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Preliminary Observations on the Feeding Behavior of *Pan paniscus* in the Lomako Forest of Central Zaïre

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ABSTRACT. The feeding behavior and ecology of *Pan paniscus* was studied over a seven-month period in Equateur, Republic of Zaïre, during 1974–1975. Additional data were gathered during four weeks in 1979. *Pan paniscus* was found to be primarily frugivorous but bonobo foods also consist of leaves, flowers, pith, invertebrates and small mammals.

INTRODUCTION

Although the bonobo or "pygmy chimpanzee" was discovered in 1929 amid much speculation on its important role in deciphering the puzzle of human evolution (COOLIDGE, 1933), field studies were carried out only in the last decade (NISHIDA, 1972; KANO, 1974, 1979; HORN, 1976; KURODA, 1977, 1979; UEHARA, 1976). The present paper is based on two periods of fieldwork, one in 1974–1975 (BADRIAN & BARDIAN, 1977, 1978) and the second in 1979 (SUSMAN, BADRIAN & BADRIAN, 1980). Data were collected on diet, feeding behavior and other aspects of bonobo socioecology. Herein we report on the foods eaten by bonobos of the Lomako Region.

METHODS

Although existing distribution maps indicate that bonobos occur throughout the forested region of the Congo Basin, south of the Zaïre River (SCHWARZ, 1929; COOLIDGE, 1933; HILL, 1969), it took weeks of reconaissance to locate an isolated area of forest with an undisturbed population of free-ranging bonobos. It appears that the range of *Pan paniscus* today is much more restricted and discontinuous than originally indicated by SCHWARZ (1929, 1934) and later workers. The area for study selected in 1974 is an isolated tract of rainforest between the Lomako and Yekokora rivers. This area represents the center of the presumed distribution of bonobos (Fig. 1) and its remoteness probably accounts for its suitability for studying naturalistic behavior of bonobos. We spent seven months in the study area site between November 1974 and June 1975 and four weeks at the same site in February and March of 1979.

The study area of approximately 35 km^2 consists of primary rainforest with patches of secondary growth. Some swamp forest is also found in the area bordering the rivers and small streams. We conducted a survey to determine tree species composition and frequencies in these three types of forest, counting and recording all trees over 80 mm in diameter in four blocks (three measured 10 m $\times$ 120 m and one measured 10 m $\times$ 90 m). The primary forest where most of our observations of bonobos occurred was on firm sandy soil and had a continuous canopy layer at 30–40 m with emergent trees reaching 45–55 m. The middle story of the primary forest was quite open and did not form a continuous layer. The shrub and her-

