COMPARATIVE DIETARY ECOLOGY OF A COMMUNITY OF FRUGIVOROUS FOREST UNGULATES IN ZAIRE

By

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ABSTRACT

COMPARATIVE DIETARY ECOLOGY OF A COMMUNITY OF FRUGIVOROUS FOREST UNGULATES IN ZAIRE

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Factors affecting diet and food choice in a guild of seven species of frugivorous ungulates (six duikers, genus *Cephalophus*, and the chevrotain, *Hyemoschus aquaticus*) were investigated in the Ituri Forest of Zaire. The methods used included radio-telemetry, feeding experiments with captive individuals, analyses of rumen contents of free-ranging animals in relationship to food availability and distributions of animals flushed on hunts.

Radio telemetry and feeding trials contrasted a large and a small duiker species. The larger species was more mobile and had a greater digestive capacity for low quality foods. The smaller species was more selective in its choice of food but also had relatively smaller total food needs.

Studies of mouth morphology, rumen contents, food availability and animal distributions involved all species in the guild. Fruits and seeds on the forest floor occurred in discrete patches. Relative to larger species, a small species of duiker selected foods of high nutritional quality but foraged on food patches of both small and large total food weight. The larger species selected foods of variable nutritional quality but preferred foods which occurred in patches of high total food biomass. Mouth size limited the size of food items

which could be ingested. Species with narrow mouths included smaller food items in their diets. Species with broad mouths avoided these. Diets of all species converged when high quality fruits and seeds were abundant in the upland forests. Diets diverged when high quality foods were scarce, but overall food diversity was high. During periods of food scarcity, two of the ungulate species foraged mainly in riverine habitats. Five species remained in upland habitats but specialized on fruits of varying nutritional and distributional characteristics. Abundances of two of these upland duikers of similar body size were negatively correlated indicating possible competition.

Ungulate abundance was contrasted in two forest types, a mixed forest and a forest dominated by the single species *Gilbertiodendron dewevrei*. Ungulate abundance was lower in the single-species dominant forest. Compared to mixed forest, food abundance in the single-species dominant forest fluctuated strongly, but food diversity was always low. Diet overlap occurred in the mixed forest when both food abundance and diversity were low, indicating possible competition.

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Terese B. Hart contributed in a major way to every phase of this study. Her botanical and ecological studies of the Ituri Forest served as the basis for the analysis of the food habits of the ungulate community reported here. Her field assistance proved indispensible. Her freely shared insights were a continuous source of inspiration and direction.

Dr. Peter G. Waterman of the University of Strathclyde generously analyzed the bulk of the food samples for this study and has been a source of objective criticsm and insight throughout the writing. Drs. George Petrides, Thomas Struhsaker and Richard Wrangham visited the project in Zaire. There observations helped focus my efforts on specific problems. Dr. Duane Ullrey suggested I attempt feeding trials with captive duiker and Dr. M. Demment generously shared insights and unpublished papers on relationships between ruminant nutrition and ecology and criticized earlier drafts of chapters of this dissertation. Drs. J. Haufler and N. Phu provided me with laboratory space and assisted in the chemical analysis of samples from the duiker digestion trials. Dr. Peter Murphy generously made his personal computer available to me to complete the typing of the manuscript. The criticisms of Dr George Petrides and Dr. Donald Hall added substatially

to the analysis and presentation of the results. This dissertaion has benefited from the comments and helpful criticisms of my doctoral committee consisting of Drs. George Petrides (chairperson), John King, Donald Hall and Jon Haufler.

Throughout the research period in Zaire and subsequent analysis and writing at Michigan State University I have had the support of my entire family. My parents, Joanne and Nathaniel Hart and my parents-in-law, Kathleen and Aruther Butler provided encouragement and finacial support. I am especially grateful to my wife Terese and our daughters, Sarah and Rebekah who made it possible for me to perservere with this project.

Finally, I owe my deepest gratitude and a special thanks to the Mbuti hunters of the Epulu area in the Ituri Forest. Without their enthusiastic co-operation, lively interest and continuous assistance, this project would not have been possible. This dissertation is dedicated to them in their forest home.

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CHAPTER ONE

Introduction

The Ituri Forest of Zaire (Figure 1-1) contains one of the richest assemblages of forest ungulates on earth. Prominent among these is a guild (sensu Root 1967) of six species of duikers (genus *Cephalophus*, Bovidae) and the chevrotain (*Hyemoschus aquaticus*, Tragulidae) (Table 1-1). These species span a size range from 5 to 70 kilograms but share a similar diet consisting of a wide array of fallen fruits, soft seeds and flowers (Dubost 1984).

Studies of this group of species in Gabon (Dubost 1979, 1984, Gautier-Hion et al. 1980, Emmons et al. 1983) have indicated that despite differences in fruit sizes eaten and in habitat and activity patterns, the duikers and chevrotain shared a number of food species. These observations indicated the possibility of competition between guild members. Mechanisms mediating coexistence, however, have been little investigated.

The purpose of this study was to investigate ecological relations within the frugiovrous ungulate community by a study of factors affecting food choice and diet. This research is reported as three separate papers.

In the first paper (Chapter 2), radio telemetry, morphological studies and feeding trials with captive animals were used to examine how differences in body size may be linked to physical and

Figure 1-1. The Ituri Forest of Zaire.

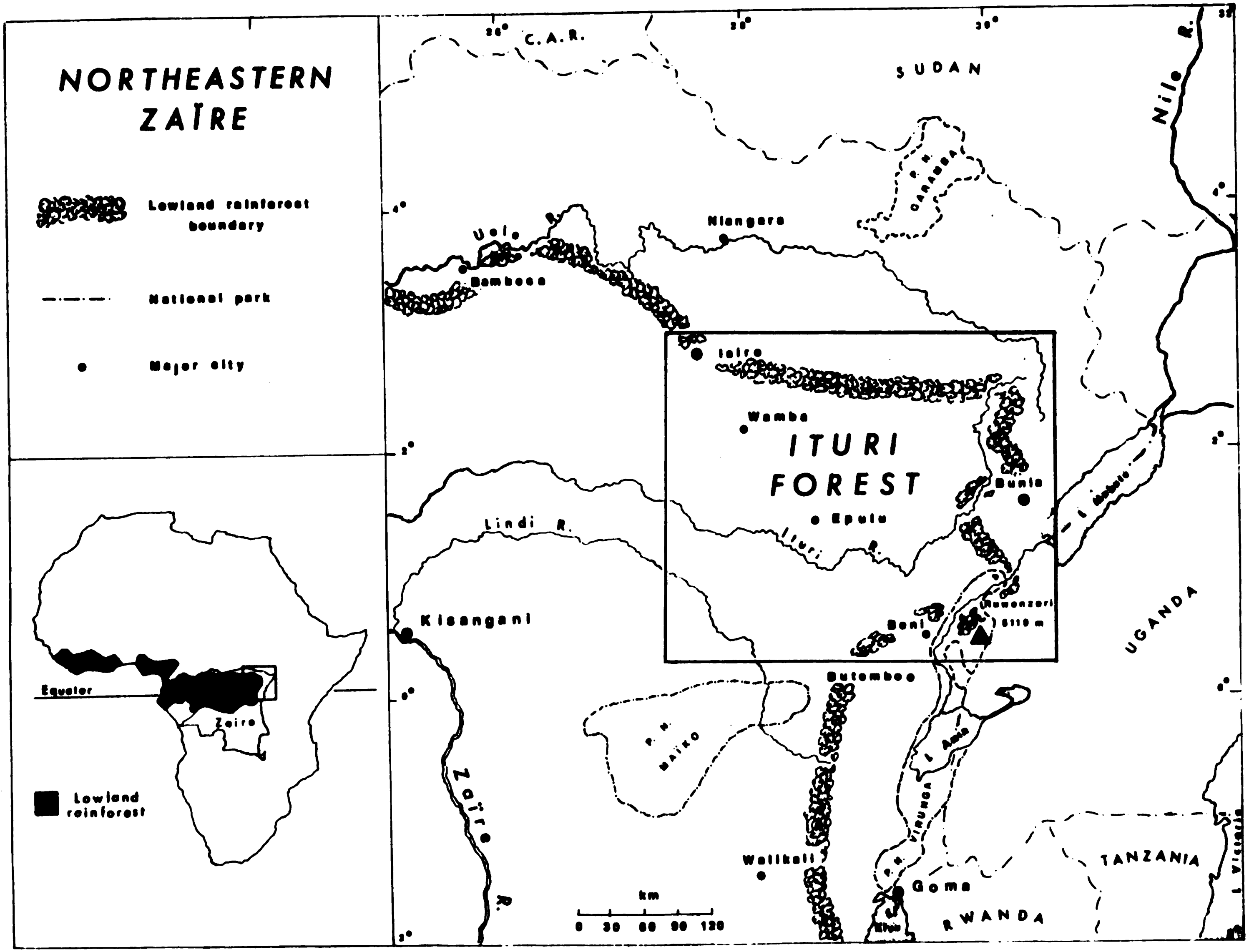
NORTHEASTERN ZAÏRE
Lowland rainforest boundary
National park
Major city
Lowland rainforest
Equator
Zaïre
C.A.R.
SUDAN
UGANDA
TANZANIA
RWANDA
26°
28°
30°
32°
4°
2°
0°
2°
Nile R.
Uele R.
Bambesa
Niangara
P. N. GARAMBA
Isiro
Wamba
ITURI FOREST
Epulu
Bunia
Ituri R.
Lindi R.
Kisangani
Zaïre R.
L. Mobutu
Ruwenzori
5119 m
Beni
Butembo
P. N. MAIKO
L. Amin
P. N. VIRUNGA
Walikali
Goma
L. Kivu
L. Victoria
km
0 30 60 90 120

Table 1-1. species of frugivorous ungulates studied in the Ituri Forest, Zaire, 1981 - 1983.

Species	Vernacular	Size (kg)[a]
Cephalophus monticola	blue duiker	4.7
Hyemoschus aquaticus	chevrotain	11.2
C. nigrifrons	black-fronted duiker	13.9
C. leucogaster	white-bellied duiker	16.7
C. callipygus	Peter's duiker	17.7
C. dorsalis	bay duiker	22.0
C. sylvicultor	yellow-back duiker	68.0

[a] Average adult body weight data from this study (Chapter 4), except for *C. sylvicultor* (Emmons et al. (1983).

physiological constraints affecting foraging. These studies were limited to two species, the blue duiker (*C. monticola*), the smallest member of the guild, and the bay duiker (*C. dorsalis*) one of the largest.

The second paper (Chapter 3), reports the results of food preference tests with these same two duiker species. The trials were designed to investigate the relation of food nutritional quality to diet choice and food intake.

