture (Nishida, 1990).

The study subjects were yellow baboons and the M group chimpanzees in the Mahale Mountains. Chimpanzees have been studied since 1965. During more than

30 years of observation, a total of 198 plants, 25 insects, 5 birds and 12 mammals have been listed as dietary items selected by chimpanzees (Nishida & Uehara, 1983). The chimpanzee group size during this study was approximately 50 individuals with 2-2.5 heads/km^2. Baboons have not been habituated. Their minimum group size has been reported as 26 with 24.9-25.1 heads/km^2 (Uehara & Ihobe, 1998).

II. Data Collection

Field data on chimpanzees were collected by AMO, and on baboons by AMO and MBK from December 1998 to January 1999. One of the major chimpanzee dietary fruits, *Saba florida* is abundant from December to January in Mahale, when the chimpanzee gregariousness is the largest during the year (Nishida, 1979; Masumoto-Oda *et al.*, 1998).

We called the focal group, "subgroup," in this study. Baboon or chimpanzee subgroup size was determined as the maximum number of individuals seen during a day-long follow. The habituated chimpanzees were followed individually. We followed baboon groups since they were not habituated. Our proximity to a group of baboons was 100m at the closest. We followed subgroups of baboons that ranged around the Kansyana camp, the research base 1km inland from the lakeshore (Fig. 1), and recorded data on the individuals at the center of the subgroup. We were not able to identify the baboon subgroups observed serially.

The data collected were subgroup size, location, activity, dietary items, and encounters with other animals per 1min. Baboons and chimpanzees were observed 1-2 times and 2-4 times a week, respectively, throughout the study period. Total observation time was 12 days and 3,141 sample points (262±156 sample points/day) for baboons, and 21 days and 6,353 sample points (303±110 sample points/day) for chimpanzees. We analyzed data obtained between 8:00 and 18:00. The proportion of 2-hour period in total observation time did not differ between chimpanzees and baboons (Wilcoxon's signed-rank test, $n=5$, $z=-0.14$, ns). Baboon sample points were 22.2% male and 79.8% female, while chimpanzee sample points were 16.6% males and 83.4% females. Female bias in the sample points were due to AMO collection of data on female behaviors. Activities were categorized into feeding (preparation and ingestion), moving (locomotion activity other than position shift of less than one meter during resting), and resting (excluding feeding and moving). Using the Minimum Convex Polygon method (White & Garrott, 1990), the range areas were calculated from travel routes during follows, which were digitized into a geographical information system (Arc/Info).

RESULTS

I. Subgroup Size and Range Use

The baboon subgroups were smaller than the chimpanzees' (Fig. 2). The mean baboon subgroup size was 15.8±7.5 (Mode=14, n=12), and that of chimpanzees was 32.5±10.8 (Mode=46, n=21). The distribution of baboon subgroup sizes had

two peaks. The large subgroups of baboons were observed only at the lakeshore, while smaller subgroups moved between the shore and the camp. Chimpanzees did not use the lakeshore during study period.

The range of baboons was 87.0ha and smaller than that of chimpanzees at 628.7 ha (Fig. 1).

II. Encounter

During one baboon follow, we heard chimpanzee vocalizations. The chimpanzees encountered baboons once on the southern bank of the Ntale River about 2km from the camp (Fig. 1). The encounter point was outside the focal baboon range.