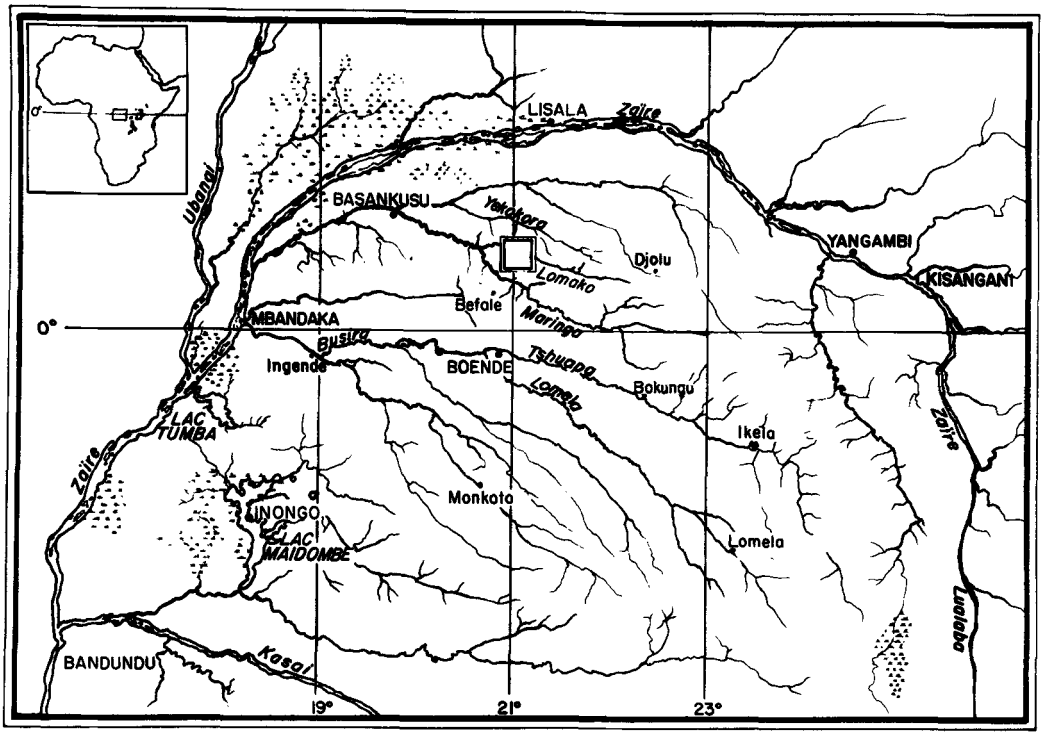

Fig. 1. Map showing location of Lomako Forest and study area.

baceous layers were usually poorly developed. In places where large trees had fallen and sunlight reached the ground there was prolific growth of herbaceous plants. The study area contained a rich diversity of fauna, including four species of monkey (black and white colobus, *Colobus angolensis*; black mangabeys, *Cercocebus atterrimus*; red-tailed monkeys, *Cercopithecus ascanius*; and the mona monkey, *Cercopithecus mona*).

The bonobos were difficult to locate and when found they proved to be very timid. Solitary animals and small groups (2–4 animals) were particularly wary. We usually attempted to remain hidden, but once detected we found that the bonobos calmed most quickly if we came out into the open and engaged in activities such as nest building, eating leaves or self-grooming. These methods of reassurance had been used by SCHALLER (1961, 1963), GOODALL (1965) and MACKINNON (1974) to habituate the other great apes. It was normally not possible to follow bonobos once they had descended to ground level. Thus the majority of our observations were made on animals in trees.

Daily searches were made along trails throughout the study area and the bonobos were located either by following the sound of their vocalizations or by visiting known fruit trees. Trees bearing ripe fruit were often located by the loud calls of hornbills or other fruit-eating birds. These trees were often visited by the bonobos as well. Upon locating bonobos we made detailed observations using standard 8×30 binoculars. Additional data on food items were gathered by analyzing food remains and fecal samples unequivocally attributable to the bonobos.

RESULTS

During 2,300 hr in the field we made visual contact with bonobos on 106 occasions and recorded a total of 98 hr of observations. The longest period of uninterrupted observation lasted for 5.75 hr. Feeding activity was observed in 56% of contacts. Although we were unable to follow the bonobos for an entire day, our combined observations sample all times of the day.

Bonobos seem to spend the greater part of their day feeding and traveling between food sources. They traveled mainly along the ground, but on a few occasions we were able to follow them as they traveled for some 2 km through the canopy from one food tree to another. There were two peak feeding periods, one between 06:00 and 09:00 hours and the other between 15:00 and 17:00 hours (daylight being approximately 05:30 to 17:00 hours). On very wet mornings, or on mornings after a night of heavy rain, however, the bonobos began their activities at a later time; on one occasion they did not leave their nests until 09:30 hours.

The number of members in each group of bonobos we observed varied throughout the course of both study periods. The largest group we encountered was estimated to number 20–25 adult individuals. This group was observed three times over a two-week period. On all three occasions there were three oestrous females in the group. The largest group other than the above contained 6–9 members. On approximately 83% of encounters with bonobos, the groups comprised 1–4 individuals (adult females with infants were counted as two individuals). In 21 sightings of single animals, 11 proved to be males, 1 was a female with infant and in 9 cases we could not determine the animal's gender. Many of the groups we observed consisted of two or three members with an adult female and her young. Most larger goups (4–9) contained at least one adult male.

Diet

The bonobos in our study area were omnivorous with the greater part of their diet consisting of fruit and other plant foods. Forty-seven plant foods from 39 species were recorded by direct observation and by fecal analysis during the course of both study periods (Table 1). Fruit accounts for 49% ($N = 23$) of the total number of these foods; leaves (both young and mature) for 21% ($N = 10$); stems and pith for 15% ($N = 7$); seeds for 9% ($N = 4$); and flowers for 6% ($N = 3$).