The third paper (Chapter 4) expands the focus of study to the entire guild. The results of a study of the diets and distributions of free-ranging animals in relation to food availability are reported. The questions posed in this chapter include the following: What are the patterns of diet selection in free-ranging animals and how are these correlated with morphological and size differences in the animals? What are the patterns of dietary divergence and convergence within the guild and how are these related to the abundance and diversity of food reosurces. Finally, what are the patterns of ungulate distibution and how are they correlated with food abundance?

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LITERATURE CITED

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CHAPTER TWO

Mobility, Food Handling and Digestive Capacity in Two Species of Duikers of Differing Body Size

Differences in body size have been seen as important in the ecological segregation of animal species in a number of communities including ungulates (Bell 1970, Hoffmann 1973, Schoener 1974, Hanley 1980, Owen-Smith 1980, Foose 1982, Demment and Van Soest 1985, Bunnell and Gillingham in press). While differences in body size affect a number of ecologically significant parameters (Clutton-Brock and Harvey 1983), the relationship betweeen body size, foraging and diet have received special attention.

The frugivorous ungulates of African forests present a potentially interesting community to study from this perspective. Up to seven species, including six duikers (*Cephalophus*) and the chevrotain (*Hyemoschus aquaticus*), may co-occur in the same forest. These species, in particular the duikers, vary to some extent in habitat and activity patterns (Emmons et al. 1983) but overall are similar in general morphology (Kingdon 1982), rumen anatomy (Hoffmann 1973) and diet (Dubost 1984). Co-occurring species do vary in body size and in the richest communities may span a range from 5 to almost 70 kg (Dubost 1979). Factors determining diet across this size range, however, remain little known.

This paper presents the results of observations and experiments on two species of duikers, a small species, the blue duiker, *C. monticola* (5 kg adult weight) and a large species, *C. dorsalis* (22 kg adult weight). The purpose of these studies was to develop a basis for evaluating how differences in body size might be related to differing constraints on the use of the available food supply (Chapter 4).

Food availability for ungulates in tropical forests differs from that of many species in more open environments. Leafy browse in the shady forest understory may be scarce and unpalatable (Chapter 3). A high diversity of fallen fruits, seeds and flowers represent the bulk of available food but many species may be rare and dispersed. Fruits further vary in texture, shape and nutrient composition (Chapter 4). These conditions suggest that differences in the relative ability to find, swallow and digest foods of differing distribution, size and nutritional quality may be important in segregating diets of related species.

Reported here are observations on relative mobility, gut capacity, food handling and diet digestibility. Diet digestibility was investigated in relationship to plant cell wall (fiber) levels in fruits. Dietary fiber is only slowly and incompletely digested. Fiber thus has been identified as a determinant of ungulate diet quality. Differences in ability to digest fiber are correlated with ruminant body size (Short 1963, Short et al. 1974, Demment and Van Soest 1985).

The relationship of diet quality, digestibility and body size was examined according to three general hypotheses:

1. A large duiker species will digest a low quality diet more completely than a small species.

2. Both large and small species will digest a high quality diet more completely than they will a low quality diet.

3. The digestion of a high quality diet is equally complete in both species.

MATERIALS AND METHODS

All studies were conducted at Epulu in the Ituri Forest between 1982 and 1983.

Home Range and Mobility

Four free-ranging adult and sub adult blue duiker (2 males and 2 females) and a subadult female bay duiker were caught, equipped with radio collars and followed on the same 70 hectare study area between February 26 and April 30, 1983. The study area was divided into 100 ha grids by a path system. Animal locations were monitored once an hour during recording sessions lasting 4 to 5 hours each. A total of 92 hours of observation were made at all hours of day and night. The total area area utilized by an animal during the study period was estimated by the area of a polygon connecting outermost location points on a map. Two indices of relative mobility were calculated as meters/hour (the average distance the animal moved between hourly locations) and meters/move (the average distance the animal moved when it relocated between grids).

Ruminoreticular Capacity

Ruminoreticular capacity was measured as weight of contents and by liquid volume fill. Adult blue and bay duiker killed by local hunters were weighed at the site of capture. The rumen and reticulum were weighed full and empty. The rumen was then filled with water to the ruminoreticular junction through an opening in the reticulum. Rumen volume (without reticulum) was determined by filling the rumen with water (to nearest 0.1 liter) while holding it submerged to avoid distention and overestimation of capacity (Demment 1982).

Food Handling

Food handling was tested using a captive adult female blue duiker and a nearly full-sized subadult female bay duiker. Handling time was defined as the number of seconds elapsing between the time an item was picked up until it was swallowed. During trials surplus quantities of fruits were offered in piles on the ground. Handling times were recorded for each item until the animal stopped and moved away (1 to 10 items). Six species of fruit, varying in size, shape and texture, depending on the species, were tested. Fruit size was measured by its total length. Five size classes were distinguished: I (< 0.5 cm), II (0.5-1.0 cm), III (1.1-2.5 cm), IV (2.6-5.0 cm), V (5.1-10.0 cm) and VI (> 10.0 cm).

Digestion Trials

General procedures for digestion trials followed those outlined for domestic species on cultivated forages by Schneider and Flatt (1975) and extended to wild species on natural diets by Ullrey et al. (1969), Robbins et al. (1975) and Milton et al. (1980).

Prolonged trials using only fruit originally were attempted. These were abandoned, however, after blue duikers lost weight and sickened when fed a pure *Klainedoxa gabonensis* fruit diet. Diets containing a single fruit species offered with the readily available and palatable foliage of the sweet potato vine *Ipomea batata* Two diets were tested, a low quality diet, consisting of ripe *K. gabonensis* (Trial I) and a high quality diet (Trial II) consisting of ripe *Ricinodendron heudelotii* Both fruits were eaten by bay duiker and to a lesser extent by blue duiker in the wild (Chapter 4).

Fruits used in the trials were all gathered from the same trees and at the same stage of ripeness. Fruits were cut into uniform pieces (3 cm) and the seeds removed. Fresh, young, fully expanded leaves of *Ipomea* foliage were cut from the vines and used in all trials. Every attempt was made to make food offerings as uniform as possible.

Experimental animals were caught with nets in the forest near Epulu and kept in adjacent 10 m by 10 m enclosures constructed in the forest. The pens were cleared of small saplings and herbaceous growth, but all trees and larger saplings (> 2.5 cm dbh) were left. Each pen was provided with a lean-to shelter, salt block and water pan. These additions did not appear to alter feeding behavior or food choices. The pens were swept daily during the trials to remove extraneous food (foliage, flowers, fruit) falling from the canopy in order to assure that the experimental diets being tested were the only source of food.

Two pairs (male and female) of adult blue duiker, E/K and R/D and two individual bay duiker, M (subadult female) and P (adult female) were used for each trial, except for Trial II when only one bay duiker, M, was available.

Experimental animals were acclimated to a given test diet for 2-3 weeks before the 7-8 day total collection period. During the trials, ad libitum quantities of each food were presented twice a day, and the amount consumed calculated by subtraction, taking into account changes due to drying as determined by controls. Fecal collections were made every half day on a precise schedule. Urine was not collected but did not appear to contaminate the droppings.

Samples of foods fed during each trial and all feces were collected and dried under low heat to a constant weight. Three to seven daily samples of feces and samples of all foods were randomly selected from each experimental unit for chemical analyses.

Field dried samples were prepared for analyses by grinding in a Wiley Mill to pass a 1 mm mesh. Total dry matter (DM) was determined by dehydration at 100° C for 24 hours. Total ash was determined by combustion of sample organic matter at 600° C. The plant cell wall fractions extracted included neutral detergent fiber (NDF), acid detergent fiber (ADF) and sulphuric acid digested acid detergent lignin (ADL). Extractions for these components followed standard procedures of Goering and Van Soest (1970), with the modification that sodium sulfite was not included in the extracting solution. The difference between NDF and ADF extractions defined the cellulose component of the sample. Total Kjeldahl nitrogen (N) was determined following methods in Horowitz (1970). Levels of condensed tannins (CT) were measured from a methanol extract using the acid hydrolosis method of Bate Smith (1973). Total phenolics (TP) were determined by the Folin-Denis method (Horowitz 1970). Further details on these methods as applied to samples in this study are contained in Oates et al. 1977. All calculations of composition were done on an ash-free dry matter basis to accommodate soil contamination in the food and fecal samples (Mould and Robbins 1982).

The proportion of the diet, or of a given nutrient, which disappears during passage through the gut is a measure of apparent digestibility and can be defined by the digestion coefficient (DC) (Schneider and Flatt 1975), where

$$DC = 1 - (DM\ excreted\ /\ DM\ ingested).$$

Digestion coefficients for nitrogen must accommodate the presence of fecal nitrogen of metabolic origin. The proportion of fecal metabolic nitrogen can be estimated by extracting fecal NDF and determining its nitrogen content. The undigested portion of the nitrogen consumed was assumed to be contained in the NDF residue (Goering and Van Soest 1970). Fecal NDF content was used in calculating nitrogen digestion coefficients.

Differences in digestibility between species and between diets were tested by analysis of variance for unequal sample sizes using a pooled error variance to which the unreplicated trial did not contribute (Steel and Torrie 1980: 146). In the tests reported here, probabilities of $p < .05$ were considered significant.

RESULTS

Home Range and Mobility

The total area utilized by the radio-collared blue duikers over the 2 month study period ranged from 3.7 to 6.4 ha and averaged 5.0 ha. There was no significant difference in the areas covered by males (average 5.2 ha) and females (average 4.8 ha). Over the same period, the collared bay duiker ranged over an area over 3 times larger than the blue duikers (15.2 ha). The blue duikers were primarily diurnal whereas the bay duiker was nocturnal. The average distance between hourly locations for the blue duikers (during daylight recording sessions) averaged 41.3 m/hr (range 25 m - 56 m). The average distance recorded for the bay duiker during night recording sessions was 82 m (range 38 m - 138 m). When the bay duiker moved between grids it moved further than the blue duiker averaging 179 m/move, (range 75 m/move - 223 m/move). The smaller blue duikers' average movement distance was 82 m/move (range 66 m/move - 94 m /move).

Gut Capacity

Both the total rumen volume and the weight of ruminoreticular contents were significantly greater in the larger bay duiker than in the blue duiker (Table 2-1). On a per body weight basis, bay

Table 2-1. Measures of rumen capacity and ratios to body weight in adult blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*).