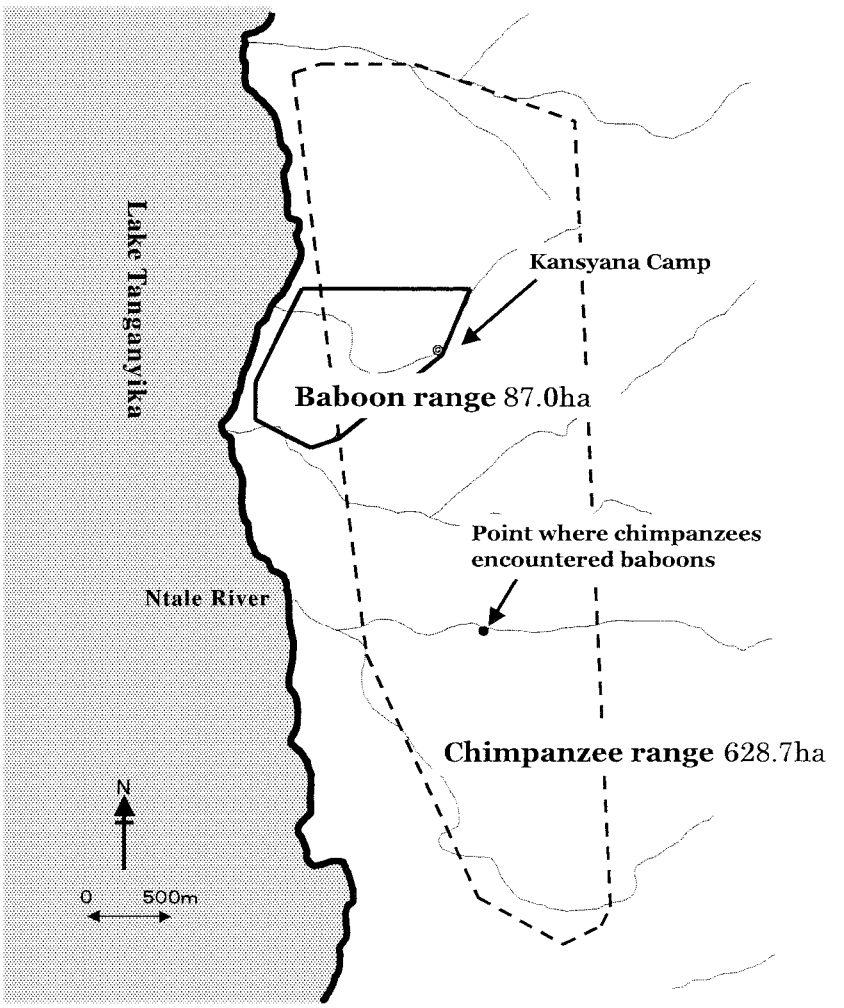

Fig. 1. Map of the Ranges used by Baboons and M Group Chimpanzees.

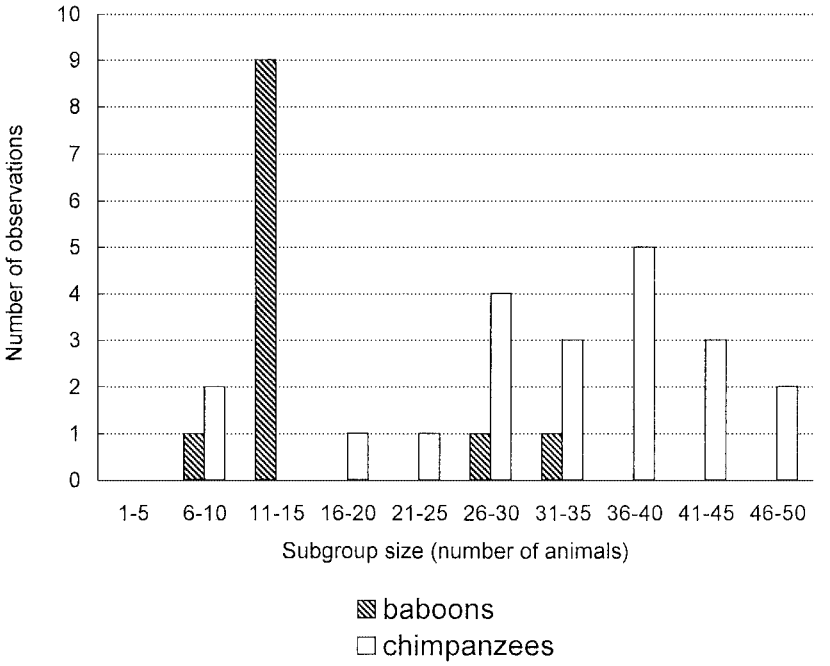

Fig. 2. Observed Baboon and Chimpanzee Subgroup Sizes.

III. Feeding and Diet

The actual observed feeding times of the baboons and chimpanzees were almost equal, 26.3 and 25.7hr, respectively, but baboons spent a greater proportion of their time feeding than chimpanzees. The proportion of time spent feeding, resting, and moving by baboons was 50.4, 22.4 and 27.2%, respectively, and those by chimpanzees were 24.2, 45.2 and 30.6%.

Both species spent their time mostly feeding on fruits (Table 1). Chimpanzees especially depended on a specific fruit (*Saba florida*) (Appendix). In the dietary repertoire of baboons, *Saba florida* also ranked first. The largest difference in feed-

Table 1. Overlap of Dietary Items between Baboons and Chimpanzees.