Food Gathering

When bonobos arrived at a fruit tree, they were often wasteful to begin with, picking a fruit, biting into it and discarding it if it was not ripe. After feeding for a while, however, they would test the fruit by smell and touch before picking it. As the bonobos became satiated and their feeding pace slackened, they often rested and chewed wadges made up of fruit skins, seeds and leaves. On occasions when bonobos nested in a food tree, they ate leaves and fruit and constructed nests from the same branches. Bonobos had various techniques for picking and eating different foods. Larger fruits were usually picked by hand and eaten in several bites or put into the mouth whole. Smaller fruits were picked by hand and transferred to the mouth singly, several at a time or plucked directly from the branch with the teeth or lips. Leaves and flowers were treated in much the same manner as the smaller fruits. The bonobos opened the large seed pods of *Anthonotha fragrens* and *A. macrophylla* with their anterior

Table 1. Plant foods.

Family	Species	Fruit	Leaves	Flowers	Seeds	Pith
Annonaceae	*Anonidium mannii*	+				
	Monodora angolense	+				
	Polyalthia suavolens	+				
Cesalpiniaceae	*Anthonotha fragrans*				+	
	A. macrophylla				+	
	Crudia harmsiana		+			
	Dialium pachyphyllum	+	+	+		
	D. zenkeri	+				
	Scorodophloeus zenkeri		+			
Commelinaceae	*Palisota ambigua*					+
Euphorbiaceae	*Uapaca guineensis*	+				
Flacourtiaceae	*Caloncoba welwitschii*	+				
	Scotellia conensis				+	
Guttiferaceae	*Garcinia punctata*	+				
Irvingiaceae	*Irvingia wombolu*	+				
Lauraceae	*Beilschmiedia corbisieri*	+				
Marantaceae	*Haumania librechstsiana*		+			+
	Megaphrynium macrostachum		+			+
	Sarcophrynium schweinfurthii		+			+
	?Trachyphrynium braunianum		+			+
Moraceae	*Antiaris toxicaria*	+	+	+		
	Ficus exasperata		+			
	Ficus sp.	+				
	Ficus sp.	+				
Myristicaceae	*Pycnanthus angolensis*	+				
Olacaceae	*Dioga zenkeri*				+	
Palmaceae	*Sclerospermum mannii*					+
Rosaceae	*Parinari excelsa*	+				
Sapindaceae	*Pancovia laurentii*	+				
Sapotaceae	*Gambeya lacourtiana*	+				
	Synsepalum dulcifecum	+				
Tiliaceae	*Grewia louisii*	+				
Ulmaceae	*Celtis brieyi*	+				
	C. soyauxii		+			
Verbenaceae	*Vitex* sp.	+				
	Afromomum sp.	+				

teeth and picked out the big soft seeds by hand or with their lips. The fruits of *Scotellia conensis* and *Dioga zenkeri* were bitten open and the soft seeds picked out with the lips or the whole fruit was put in the mouth and the pericarp subsequently ejected. The fruits of *Pycnanthus angolensis* were opened by hand and the stone picked clean of the thin covering of flesh by scraping at it with the incisors or finger nail. Observations of feces revealed that large quantities of these stones were swallowed whole. The very large fruits of *Anonidium manii* were eaten only after they had fallen to the ground; they were held in the hand and the succulent fruit was sucked and nibbled off the stone. Often the bonobos would pull a branch toward themselves by hand or foot, sometimes standing up or hanging by one arm in the process. Branches were often snapped off and carried to a more secure or comfortable site where the food was consumed. In the process of food gathering high in the trees, bonobos often performed extraordinary and dangerous acrobatic manoeuvers (SUSMAN, BADRIAN & BADRIAN, 1980).

Important staples in the bonobos' diet were found at ground level in the herbaceous layers of the forest. The majority of these foods were leaf shoots or pithy stems. The spear-like shoots of *Megaphrynium macrostachum* and *Sarcophyrynium schweinfurthii* were pulled up by

hand and torn open using the incisors and fingers. The soft pith and tender, rolled-up leaf shoots were then extracted with the fingers or lips and eaten. The spiky shoots of the cane-like *Haumania librechtsiana* do not contain rolled up leaf shoots but the bonobos frequently ate the growing tip of this plant (the outer sheath of the shoot is tough and fibrous and is used by the local people for basket work and rough tying jobs). Just above the nodes, however, the sheath encloses a soft juicy pith up to 200 mm in length that the bonobos eat. The rest of the stem up to the next node is very tough and is discarded. The method of opening this food plant varies. Some bonobos stripped the sheath off downwards with their teeth and/or hands, other bit or snapped the stem off just above a node and peeled the sheath back, i.e., pulled it upwards. Food remains from this plant were found almost daily along the animal paths which laced the study area. The thicker stems of *Palisota ambigua* also contain pith which was processed in much the same manner as *H. librechtsiana*. These herbaceous plants were widely dispersed in clumps in secondary growth thickets. Only small numbers of their remains were found at any one site, indicating that although they probably formed an important staple of the bonobo's diet they were not highly preferred foods.