		Rumen Capacity		Rumen capacity/Body weight	
		Volume (l)	Contents (kg)	Volume (l)	Contents (kg)
Blue duiker 4.7 kg	mean	1.51	0.41	0.41	0.089
	SE	0.36	0.02	0.01	0.004
	n	19	57	21	33
Bay duiker 21.8 kg	mean	7.29	1.87	0.48	0.098
	SE	1.10	0.12	0.01	0.010
	n	5	12	6	11
Difference (t-test)		p<.001	p<.001	p<.01	N.S.

duiker had significantly greater rumen volume than the blue duiker ($p < 0.01$). The relative weights of the ruminoreticular contents were not statistically different. Wet weight contents averaged 0.89 kg/kg body weight and 0.98 kg/kg body weight (8.9 % and 9.8% body weight) for blue and bay duiker respectively.

Food Handling

Handling times for bay and blue duiker varied between food size classes, as well as within food size class between species of fruit (Table 2-2). Both blue and bay duikers handled small items with comparable efficiency. The bay duiker had shorter handling times for many of the larger items (Class IV and Class V) than did the blue duiker, especially for fruits which were tough and fibrous such as *K. gabonensis*. Indeed, many large *K. gabonensis* fruits (size class V) could not be handled by blue duiker. The largest fruits (Class VI), with the possible exception of unripe pods of some legumes, not included in the experiments, could not be handled by either species.

The time needed for an animal to fill its rumen with items of a specific size class (rumen-fill time) was calculated from estimates of rumen capacity (above) and data on numbers of differently sized itmes in rumens of wild caught animals (Hart, unpublished data). Although these estimates would be expected to vary, depending on fruit species, they nevertheless provided a measure of major differences in relative time costs for large and small duikers to specialize on feeding on differently-sized items (Table 2-3).

In both species rumen-fill time decreased with increasing

Table 2-2. Handling times for fruits by an adult female blue duiker (*C. monticola*) and a subadult female bay duiker (*C. dorsalis*).

Item size class	Fruit Species	Blue duiker n	Blue duiker mean	Blue duiker SD	Bay duiker n	Bay duiker mean	Bay duiker SD
II	*Ficus capensis*	4	10.0	5.0	5	8.9	4.1
III	*Celtis adolfi-fridericii*	1	14.0	--	14	6.2	1.2
	Klainedoxa gabonensis	7	13.9	2.4	5	7.5	1.0
IV	*Donella pruniformis*	21	16.6	2.3	18	17.3	2.4
	Klainedoxa gabonensis	3	49.3	11.7	5	7.8	1.0
	Ricinodendron heudelotii	3	44.0	12.7	7	23.3	6.5
	Ficus mocuso	7	49.6	12.5	not tested		
V	*Klainedoxa gabonensis* [a]	2	51.5	24.4	5	21.7	3.0

Handling Time (sec)

[a] Most size size V *K. gabonensis* fruits were too large for blue duiker to handle. Handling times reported do not include these fruits.

Table 2-3. Estimated number of fruits to fill rumen, fruit handling times and time to rumen-fill for fruits of different sizes for blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*). [a]

Item Size	Number to Fill	Unit Handling Time (seconds)	Time to Rumen Fill (minutes)
		Blue Duiker	
I	500	10	83.3
II	250	10	41.7
III	70	14	16.3
IV	40	40	26.7
V	10	49 +	8 +
		(many too large too handle)	
VI	7	too large to handle	
		Bay Duiker	
I	4,000	10	666.7
II	1,350	9	202.5
III	200	7	23.3
IV	50	16	13.3
V	20	22	7.3
VI	10	too large to handle	

[a] Time to rumen-fill (minutes) estimated for each food size as Number to Fill x Unit Handling Time.

fruit size up to a point where items were too large to handle. There was a marked difference, however, between the two duikers in the relative time reduction in feeding on the smallest and largest food species. In blue duikers, estimated rumen-fill times increased 10.4 times from 8 minutes (for size class V fruits which could be swallowed) to 83 minutes for foods of the smallest size class. In the bay duiker, rumen-fill time increased 91.4 times over the same range of food sizes. It seems even from these limited data that the bay duiker would have to spend considerably more time to fill its rumen than the blue duiker when feeding on small-sized items.

Digestion Trials

The nutritional composition of the fruits and foliage utilized in the feeding trials is shown in Table 2-4. Total dry matter, fiber and lignin levels were higher in *K. gabonensis* fruits than in *R. heudelotii* fruits, while percentage nitrogen was lower ($p < 0.05$). *Ipomea* foliage, in contrast to the fruits, had lower dry weight content, but higher percent dry weight nitrogen. Fiber levels in *Ipomea* foliage were intermediate between the two fruit species and lignin content was relatively high. Condensed tannin levels in all foods were relatively low. Total phenolic content of the fruits, on the other hand, was quite high, averaging almost one sixth dry weight content in *K.gabonensis* and nearly one third dry weight content of *R. heudelotii*. The identity of the phenolic compounds has not been determined, although samples of *R. heudelotii* were particularly rich in hydrolysable tannins (P.G. Waterman pers comm).

Table 2-4. Nutritional composition of foods utilized in feeding trials with blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*).

		Percentage Composition [a]							
		Dry matter	Lignin ash	Neutral detergent fiber	Acid detergent fiber	Acid detergent lignin	Nitrogen	Condensed Tannins	Total Phenolics
Food species	Material	DM	ADL ash	NDF	ADF	ADL	N	CT	TP
Klainedoxa	ripe fruit	27.6	1.13	42.8	26.4	6.8	0.60	1.88	15.51
gabonensis	n = 4	(1.1)	(1.32)	(3.3)	(1.7)	(1.0)	(0.10)	(0.73)	(4.49)
Ricinodendron	ripe fruit	24.2	0.01	13.5	10.9	1.5	1.03	1.38	31.12
heudelotii	n = 3	(0.4)	(0.00)	(2.3)	(1.1)	(0.6)	(0.60)	(0.62)	(5.09)
Ipomea	mature leaf	17.0	2.3	26.7	17.7	6.2	4.84	0.80	2.03
batata	n = 7	(0.6)	(2.04)	(5.0)	(4.7)	(3.0)	(0.34)	(0.18)	(0.25)

[a] Values are means (and standard deviations) for sample sizes shown (n).
Values for ADL Ash, Condensed Tannins and Total Phenolics are based on total dry matter. all other values are based on ADL Ash-free dry matter.

The purpose of the trials was to test digestibility of a given diet by both duiker species. This was not possible on the low quality fruit diet (Trial I) because the two species selected significantly different portions of fruit and leaf (Table 2-5). The bay duiker averaged 72% *K. gabonensis* fruits, whereas blue duikers averaged 58% fruit. The bay duiker's consumption of *K. gabonensis* fruit resulted in a diet higher in NDF and cellulose ($p < .05$) and lower in nitrogen ($p < .01$). Only ADL densities (6.7%) were the same for both species on this diet.

On the high quality fruit trial (Trial II) the composition of the diets of both duiker species was the same (Table 2-5). Both species averaged over 80% fruit on a dry weight basis. Fiber composition (16% NDF, 10% cellulose, 2% ADL) and nitrogen levels (1.6% - 1.7%) were also equivalent in both species diets and lower than on the *K. gabonensis* diet.

There was no difference in dry matter digestion between the two duiker species in Trial I despite differences in the relative composition of the diets (Table 2-6). Both species digested comparable percentages of dietary NDF even though the bay duikers' diets averaged twice the levels of those in the blue duikers' diets. Cellulose digestion by the bay duikers averaged even higher than the blue duikers (67.6% versus 60.4%, $p < .05$, $n = 2$), though here again levels in the bay duikers's diets were almost three times those of the blue duikers (Table 2-5).

Dry matter digestion in both species' diets did not differ in Trial II (Table 2-6). Both dry matter and cellulose digestion were

Table 2-5. Percentage dry weight composition of diets of blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*) on feeding trials containing *K. gabonensis* fruit and *I. batata* foliage (Trial I) and *R. heudelotii* fruit and *I. batata* floiage (Trial II).

A) Percent Composition of Diets

	blue duiker					bay duiker					
Replicate	Fruit	NDF	Cellulose	ADL	N	Replicate	Fruit	NDF	Cellulose	ADL	N
I E/K	59.1	37.1	16.5	6.6	2.34	M	73.5	39.4	17.7	6.7	1.73
R/D	56.2	36.6	16.3	6.7	2.46	P	70.8	38.8	17.5	6.7	1.84
Trial I Average	57.7	36.9	16.4	6.6	2.40		72.2	39.1	17.6	6.7	1.79
II E/K	90.6	14.7	9.6	2.0	1.39	M	81.7	16.0	9.8	2.4	1.74
R/D	80.7	16.1	9.9	2.4	1.78						
Trial II Average	85.6	15.4	9.8	2.2	1.59						

B) Tests of hypotheses: Percentage composition of diets[a]

	Fruit	NDF	Cellulose	ADL	N
1) blue vs bay, low quality diet (Trial I)	*	*	*	N.S.	*
2) blue vs bay, high quality diet (Trial II)	N.S.	N.S.	N.S.	N.S.	N.S.
3) high quality diet vs low quality diet, blue	*	**	**	**	*
4) high quality diet vs low quality diet, bay	N.S.	**	**	**	N.S.

---

[a] N.S., difference not significant; difference siginficant, $p < 0.05$ (*); $p < 0.01$ (**).

Table 2-6. Digestion coefficients for blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*) on diets of *K. gabonensis* fruit and *I. batata* foliage (Trial I) and *R. heudelotii* fruit and *I. batata* foliage (Trial II.

A) Digestion Coefficients [a]

	blue duiker					bay duiker				
Trial	Replicate	Dry Matter	NDF	Cellulose	N	Replicate	Dry Matter	NDF	Cellulose	N
I	E/K	76.7	59.1	61.8	77.1	M	76.8	61.6	64.4	73.8
	R/D	74.9	57.2	58.9	75.2	P	80.0	65.5	69.6	77.4
Average		76.3	58.2	60.4	76.2	Average	78.4	63.3	67.0	75.9
II	E/K	81.0	57.2	72.2	58.3	M	83.4	62.1	86.0	66.7
	R/D	83.5	55.5	76.1	63.7					
Average		82.3	56.4	74.2	61.0					

B) Tests of Hypotheses: Digestion Coefficients.[b]

	Dry Matter	NDF	Cellu lose	N
1) blue vs bay, low quality diet (Trial A)	N.S.	N.S.	*	N.S.
2) blue vs bay, high quality diet (Trial B)	N.S.	*	*	N.S.
3) high quality diet vs low quality diet, blue	*	N.S.	**	*
4) high quality diet vs low quality diet, bay	N.S.	N.S.	*	*

[a] Digestion Coefficients (DC) = 1-(Dry Wt Excrete/Dry Wt Ingest) times 100%.

[b] N.S., difference not significant; *, difference significant, $p < .05$; **, $p < .01$.

higher in the blue duiker in Trial II than in Trial I, and cellulose digestion was higher for the bay duiker . The bay duiker also digested cellulose more completely than the blue duiker on this trial.