Dietary items	% Time spent feeding (/feeding time)		The number of species eaten		Percentage of dietary overlap		
	Baboons	Chimpanzees	Baboons	Chimpanzees	of chimpanzee diets with baboon diets	of baboon diets with chimpanzee diets	of baboon diets with chimpanzee dietary list*
Fruit	55.9	60.5	11	4	18 (%)	50 (%)	91 (%)
Leaf	13.3	11.6	11	7	36	57	73
Pith	12.9	14.5	9	4	22	50	56
Insect	11.5	12.5	3	2	33	50	33
Other	6.4	0.9	2	1	0	0	50
Total	100	100	36	18			

*Nishida & Uehara (1983)

ing on fruit was for oil palm nuts (*Elaeis guineensis*). Baboons spent 18% of their feeding time on the oil palm nuts, while chimpanzees have never been observed to eat them at Mahale during 35 years (Nishida *et al.*, 1983).

The number of baboon dietary items was twice as many as that of chimpanzees (Table 1). About half of the chimpanzee dietary items overlapped with those of the baboon. The percentage of dietary overlap in chimpanzees was larger than that in baboons. Moreover, all the dietary fruits of baboons, except palm nuts, were also eaten by the chimpanzees.

DISCUSSION

In general, species with similar life styles show subtle differences in their habitat, feeding, or activity. There have been reports of interspecies feeding competition from chimpanzee research sites. At Kibale, Uganda, anubis baboons live with chimpanzees. As the chimpanzees in Kanyawara, baboons concentrate heavily on non-fig fruit trees in approximate proportion to fruit availability (Wrangham *et al.*, 1991). Moreover, Wrangham *et al*. (1991) reported that the monthly variation in fibrous strands consumed by baboons and chimpanzees agreed in Ngogo. Such findings suggest feeding competition between baboons and chimpanzees. Wrangham *et al*. (1998) tested the dietary responses of chimpanzees and three other monkeys. The results showed that chimpanzees were ripe-fruit specialists, whereas cercopithecines had a lower-quality diet including a higher antifeedant intake. Cercopithecines might coexist with chimpanzees as a result of dietary segregation. Also at Gombe, Tanzania, where both baboons and chimpanzees live, the studies on interspecies interactions focused on predation-prey relationships (Goodall, 1986; Stanford, 1995). Chimpanzees occasionally preyed on baboons, but members of the two species usually ignored or avoided each other in the majority of 95 encounters (Ranson, 1981).

There has been a preliminary report compiled at Mahale for diet, ranging pattern, group size and interaction between baboons and other mammals in 1973-1979 (Hasegawa *et al.*, 1980). Leaves, fruits and roots ranked the highest in the baboon's dietary repertoire, their range was exclusively along the lakeshore, and their group size was about 40. Baboon-chimpanzee aggressive encounters were sometimes observed. Although baboons were detected more frequently in the woodland (Uehara & Ihobe, 1998), baboons have recently expanded their range inland (Nishida, 1997).

In summary, this study primarily found that:

1) chimpanzees had larger ranges than baboons,
2) small sized baboon subgroups, ranged inland,
3) direct baboon-chimpanzee encounter seldom occurred,
4) both baboons and chimpanzees spent most time feeding on fruits, but baboons had a broader diet than the chimpanzees,

and 5) all the fruits eaten by baboons were also among the chimpanzee diet.

The two species may avoid feeding competition by two ways: first, by avoiding direct encounter. Whether the two species avoid each other because of feeding com-

petition or due to a baboon strategy of predation avoidance is not known. As in Gombe, a Mahale chimpanzee was observed to eat a baboon (Nakamura, 1997). Second, competition may be avoided by different feeding behaviors. In the fruit-abundant season, the Mahale chimpanzees depended on few specific fruits and move a wider range. In contrast, the large subgroups of baboons used the lakeshore not used by chimpanzees during the same period. When baboons invade the forest, their subgroup size may become small. Baboons eat various fruits including non-chimpanzee dietary items.