Foraging Pattern

How the bonobos utilized their food resources was affected by the seasonal availability of plant foods and especially that of preferred fruits. Their foraging pattern changed throughout the initial study period. Between December and March we located groups of bonobos fairly frequently and they were observed to make repeated visits to large fruit trees. For example, one group of bonobos visited a very large *Parinari excelsa* tree on 15 occasions over a 17-day period, spending a total of nearly 28 daylight hr in the tree. They also constructed nests in this tree and slept there on two occasions. On the two occasions that they spent the night in the tree, they arrived in the afternoon and fed for a couple of hours building their nests shortly before and after darkness fell. On the following mornings they fed in the tree again for some time before moving off. On two other occasions the same group visited the tree to feed in the late afternoon. They constructed their nests about 500 m away, but returned to feed in the tree the following mornings.

From March to June this pattern of repeated and prolonged visits to individual food sources gradually changed. The bonobos traveled around the forest more and were consequently more difficult to locate than during the previous period. They spent less time in individual fruit trees even when the trees were in fruit.

Meat Eating

Fecal samples that we washed contained the remains of 12 species of invertebrates and 3 species of vertebrates. In March 1975 we observed a bonobo eating the larvae of the ant *Pachysemia aethiops* which are found in the hollow leaf stems of three tree *Barteria fistulosa*. The bonobo stripped the leaflets off the stem, dislodging the stinging adult ants that were swarming over it. He then bit open the stem using his incisors and picked out the larve with his lips. In May we observed a large male bonobo squatting on a path beside a broken termite mound, picking up termites between his thumb and index finger and placing them in his mouth. The termite mound (approximately 250 mm high and 100 mm in diameter) had been carried a short way by the bonobos and broken over a tree root in the path. The base of the

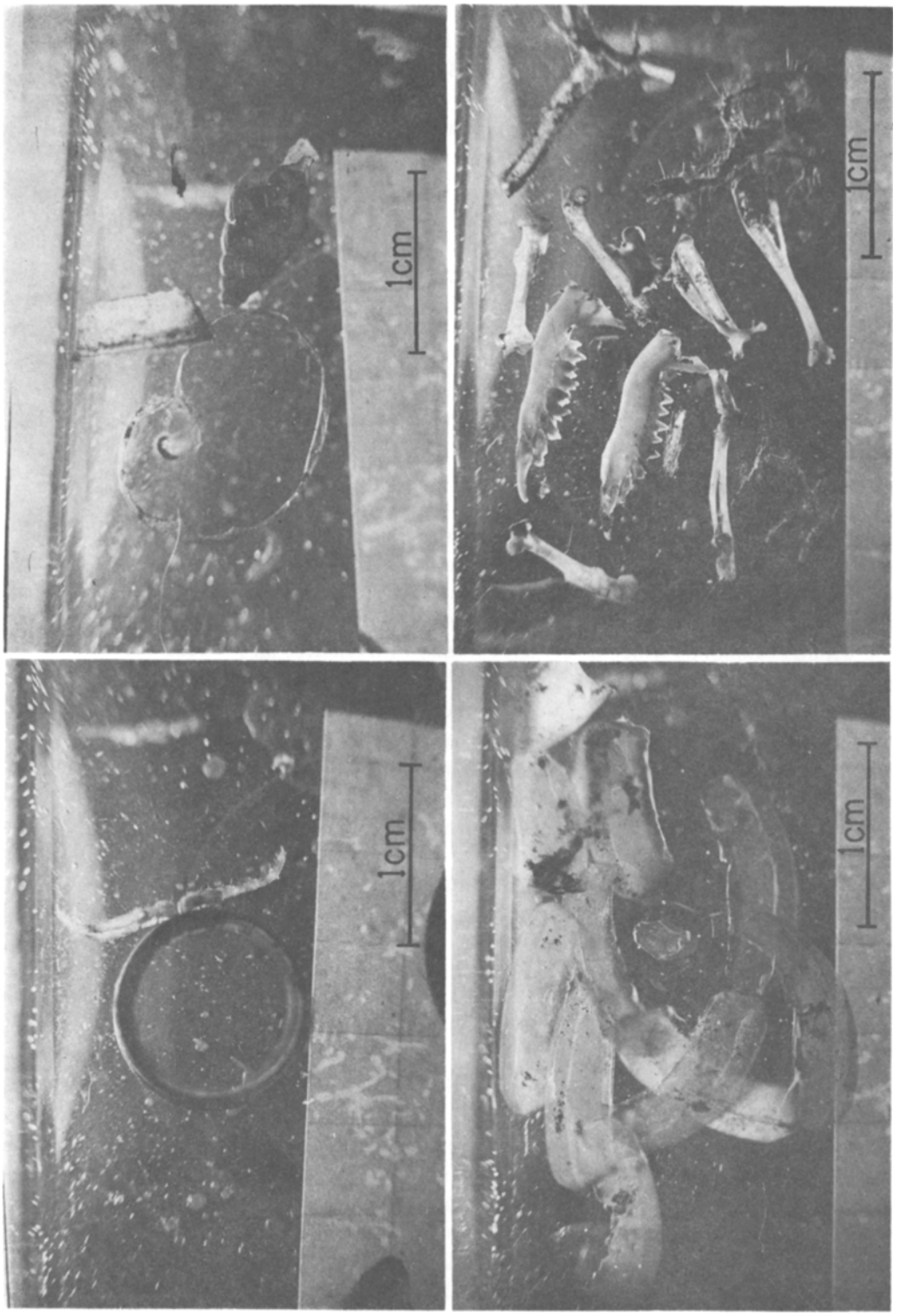
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Table 2. Animal foods.