Patterns of nitrogen digestion were at variance with those of plant cell wall constituents. Both duikers exhibited comparable nitrogen digestibilities on the *K. gabonensis* diet (76%). On the *R. heudelotii* diet, however, the bay duiker's digestion coefficient fell to 67% whereas bay duikers' dropped to 61%.

Lignin, a complex plant cell wall constituent is theoretically indigestible (Van Soest 1982), and ADL digestion coefficients were expected to be zero. Values close to the expected were obtained on the *K. gabonensis* diet (Table 2-8). In contrast to these results, there was an accumulation of an apparent lignin-like artifact in the feces of both duiker species on the *R. heudelotii* diet. Apparent fecal ADL increased 89% in the bay duiker trial and an average 126% in the blue duiker trial.

DISCUSSION

Though limited by small sample sizes, especially for the bay duiker, the results of the mobility and food handling studies indicated that size and spatial distribution of food is likely to have an impact on foraging and food choice in duikers of differing body size.

It was not possible to relate the movements and home range use of collared duikers to specific food distributions. It is unlikely too that all animal movements entailed food searching. Nevertheless, the

Table 2-7. Apparent lignin digestion coefficients for blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*) on diets of *K. gabonensis* fruit and *I. batata* foliage (Trial I) and *R. heudelotii* fruit and *I. batata* foliage (Trial II)[a]

	Blue duiker		Bay duiker	
Trial	E/K	R/D	M	P
I	-15.0	-9.0	6.0	14.0
Average	-12.0		10.0	
II	-160.0	-91.0	-89.0	
Average	-126.0			

[a] Digestion Coefficients DC = 1-(Dry Wt Excrete/Dry Wt Ingest) times 100%. Negative values indicate accumulation of lignin artefact in the feces.

larger home range and apparently greater mobility of the bay duiker indicated a greater potential for the larger animal to find and exploit widely-dispersed food resources. The fact that the collared bay duiker tended to make direct, relativlely long-distance moves during its activity periods suggested that the animal visited specific, known food sources, and tended to avoid patches in between.

Based on the amount of time needed to manipulate and swallow a food item, both the bay and blue duikers were equally adept at handling small-sized foods. The large species required less time to handle large foods. In both species, however, rumen-fill times were minimized by feeding on the larger items up to the apparent limits of mouth size. The major difference between the two species became apparent in the relative time costs in filling the rumen with small-sized items. Based on calculations, it was estimated that it would take the larger bay duiker eight times longer than the blue duiker to fill its rumen with foods of the smallest size class (< 0.5 cm), and 4.5 times longer to fill its rumen with items of the next size class (0.5 - 1 cm). Thus while both species incurred time costs in feeding on small items, these are relativley greater for the bay duiker than for the blue duiker. These estimates assume no search time between items. The addition of search time would clearly reduce the potential utility of small items to the bay duiker even more.

Diets of free-ranging animals were diverse (Chapter 4). Test diets were simplified to examine the relative importance of the fiber content of the diet in affecting preference and digestibility. An evaluation of the feeding trial results in the light of the initial hypotheses, nevertheless pointed to a role for multiple factors in determining dietary quality.

Hypothesis 1. The large-bodied bay duiker was hypothesized to have higher digestion coefficients than small-bodied blue duiker on the low-quality *K. gabonensis* diet. This hypothesis could not be evaluated on diets of equal quality because the two duiker species selected foliage and fruit in different proportions. The fact that bay duiker replicates had equal or higher digestion coefficients for cell wall components on diets with twice the plant cell wall levels provides, nevertheless, supported for the hypothesis that larger-bodied ruminants were better able than small-bodied species to utilize foods over a range of dietary quality. (see reviews in Owen-Smith 1980 and Demment and Van Soest 1985). The results of Trial I were somewhat confounding, however, in that despite its higher fiber content, *K. gabonensis* fruit was favored to foliage, at least by the bay duiker. Fiber alone is thus not the only dietary component affecting food preference and quality.

Hypothesis 2. Digestion coefficients for both species were predicted to converge on the high quality diet. Dry matter digestion coefficients were equivalent for both species but fiber fractions were digested more efficiently by the bay duiker. The results of this trial were not confounded by differences in diet composition, as both species ate equivalent proportions of leaf and fruit.

Hypothesis 3. High quality (low fiber) diets were predicted to be more digestible than low quality (high fiber) diets. This generally proved to be the case for dry matter and at least some plant cell wall components of the diet. The lower apparent nitrogen digestion on the *R. heudelotii* diet, however, was unexpected. This might have been due due to high levels of phenolics in this fruit. Recent studies have ascribed a digestion inhibitory role to plant phenolics (Mould and Robbins 1982), but results are not entirely unequivocal (Horvath 1981).

The accumulation of indigestible lignin-like compounds in the feces of animals on *Ricinodendron* diets was similar to those reported for other species fed diets high in tannins (McLeod 1974). The urine of duikers on the *Ricinodendron* diet was dark reddish brown. This has also been reported in elk on diets high in total phenolics (Mould and Robbins 1982), and is similar to the hematuria reported in tannin-dosed sheep (McLeod 1974). *R. heudelotii* fruits may well be somewhat toxic. The fact that they were also highly digestible and eaten freely is an indication that phenolic compounds will not deter feeding, though they may limit the amount of a food which may be ingested (Freeland and Janzen 1974).

CONCLUSIONS

Comparisons of mobility, food handling and diet digestion in two species of duikers, a large species, the bay duiker and a small species the blue duiker, demonstrated the potential for size-related differences in foraging behavior in the forest ungulate community.

The bay duiker was more mobile and could better digest foods over an apparent range of quality. Relative to the blue duiker, however, it was more constrained by its larger total needs from effectively utilizing small food items, especially if foraging on these involved extensive searching.

The digestion trials revealed that plant cell wall content was one element of fruit quality, however, digestibility appeared to be affected by phenolic compounds in fruits as well.

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LITERATURE CITED

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CHAPTER THREE

A Study of Factors Affecting Food Preference and Intake in Two Species of Duikers

Six species of duikers (genus *Cephalophus*) and the chevrotain (*Hyemoschus aquaticus*) spanning a size range from 5 to 70 kg co-occur in the humid evergreen forests of central Africa (Emmons et al. 1983; see also Chapter 4). The diets of all species are dominated by fruits and seeds (Dubost 1984). Gautier-Hion et al. (1980), in a comparative study of primary consumers, including the duikers and chevrotain, of the forests of Gabon, suggested the hypothesis that complimentarity in diets of different frugivores may reflect differences in their physical and physiological capacities in response to a range of nutritional and physical properties of the fruits. While this hypothesis suggests possible mechanisms for coexistence in related species of frugivores, it has been difficult in the field to determine how different species respond to variations in speciifc dimensions of the fruit resources.

This paper reports the results of palatability trials conducted with two species of captive duiker. These trials were designed to ascertain the importance of food nutritional quality, independent of food distribution, as a factor affecting diet choice. The duikers chosen, the blue duiker *Cephalophus monticola* (4.7 kg adult weight) and the bay duiker, *C. dorsalis* (22.0 kg adult weight) were at opposite ends of the local body-size spectrum within the guild of frugivorous ungulates. Thus the relationship of body size and food preference will also be considered. The foods tested in the trials included fruit and foliage species available to duikers in their natural environment. The questions addressed by these experiments were:

1) What are the duikers' food preferences and are they consistent from test to test?
2) What are the nutritional and chemical correlates of food preference?
3) What is the relationship between the preference for a diet and its intake?

These specific questions are posed in a broader ecological framework that will also be addressed by a consideration of the following problems:

How do preferences for fruits compare with those of foliage and why is foliage uncommon in the diet?

How are food preference and intake related to body size in duikers?

Plants contain a wide array of compounds which affect their quality as food for primary consumers (Freeland and Janzen 1974, Crawley 1983). One way to relate these to food preference and diet is to consider these compounds in terms of the costs and benefits of ingesting a given food. The major nutritional benefits of a food are contained in the ready sources of protein and energy which can be contributed to the diet (Barnes and Marten 1979, Van Soest 1982, Waterman 1984). Other groups of compounds including plant cell wall components and certain defensive compounds are difficult to digest, reduce palatability, inhibit digestion or are even toxic (Rosenthal and Janzen 1979 and references therein, Waterman et al. 1980). These can be thought of as the costs of ingesting a particular food.

Compounds in both these cases are concentrated in different ways in plant tissue and may determine the value of different plant parts to consumers (McKey 1979). Differences in the relative nutritional quality of foliage, fruits and seeds may be especially apparent (C. Hladik 1978, McKey et al. 1981). Leaves serve the plant as the primary organs of photosynthesis. They contain appreciable quantities of protein (Mattson 1980) but often have high levels of cell wall constituents which make them poor sources of energy (Van Soest 1982, Waterman 1984).

Fleshy fruits protect the ovule as it ripens but when ripe must attract animal seed dispersers (Snow 1971, van der Pijl 1972, Janzen 1983). Relative to leaves, fruit pulp often contains less protein but may have concentrations of sugars, pectin and other readily-digested carbohydrates and may contain appreciable levels of energy-rich oils and fats (Waterman 1984). Some fruits also contain toxins (Herrera 1982).

Seeds protect the embryonic plant until germination and thereafter provide energy for seedling establishment. Seeds generally contain high levels of oils or starches in the endosperm or cotyledon. In some species nitrogen levels also may be high. Seeds may be protected, however, by toxins and digestive inhibitors (Janzen 1971, McKey 1979, Waterman 1984), or by hard, resistant seed coats in which case seeds are essentially inedible ballast in the diet (Herrera 1981).

METHODS

Palatability Trials

Experiments were conducted at Epulu in the Ituri Forest of Zaire from November, 1982 to March, 1983. See Chapter 4 for a description of the Epulu area and its fauna.

Free-ranging duikers are known to eat a large number of fruit species (Dubost 1984, see also Chapter 4). It was possible to test preferences for only a minority of these, however. Five to six food species were selected for each of three trials, A, B and C conducted during the late wet, dry and early wet seasons repsectively (Table 3-1). Preferences were determined for these species and related to their nutritional composition. The nutritional correlates of preference then provided a basis for evaluating the potential food quality of other foods which were not tested.

The amount of a food eaten when offered by itself without alternative choices provides an inadequate measure of food preference since animals may be able to compensate for a poor quality food in the

Table 3-1. Design of fruit palatability trials.

			Test Animals[a]	
Trial	Season	Number Food Species	Blue Duiker	Bay Duiker
A	late wet	5	E/K, R/D	M
B	early dry	5	E/K	M
C	early wet	6	E/K	none

[a] Abbreviations refer to individual captive animals. See Chapter 2 for details.

diet by eating more of it. Thus the food eaten in greatest quantity is not necessarily the most favored.