We believe that feeding competition is against the chimpanzees by the following reason. The caloric content of fruits is the crucial factor determining the chimpanzee choice of dietary items (Matsumoto-Oda & Hayashi, 1999). In addition, chimpanzees depend on specific fruits, as they selectively eat the ripe fruit (Goodall, 1986; Nishida, 1990, 1997; Wrangham *et al.*, 1998; Newton-Fisher, 1999). All the fruits eaten by baboons during the study, except palm nuts, were among the chimpanzee dietary items listed by Nishida & Uehara (1983). This suggests that baboons may eat unripe fruits before the chimpanzees do. Damage from competition might be serious for the chimpanzees in the fruit scarce season. The critical issue in this interspecific relationship is the balance: is there only one dominant species, or is there a more complex and dynamic relation? To understand how baboons and chimpanzees reach a balance in their diet, feeding, or activity in the same habitat, more investigations in other seasons are needed.

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Appendix. Dietary Items of Baboons and Chimpanzees.

Parts	Family	Species	Local name	Baboons 1579 sample points	Chimpanzees 1539 sample points	List of chimpanzee diets (Nishida & Uehara, 1983)
Fruit				882 sample points	931 sample points	
	Annonaceae	*Annona senegalensis*	Lufila	14		*
	Apocynaceae	*Saba florida*[*1]	Ilombo	439	877	*
	Boraginaceae	*Cordia millenii*	Mkibu gwwsimbwa	2		*
	Euphorbiaceae	*Antidesma* sp.	Mtimpu	14		*
	Moraceae	*Ficus exasperata*	Lwago		48	*
		Ficus sur Forssk.	Ikubila	40	5	*
		Ficus urceolaris	Kankolonkombe	30	[*2]	*
		Ficus vallis-choudae	Ihambwa	44		*
		Ficus sp.	Ikuku		1	*
	Myrtaceae	*Psidium guajava*	Mpela	8		*
	Palmae	*Elaeis guineenis*	Migazi	284[*1]		
	Rutaceae	*Citrus limon*	Limau	4		*
	Zingiberaceae	*Aframomum alboviolaceum*	Itungulu	3		*
Leaf				210 sample points	179 sample points	
	Apocynaceae	*Saba florida*	Ilombo	40		*
	Asclepiadaceae	*Ceropegia* sp.	Lumpululu		25	*
		Pterocarpus tinctorius	Mwenje		1	*
	Marantaceae	*Marantochloa leucantha*	Kalubwabakulu	20	36	*
	Menispermaceae	*Tinospora caffra*	Mswamombo	5		*
	Mimosaceae	*Albizia glaberrima*	Kafunampasa	15		*
	Moraceae	*Ficus exasperata*	Lwago	5	67	*
		Ficus urceolaris	Kankolonkombe	3	43	*
	Papilionaceae	*Baphia capparidifolia*	Ijubila	65	4	*
		Vigna ambacensis	Kabwase	19		*
	Rubitaceae	*Psychotria* sp.	Lulyolwakape	17		
	Smilacaceae	*Smilax kraussiana*	Linselele		[*2]	*
	Sterculiaceae	*Sterculia tragacantha*	Kakubabolo		3	*
	Zingiberaceae	*Aframomum alboviolaceum*	Itungulu	10		
	Papilionaceae	*Mucuna gigantea* sp.	Upupu	11		

Pith				203 sample points	223 sample points	
	Apocynaceae	*Landolphia* sp.	Mpila		36	*
	Gramineae	*Beckeropsis uniseta*	Kantentwa	18		
		Pennisetum purpureum	Iswe	7	14	*
		Setaria sp.	Sibingabweha	60		
	Marantaceae	*Marantochloa leucantha*	Kalubwabakulu	5		*
	Menispermaceae	*Tinospora caffra*	Mswamombo	5		*
	Rubitaceae	*Psychotria* sp.	Lulyolwakape	42		
	Vitaceae	*Ampelocissus cavicaulis*	Lukosho		19	*
	Zingiberaceae	*Aframomum alboviolaceum*	Itungulu	50	154	*
		Costus afer	Omoji	2		*
	unknown		Lyan'gonbe	14		
Flower				2 sample points	0 sample points	
	Zingiberaceae	*Costus afer*	Omoji	2		*
Seed				20 sample points	0 sample points	
		unknown		20		
Insect				182 sample points	193 sample points	
		Camponotus spp.			131	*
		Crematogaster sp.	Sisimisi	163	62	*
		unknown	Panji (Mahaso)	14		
		unknown	Lifumbe	5		
Soil				0 sample points	13 sample points	
			Udongo wa kisuguu		13	
Unknown				80 sample points	0 sample points	
				80		

*[1]including seeds
*[2]not observed during time sampling but observed once