Invertebrates	Vertebrates
Ants (*Pachysima aethiops*) + 2 spp.	Reptile: snake
Termites 2 spp.	Mammals: shrew
Coleoptera 1 sp.	rodent?
Cricket 1 sp.	
Hymenoptera (*Melliponid* sp.?)	
Mollusca 3 spp.	
Millipede	

mound was later discovered about 2 m away. We frequently came across other termite mounds that had been broken open and we sometimes found sticks and stems lying near the mounds which had termite mud adhering to them. These "ant harvesting tools" appeared to be similar to those described in studies on common chimpanzees by GOODALL (1968), JONES and SABATER PÍ (1969) and MCGREW, TUTIN and BALDWIN (1978).

Table 2 indicates the number of animal foods recorded by direct observations and by fecal analysis. The greatest mass of invertebrate remains found in bonobo feces were those of giant millipedes. These were especially common from March to May when preferred edible fruits appear to be relatively scarce. Other invertebrates found in fecal samples were beetles, crickets, bees and snails. Vertebrates were found in four of the approximately 50 fecal samples that we analyzed. Two of these samples contained unidentified small mammal bones and fur. One contained the bones, fur and complete lower jaw of a shrew and the remaining sample contained the dorsal and ventral scales of a small snake (Figs. 2, 3, 4 & 5).

DISCUSSION

Our present data on this population of wild, unhabituated bonobos indicates that they are mainly frugivorous, the bulk of their food consisting of plant foods with the addition of some animal protein. Foraging behavior appears to be influenced by the interaction of several factors including phenology of the main fruit trees and the abundance and distribution of herbaceous food plants (also see KURODA, 1979). Whether the vertebrate remains found in bonobo feces are the result of active hunting or opportunistic gathering we cannot, at this point, determine. The effect of food dispersal on bonobo ranging patterns, group size and social organization cannot be determined at this preliminary stage in our research. KURODA (1979) suggests that the availability of preferred fruits is the main determinant of group size with the largest groups (32.5 average animals, 54 maximum) being formed by smaller social units (6–15 animals), when fruit is abundant. It also seems quite certain that the availability of fruit has a profound effect on daily ranging patterns and foraging in the animals we observed.

Fig. 2. Segment of a millipede exoskeleton with paired legs. Remains were recovered from a fecal sample of *Pan paniscus*. Bar = 1 cm. (upper left)

Fig. 3. Two mollusc shells recovered from *Pan paniscus* feces. Bar = 1 cm. (upper right)

Fig. 4. Ventral and dorsal scales of a small snake recovered from feces of *Pan paniscus*. Bar = 1 cm. (lower left)

Fig. 5. Fur, jaw and limb bones of a small insectivore found in feces of *Pan paniscus*. Bar = 1 cm. (lower right)

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