Cafeteria-style presentations of a number of foods simultaneously provides a means of assessing preference. Lack of adequate numbers of animals and fruit supplies in this study, however, made it impossible to test all possible combinations of even three or four food species offered at one time.

As a compromise, a test protocol in which foods were offered two species at a time was used. Each combination was offered in known-weight ad libitum quantities with *Ipomea batata* foliage for a 12 hour period. The preferred fruit was considered that species eaten in the greater quantity. If the amount of each choice eaten differed by less than 10% both species were considered equally preferred. All possible fruit combinations were replicated (n = 2) if availability of forest fruits permitted. Combinations were presented randomly so that animals did not have the opportunity to habituate to any given choice.

The rank preference of a given fruit species, *i* was based on the summed frequency of test combinations in which *i* was the preferred choice. Tests in which both fruit offerings were eaten in equal amounts were scored as one half in accumulating rank preference values.

This protocol had several advantages. First it allowed preference for every food species to be evaluated in relation to every other in the trial. Secondly, it provided a means of examining whether food preferences were consistent. Consistent food preferences were defined as tests in which the same species was preferred in both replicates of a specific two-species offering. Finally, it permitted an examination of the relationship between the quality of a diet and its intake, where a measure of diet quality is provided by the preference rank of the preferred of the two constituent food species. In testing all combinations of foods, two species at a time, animals were presented diets in which one or both fruits offered were preferred. They were also forced to choose between combinations of less favored foods. Of interest here was not only which food was selected in each combination, but how much total food was eaten. The relative ability of an animal to maintain intake over a range of diet quality provides some indication of the importance of food quality as a constraint in foraging.

Although diets of free-ranging animals often contained a number of food species, between 67% and 100% of the diet by weight could generally be accounted for by one or two food species (J. Hart, unpubl. obs., see also Chapter 4). Thus the two-species food offerings used here were not necessarily at variance with the animals' natural dietary habits.

Test animals included two mated pairs of adult blue duikers identified as E/K and R/D (Male/Female). Each pair was treated as an experimental unit and compared with a single subadult female bay duiker, labelled M. The experimental animals had been captured locally and were kept in 10 m by 10 m pens in the forest. These were swept daily during experiments to remove extraneous foods fallen from the canopy. Preferences of both blue duiker pairs and the bay duiker were determined in Trial A. Only blue duiker pair E/K and the bay duiker were studied in Trial B. The blue duiker pair E/K was tested alone in Trial C.

Available supplies of test foods from the forest permitted two replications of almost all test combinations in Trial A. This was not possible in Trials B and C because fruits were more scarce in the forest. Nevertheless, the majority of fruit offerings were replicated in each test. *Ipomea batata* foliage intake was measured in Trial A, but not in Trials B and C. Most test foods were presented entire, just as they would be encountered in the forest. Some fruits of *I. wombolu, K. gabonensis* handle effectively. Fruits of these species were cut into 2 - 3 cm pieces and the seeds removed, before being offered to all test animals.

Preference tests for forest foliage differed from those for fruits because duikers often refused to eat large quantities of many foliage species. To test preferences for foliage, an alternative protocol was established. The test animals (blue duiker pair E/K and bay duiker M) were put on a diet of unripe *K,. gabonensis* fruits. Newly-expanded fresh leaves and petioles of different foilage species were presented to duikers in small, loose bunches of similar size. Three selection classes were established based on the amount of leaves eaten: Foliage uneaten (scored 0), less than half the bunch eaten (scored 0.5) and most or all of the foliage consumed (scored 1.0). Each species of foliage was presented on three different occasions and the scores summed and ranked. Ten species (both climax and pioneer) were tested. These comprised some of the more common species whose fallen leaves were likely to be most available to free-ranging animals. Preferences for four common understory species was also tested.

Nutritional Composition

Samples of all fruits, seeds and foliage offered in trials were retained for analyses. In fruits which contained hard, inedible seeds which are usually regurgitated, the seeds were removed from the flesh and weighed separately. Total dry matter (DM), total phenolic content (TP), condensed tannin content (CT), acid detergent fiber content (ADF) and total nitrogen content (N) were determined for edible parts of all samples by Dr. P.G. Waterman, Department of Pharmaceutical Chemistry, University of Strathclyde, Glasgow, Scotland. Procedures followed those detailed in Oates et al. 1980.

For each food species, edible dry matter yield (Y), as defined by (Herrera 1981), was calculated as

$$Y = (T - S) \times DM$$

where T equals the total fresh weight (g), S is the inedible seed weight (g) and DM equals percentage dry matter of the edible portion. In cases where S = 0, Y simply equals the grams dry matter in the sample.

Ratios of nutrient to digestion inhibitors were calculated for each food tested based on nutritional composition data. Three ratios were considered: N/ADF, N/(ADF + TP) and N/(ADF + CT). Each ratio was multiplied by the edible dry matter content of the food to provide a measure of adjusted dry matter yield of the food (Y_Q).

Values of all nutritional measures are expressed in milligrams per gram (mg/g) fresh weight of the food.

The plant constituents measured in this study do not comprise the total array of nutritionally significant compounds. The chemical constituents chosen for analysis here have been associated with preference in other studies (see bleow). Their use here provides a means of comparing food preferences and diets of duikers with those of other species.

Spearman's coefficient of rank correlation (r_S) (Steel and Torrie 1982) was used to test association of rank preference with other variables. Probabilities of $p < .10$ will be considered significant.

RESULTS

Preference Ranks

Rank preferences for each food (Table 3-2) were determined by four to eight test offerings to each of the animals or animal pairs being tested (Appendix 3-A). Four species of ripe fruit and one seed species were used in Trial A. Three species of ripe fruit and two species of unripe fruit were tested in Trial B. In Trial C four unripe fruits were tested. The fruits tested in Trial C included two species tested in Trial B: *Klainedoxa gabonensis* (unripe fruits tested in B, ripe fruits tested in C) and *Musanga cecropioides* (full size, unripe fruits tested in B, ripe fruits and small unripe fruits tested in C).

In all three trials, the first ranked species was the

Table 3-2. Rank preferences of fruits and seeds as determined by palatability trials with captive blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*).

			Blue duiker				Bay duiker	
			E/K		R/D		M	
Food Species	Symbol	Food Type	rank	tests	rank	tests	rank	tests
TRIAL A								
Brachystegia laurentii	B.l.	ripe seed	1	8	1	8	1	8
Canarium schweinfurthii	C.s.	ripe fruit	2.5	8	2	8	5	6
Donella pruniformis	D.p.	ripe fruit	2.5	8	3	8	3.5	6
Ricinodendron heudelotii	R.h.	ripe fruit	4	7	4	8	2	6
Phyllanthus pynaertii	P.p.	ripe fruit	5	8	5	8	3.5	5
TRIAL B								
Irvingia wombolu	I.w.	ripe fruit	1	7			2	6
Klainedoxa gabonensis	K.g.	unripe fruit	2	8			1	5
Musanga cecropioides	M.u.	unripe fruit	3.5	7			3	5
Ficus mocuso	F.m.	ripe fruit	3.5	6			4	4
Klainedoxa trillesii	K.t.	ripe fruit	5	7			5	4
TRIAL C								
Musanga cecropioides	M.r.	ripe fruit	1	8				
Irvingia grandifolia	I.g.	unripe fruit	2	8				
Klainedoxa gabonensis	K.g.	ripe fruit	3	6				
Dacryodes edulis	D.e	unripe fruit	4	8				
Cleistanthus michelsonii	C.m.	unripe fruit	5	7				
Musanga cecropioides	M.u.	unripe fruit	6	6				

preferred choice in every test combination. The lowest ranked food offering was never the preferred choice in any combination. Foods with intermediate preference ranks were the preferred choices in some combinations but not in others. Preferred food choices were generally not eaten to the exclusion of the other fruit offering. In most cases, at least small amounts of the less preferred choices were eaten and in some combinations substantial amounts were consumed. *Ipomea batata* foliage was generally eaten in small amounts, and sometimes not at all except when combinations of less preferred foods were offered (see further discussion below).

In Trial A, *Brachystegia laurentii* seed was the most preferred food by all duikers. *Phyllanthus pynaertii* was the least-preferred blue duiker food item, while *Canarium schweinfurthii* was the least-preferred bay duiker food item. Food rank preferences (n = 5) of blue and bay duiker were not correlated in Trial A (E/K with M, $r_S = .289$, $p > .10$; R/D with M, $r_S = .205$, $p > .10$).

In Trial B, ripe fruit of *Irvingia wombolu* and unripe fruit of *Klainedoxa gabonensis* were the first and second choices of the blue duiker with these same two species in reverse order the top ranked foods of the bay duiker. For both duikers, the least-preferred food was the ripe fruit of *K. trillesii*. Food rank preferences of blue and bay duikers were correlated in Trial B ($r_S = .872$, $p < .10$, $n = 5$).

In Trial C, ripe *Musanga cecropioides* was the highest ranked food of the blue duiker pair tested while small unripe fruits of the same species had the lowest rank.

Blue and bay duiker preference scores for canopy foliage (Table 3-3) were correlated ($r_S = .902$, $p < 0.01$, $n = 10$). Understory foliage species had uniformly low preference scores. In the one case tested (*Gilbertiodendron dewevrei*), understory foliage (fully opened but still limp) had a lower preference score than canopy foliage of the same age.

Replicated test combinations in which the same fruit was the preferred choice in both offerings were labelled consistent preference choices. Given the three possible outcomes of a choice between "Food A" and "Food B": $A > B$, $A < B$, and $A = B$ and duplicated tests, only one third of choices would be expected to be repeated if food choices were random. If more than one third of choices were repeated (Chi square test of exact probability), it was concluded that food choice was not random. In each of the trials only one or two of the blue and bay duiker replicated tests did not result in the same choice of preferred food. This was significantly less than would be expected if food choices were random (Table 3-4).

Even with random presentations of food combinations, the duikers consistently favored the same fruits. The strong correlation of rank food preference values between the two blue duiker replicates in Trial A ($r_S = .975$, $p < .01$) provided further evidence that food choices were consistent, and thus likely to be correlated with particular qualities of the fruits.

Consistency in foliage trial scores was evaluated in the same manner. For leaves, evidence for consistent scores between replicate

Table 3-3. Scores and preference ranks for foliage species offered in palatability trials with captive blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*).

Foliage Species	Blue duiker Score	Blue duiker Rank	Bay duiker Score	Bay duiker Rank
CANOPY FOLIAGE				
Alstonia boonei	3.0	1	3.0	2
Ricinodendron heudelotii	2.5	2	3.0	2
Phyllanthus pynaertii	2.0	3.5	1.5	4.5
Cola lateritia	2.0	3.5	3.0	2
Albizzia gummifera	1.5	6	1.0	6.5
Dacryodes edulis	1.5	6	0.5	8.5
Gilbertiodendron dewevrei	1.5	6	1.5	4.5
Canarium schweinfurthii	1.0	8	1.0	6.5
Erythrophleum suaveolens	0.5	9	0.5	8.5
Cleistanthus michelsonii	0.0	10	0.0	10
UNDERSTORY FOLIAGE				
Gilbertiodendron dewevrei	1.0	1		
Scaphopetalum dewevrei	0.5	2.5		
Alchornea floribunda	0.5	2.5		
Brachystegia laurentii	0.0	4		

Table 3-4. Consistency of preference choices between replicated presentations of the same food combinations within trials.

	Animal		Choices made		Significance	
Trial	Species	Replicate	Consistent Choices	Inconsistent Choices	X^2	P
FRUIT TRIALS						
A	blue duiker	E/K	8	1	12.50	<.005
A	blue duiker	R/D	8	1	12.50	<.005
A	bay duiker	M	5	1	6.75	<.01
B	blue duiker	E/K	7	1	10.50	<.005
B	bay duiker	M	2	0	---	---
C	blue duiker	E/K	5	2	4.67	<.05
FOLIAGE TRIALS						
	blue duiker	E/K	6	8	0.61	N.S.
	bay duiker	M	6	4	3.30	<.10

presentations was not as strong as for fruits (Table 3-4). This may have been due to the fact that only small quantities of foliage were generally eaten at one time. It was noted, however, that animals generally sampled most leaf species when they were presented, even if they did not consume them in quantity.

Composition of Foods

The fruits and seeds offered in the trials A - C varied in composition (Table 3-5). Dry matter yield values ranged from a low of 170 mg/g fresh weight in *Ficus mucuso* and *Musanga cecropioides* to a high of 810 mg/g fresh weight in *Brachystegia laurentii* seed. Total phenolic content ranged from almost 0 to 74 mg/g, condensed tannin content from 0 to 83 mg/g, fiber from 22 to 150 mg/g and crude protein (N content x 6.25) from 8.3 to 91 mg/g.

In comparison with the fruits and seeds, the *Ipomea batata* foliage, offered during Trials A -C had a low dry matter yield (due to its high moisture content) but relatively high crude protein content. Fiber, total phenolic and tannin levels all fell within the limits exhibited by the fruits and seeds.

On a fresh weight basis, rank levels of condensed tannin in fruits were positively correlated with rank fiber levels (r_S = .692, $p < .01$ $n = 16$). Fiber levels were also correlated with crude protein content (r_S = .596 $p < .05$ $n = 16$). Total phenolics were not significantly correlated with any other chemical component.

Among the foliage species tested (Table 3-6), total phenolic levels ranged from 3 to 52 mg/g and condensed tannin levels from 0 to

Table 3-5. Chemical composition of foods offered in palatability trials.

				Milligrams / Gram Fresh Material				
Species	Description	Percent Moisture	Regurgitated Seed	Edible Dry Matter Y	Total Phenolic TP	Condensed Tannins CT	Fiber ADF	Crude Protein N
TRIAL A								
Brachystegia laurentii	ripe seed	19	0	810	45.8	82.9	149.9	91.1
Canarium schweinfurthii	ripe fruit	45	440	320	12.4	61.0	76.7	11.8
Donella pruneformis	ripe fruit	66	130	300	74.4	16.4	88.1	18.3
Ricinodendron heudelotii	ripe fruit	77	160	200	62.0	0	25.1	9.9
Phyllanthus pynaertii	ripe fruit	83	60	190	3.7	29.4	90.0	10.6
TRIAL B								
Irvingia wombolu	ripe fruit	74	0	260	28.2	0.7	31.7	8.3
Klainedoxa gabonensis	unripe fruit	69	0	310	32.0	7.8	73.8	11.7
Musanga cecropioides	unripe fruit	65	400	210	3.2	24.3	109.9	22.4
Ficus mocuso	ripe fruit	83	?	170	2.5	14.2	70.4	12.1
Klainedoxa trillesii	ripe fruit	75	0	250	8.5	37.6	57.5	7.6
TRIAL C								
Musanga cecropioides	ripe fruit	67	480	170	1.0	8.7	93.7	16.3
Irvingia grandifolia	unripe fruit	74	0	260	16.3	1.2	22.1	20.8
Klainedoxa gabonensis	ripe fruit	71	0	290	34.7	5.5	44.4	8.3
Dacryodes edulis	unripe fruit	81	0	190	15.8	7.2	30.0	13.8
Cleistanthus michelsonii	unripe fruit	58	0	420	31.3	14.2	137.8	26.0
Musanga cecropioides	unripe fruit	79	0	210	7.3	50.5	85.3	24.9
ALL TRIALS								
Ipomea batata	foliage	82	0	180	3.9	1.3	31.9	54.5

Table 3-6. Chemical composition of foliage offered in palatability trials. Values expressed as mg/g of fresh weight.

Species	Dry Matter DM	Total Phenolic TP	Condensed Tannins CT	Acid Det Fiber ADF	Crude Protein N
CANOPY FOLIAGE					
Alstonia boonei	.267	8.8	2.1	73.7	38.7
Canarium schweinfurthii	.274	51.5	10.7	76.5	58.1
Erythrophleum suaveolens	.306	18.1	13.8	95.2	83.5
Cola lateritia	.310	40.6	129.9	96.4	53.0
Ricinodendron heudelotii	.243	11.7	2.7	56.4	67.1
Phyllanthus pynaertii	.309	3.1	.00	95.8	50.7
Dacryodes edulis	.410	20.5	35.7	167.7	35.7
Albizzia gummifera	.274	18.4	19.2	100.0	103.8
Cleistanthus michelsonii	.436	49.3	9.6	159.1	50.1
Gilbertiodendron dewevrei	.239	44.7	98.9	94.4	39.2
UNDERSTORY FOLIAGE					
Brachystegia laurentii	.385	6.9	17.3	178.3	83.2
Gilbertiodendron dewevrei	.258	19.6	41.8	117.7	46.4
Scaphopetalum dewevrei	.188	12.2	22.9	47.6	35.3
Alchornea floribunda	.224	19.3	2.2	46.1	64.5

* Crude protein = N x 6.25.

130 mg/g. The fiber content of foliage was more uniform and on average higher than in fruits. Values ranged from 74 to 168 mg/g fresh weight. Crude protein levels were uniformly high, 36 to 104 mg/g fresh weight. Foliage dry matter yield values fell between 240 and 440 mg/g fresh weight. Rank total phenolics was correlated with rank condensed tannins ($r_S = .563$, $p < .10$, $n = 14$). No associations of other measured chemical variables were apparent. Compared to the *Ipomea batata* foliage offered with the fruits and seeds in Trials A - C (Table 3-5), the forest foliage species tested had markedly higher tannin and phenolic levels in all species. Dry matter yield and fiber levels were also higher, but protein levels were comparable.

Chemical Correlates of Preference: Fruit

No single chemical component measured was consistently correlated with preference over all trials (Table 3-7). For the blue duiker, rank food preference in Trial A was significantly correlated with food levels of crude protein and edible dry matter. For foods offered in Trial B preference was negatively correlated with condensed tannin levels. In Trial C, there was no correlation between blue duiker preference and any of the single chemical variables measured. If ripe *Musanga cecropioides* (see discussion below) was excluded from the analyses, however, food preferences in Trial C became negatively correlated with levels of both fiber and tannins. In the bay duiker trials, the only single variable correlated with preference was condensed tannin levels in Trial B.

In contrast with the measures of single chemical variables,

Table 3-7. Spearman's rank correlation coefficients (r_s) of rank preference with chemical measures of fruits used in palatability trials with blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*). ^{a}

	Single chemical variables					Adjusted Dry Matter Yield (Y_a)		
Trial	TP	CT	ADF	N	Y	Yx(N/ADF)	Yx(N/(ADF+CT)	Yx(N/(ADF+TP)
Trial A								
Blue duiker								
E/K	.359	.616	.359	.872 *	.975 ***	.667	.667	.872**
R/D	.200	.700	.000	.950 **	1.000 ***	.600	.600	.900**
Bay duiker								
M	.308	.462	.308	.205	.205	.821*	.821*	.051
Trial B								
Blue duiker								
E/K	.564	-.975 ***	-.154	.051	.564	.821*	.975**	.410
Bay duiker								
M	.700	-.810 *	.200	.200	.700	.821*	.810*	.500
Trial C								
Blue duiker E/K								
with M.r.	-.239	-.600	-.314	-.371	-.543	-.024	-.029	-.142
without M.r.	.200	-.900 **	-.900 **	-.600	-.200	.667	.667	.500

^{a} Significance: *, $p < .10$; **, $p < .05$; ***, $p < .01$

composite measures incorporating levels of both nutrients and digestion inhibitors were consistently correlated with food preferences. Two measures of adjusted dry matter yield, Y x (N/ADF) and Y x [N/(ADF + CT)] had coefficients of rank correlation of 0.60 or above for all animals in all three trials (Table 3-7; Trial C, ripe *Musanga cecropioides* strongly correlated with food preferences except for the two blue duiker pairs tested in Trial A.

Chemical Correlates of Preference: Foliage

Preferences for canopy foliage were negatively correlated with phenolic levels (blue duiker) and fiber levels (blue and bay duiker) but positively, though weakly correlated with a measure of adjusted dry matter yield, Y x [N/(ADF + TP)] (Table 3-8).

The three foliage species most favored by both blue and bay duiker, *Phyllanthus pynaertii, Alstonia boonei* and *Ricinodendron heudelotii*, all had the lowest total phenolic and condensed tannin rankings. The two most preferred species also had the lowest fiber rankings.

Cleistanthus michelsonii, Erythrophleum suaveolens and *Canarium schweinfurthii* were the three least preferred species. All exhibited high levels of potentially toxic, or digestive inhibiting compounds. *C. michelsonii* had high fiber and tannin content and low protein levels. *C. schweinfurthii* had low fiber and high protein contents, but also high total phenolics and a strong, resinous odor, indicating presence of essential oils. Essential oils have been shown to inhibit rumen fermentation in some tests (Nagy et al. 1964, see also

Table 3-8. Spearman's rank correlation coefficients (r_s) of rank preference with chemical measures of ten species of canopy foliage tested in palatability trials with blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*). [a]

	Single Chemical Variables				Adjusted dry matter yield (Y_o)		
Species	TP	CT	ADF	N	Y×(N/ADF)	Y×(N/(ADF+CT)	Y×(N/ADF+TP)
Blue duiker	-.712 **	-.286	-.575 *	-.140	.216	.122	.551*
Bay duiker	-.024	-.446	-.747 **	-.325	.434	.289	.554*

[a] Significance: *, $p < .1$; **, $p < .05$.

references in Bryant and Kuropat 1980). *E. suaveolens* had high protein and low fiber levels, however, this species is renowned locally for its toxic properties. The bark was used to poison fish.

None of the four understory foliage species were eaten freely by the blue duiker pair, and all four exhibited apparently effective anti-herbivore properties (Table 3-9). *Alchornea floribunda* had high protein and low fiber and tannin levels but leaves were never eaten. The foliage had a peculiar peppermint-like aroma, indicating possibly significant levels of secondary compounds. This species is a member of a group of Euphorbiaceae known for its toxic qualities (P.Waterman, pers. comm.). Although *Scaphopetalum dewevrei* foliage also had low fiber and tannin levels it too was not eaten. *S. dewevrei* foliage was strongly pubescent and harbored ants in small pockets in the leaf blade at the juncture with the petiole. The foliage of seedlings of both *Brachystegia laurentii* and *G. dewevrei* were high in fiber, and in the case of *G. dewevrei*, there were appreciable levels of condensed tannins as well. In addition, the first leaves put out by both of these seedlings characteristically become tough, fibrous and unpalatable even before the cotyledons are absorbed.

Intake on Fruit Diets

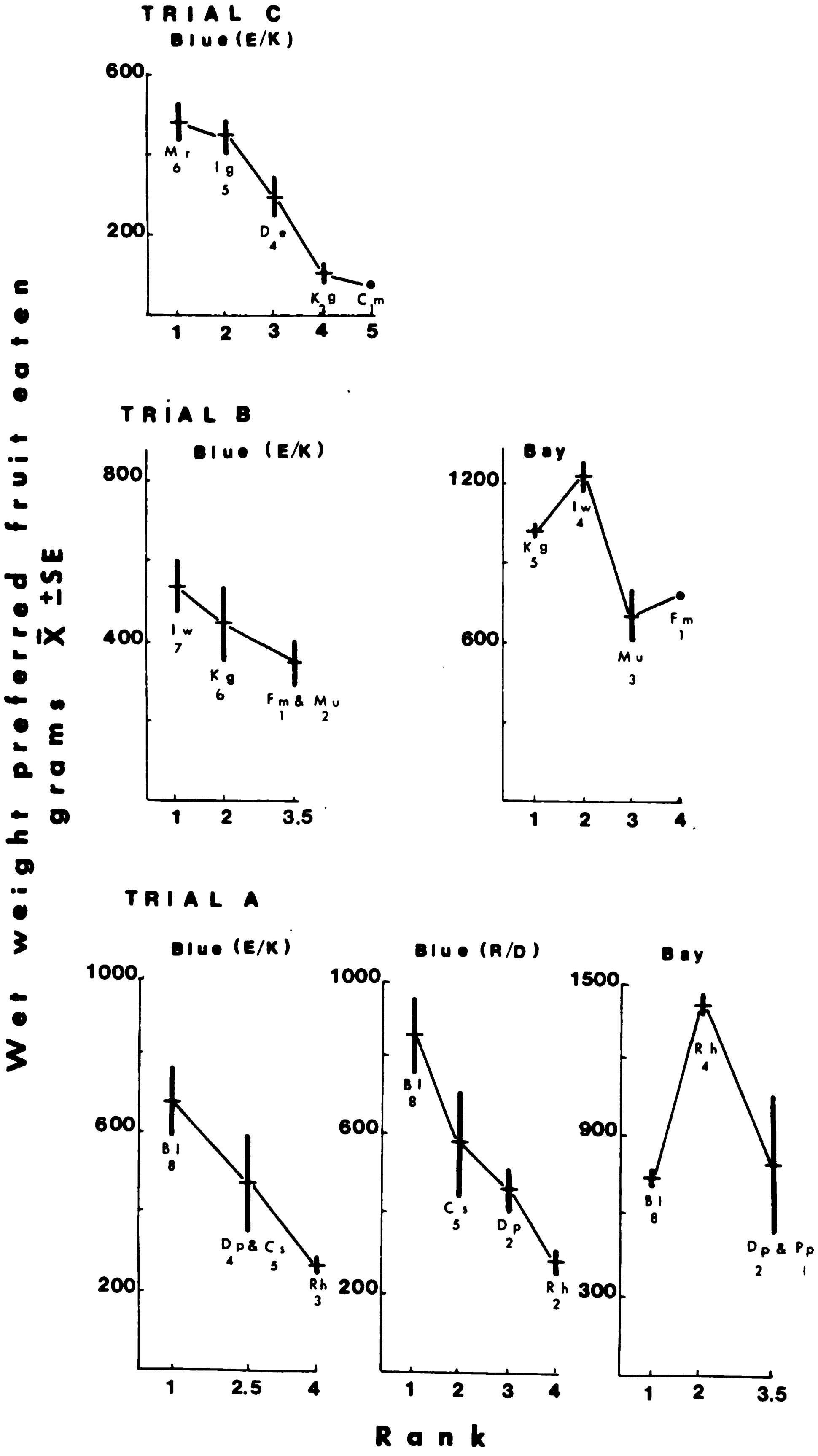
For the blue duiker in all three trials, the total amount of fruit eaten on a diet was correlated with the rank preference of the preferred of the two food choices offered (Figure 3-1). Fruit intake on test combinations which included the top ranked food species was higher

Table 3-9. Possible defensive characteristics of species of understory foliage offered to a blue duiker (*C. monticola*) in palatability trials.[a]

Species	Acceptance*	Evident Characteristic
Alchornea floribunda	sampled once	strong odor
Gilbertiodendron dewevrei	sampled twice	high fiber and tannins
Scaphopetalum dewevrei	sampled twice	copious pubescence, ants
Brachystegia laurentii	never eaten	high fiber

* Three replicate offerings made.

Figure 3-1. Average (± SE) wet weight eaten (g/day) versus preference rank of each fruit species when the indicated species was the preferred choice offered. Number of tests shown below each species. For key to species abbreviations see Table 3-2.


TRIAL C
Blue (E/K)
600
200
Mr
6
Ig
5
De
4
Kg
3
Cm
1
2
3
4
5
TRIAL B
Blue (E/K)
800
400
Iw
7
Kg
6
Fm &
1
Mu
2
1
2
3.5
Bay
1200
600
Kg
5
Iw
4
Mu
3
Fm
1
1
2
3
4
TRIAL A
Blue (E/K)
1000
600
200
Bl
8
Dp &
4
Cs
5
Rh
3
1
2.5
4
Blue (R/D)
1000
600
200
Bl
8
Cs
5
Dp
2
Rh
2
1
2
3
4
Bay
1500
900
300
Rh
4
Bl
8
Dp &
2
Pp
1
1
2
3.5
Wet weight preferred fruit eaten
grams X̄ ±SE
Rank

than on diets which contained combinations of foods of lower rank preference. In other words, if blue duiker were presented with foods they preferred, they ate more of them.

This was not the case with the bay duiker in either of the two trials it was tested. The preference score of a food and its intake were not correlated (Figure 3-1). Although the bay duiker exhibited consistent food preferences in both Trial A and B (see above), it was able nevertheless to consume large amounts of less-highly ranked foods when more favored choices were not presented.

The bay duiker's ability to eat relatively large quantities of both preferred or less-preferred foods allowed this species to maintain relatively constant levels of edible dry matter intake over a range of diet preferences. Except for diets containing *Brachystegia laurentii* seed, in which dry matter intake was high (see discussion), total fruit dry matter intakes averaged between 350 to 410 g/day for all paired fruit combinations offered in Trials A and B. This was not the case for the blue duikers. Their fruit dry matter intakes declined as the animals were forced to choose between fruits of lower preference rank (Figure 3-2).

When confronted with a choice between two less-preferred fruit species, blue duikers increased *Ipomea batata* foliage intake in their diet. In Trial A, foliage averaged only 5% to 6% of total dry matter intake when *Brachystegia laurentii* seed, the most preferred food was available. In contrast, when the two lowest ranked fruits were presented, foliage represented 45% - 52% of total dry matter intake (Table 3-10). Increased levels of *I. batata* foliage in the

Figure 3-2. Total fruit dry matter intake (mean ± SE) on fruit diets of decreasing rank preference. Diet rank equals rank of the more-preferred of the two fruit choices offered. Symbols: ●——●, blue duikers E/K; ○—○, blue duikers R/D; ★—★, bay duiker M.

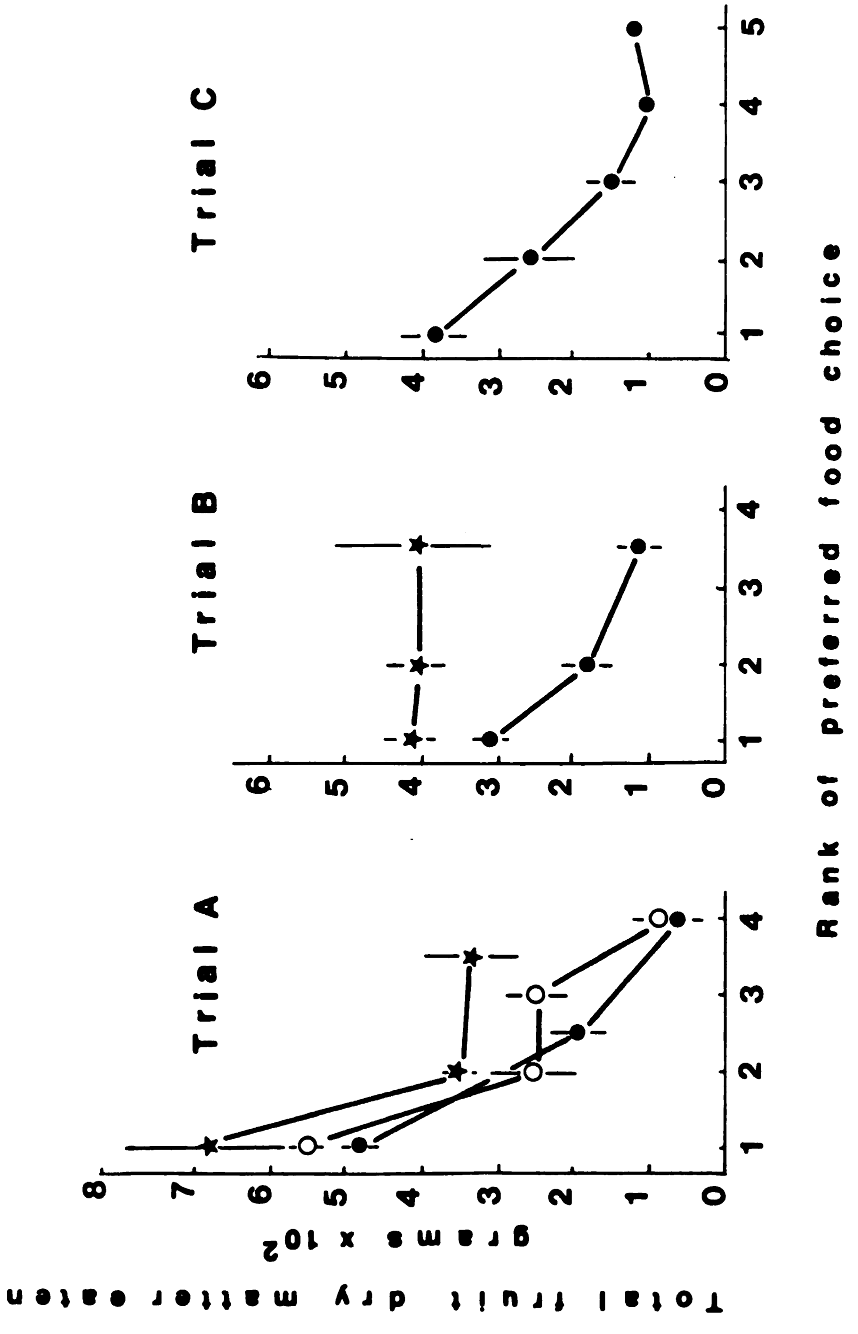

Trial A
Trial B
Trial C
Total fruit dry matter eaten
grams x 10^2
Rank of preferred food choice
0
1
2
3
4
5
6
7
8
1
2
3
4
5

Table 3-10. Percentage of total dietary dry matter contributed by *Ipomea batata* foliage in diets of blue duiker (*C. monticola*) and bay duiker (*C. dorsalis*) in which the fruits offered varied in preference rankings.

	Blue duiker (E/K)				Blue duiker (R/D)				Bay duiker (M)			
Rank*	1	2.5	2.5	4	1	2	3	4	1	2	3.5	3.5
$\bar{X}$	6.0	15.5	25.5	46.0	4.8	30.4	37.1	46.9	2.5	11.8	6.5	13.4
SE	1.4	3.1	2.2	---	1.1	8.8	4.4	15.9	0.8	4.9	0.7	7.4
n	4	3	3	1	4	3	2	2	4	3	3	2

* Rank of preferred fruit species.

diet did not offset the loss in total dry matter intake precipitated by reductions in fruit consumption on the less-preferred diets. Percentage foliage in diet and total dry matter intake were negativley correlated (Figure 3-3) (E/K, $R^2 = .45$, $p < .05$, $n = 20$; R/D, $R^2 = .54$, $p < .001$, $n = 19$).

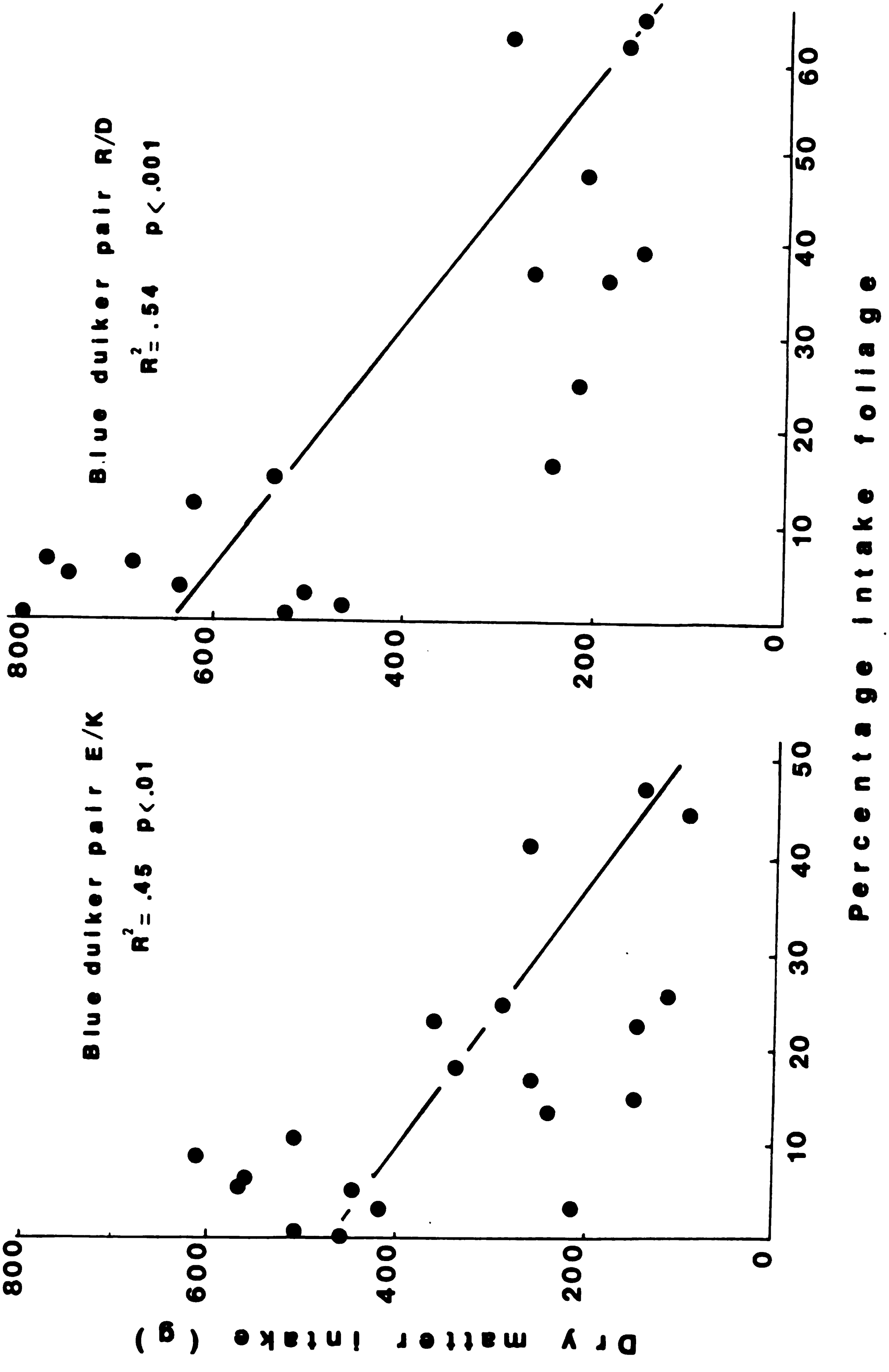
In the bay duiker diets the contribution of foliage to total dry matter intake was never more than 15%, even when the least preferred fruit combinations were offered (Table 3-10). The bay duiker thus maintained fruit intake over a range of fruit quality.

DISCUSSION

Referring to the specific questions posed in the introduction, food choices of both the blue and bay duiker in palatability trials were not random. Preferences for specific foods were generally consistent between similar replicated presentations. Although both duiker species revealed clear food preferences, neither species ate even the most favored food to the exclusion of other offerings. This result is consistent with what has been seen of herbivore food choices in general (Bunnell and Gillingham in press) and is thought to be due to nutritional inadequacies and defensive compounds in some plants (Freeland and Janzen 1974, Westoby 1978).

The results of this study are in agreement with recent findings on diets of tropical forest primates which demonstrate that nutritional correlates of food preference are not well defined by any single chemical variable (Oates et al. 1977, 1980; Milton 1979, McKey

Figure 3-3. Total dry matter intake (g) versus percent *Ipomea batata* foliage in blue duiker diets for all two-species fruit offerings in Trial A.


Blue duiker pair R/D
R² = .54 P<.001
Blue duiker pair E/K
R² = .45 P<.01
800
600
400
200
0
10
20
30
40
50
60
Percentage intake foliage
Dry matter intake (g)

et al. 1981). Composite measures incorporating apparent nutritional costs and benefits of a food were better correlated with food preferences in both species. In this study ratios of N/ADF and N/(ADF + CT), each multiplied by dry matter yield (Y) provided positive correlations with food preference.

McKey et al. (1981) found that ratios of nitrogen to fiber and nitrogen to fiber plus tannins were correlated with diet choice in the black colobus monkey (*Colobus satanus*) in Cameroon. These authors did not weight their ratios with the dry matter yield of the foods as was done in this study. Most of the important foods eaten by the colobus were either foliage or edible seeds. The proportion of these foods which was edible dry weight apparently may not have varied markedly from species to species. This was not the case for many of fruits reported here in which the relative proportions of water and inedible (reguritated) seed varied widely. As Herrera (1981) has pointed out, the relative portion of a fruit which is edible dry weight pulp can have a marked effect on frugivore preference.

Not all duiker food preferences were correlated with adjusted dry matter yield. Ripe *Musanga cecropioides* fruit was most preferred by blue duikers in Trial C yet it had low edible dry matter content and relatively low nitrogen to fiber ratios (Table 3-5). Preference for this fruit may have been due to high levels of readily fermented carbohydrates (sugars and pectins) not measured in the extractions. Use of this fruit by bats and cercopithecine monkeys, neither of which have developed capacities for fermentive digestion, also is evidence that it must contain readily available stores of energy. The apparently high levels of fiber recorded in the chemical analyses may have been due to the mixing of both fruit and seed in the samples used for extraction. Since the seeds of this species are inedible and are voided by the duikers, their inclusion in the chemical anlayses may give a distorted measure of the true nutritonal value of the food.

The blue duikers' preference for ripe *Canarium. schweinfurthii* fruits may also be a function of concentrated, readily available energy. These fruits are apparently rich in digestible lipids (Wu Leung 1968). It was not clear why they were avoided by the bay duiker.

A number of the foods preferred by the duikers contained appreciable levels of tannins. The importance of these compounds in affecting selectivity is not clear. *Canarium schweinfurthii* fruits had high condensed tannin levels. Its fruits were favored by the blue duiker, but not by the bay duiker. *Ricinodendron heudelotii* fruits had high levels of hydrolysable tannins (P. Waterman, pers comm.) and yet were eaten freely by bay duiker in the Trial A. Captive blue and bay duikers maintained on a diet dominated by *R. heudelotii*, however, exhibited what was apparently marked hematuria, (Chapter 2).

Differences in the diets of frugivorous ungulates and primates in African tropical forests may be linked to to differences in the relative tolerances of these two taxa to tannins and perhaps other plant defensive compounds. Two studies (Wrangham and Waterman 1981, 1983) have shown that at least some species of primates which lack foregut fermentation may be sensitive to condensed tannin levels in foods and will avoid foods such as some unripe fruits where levels of these compounds are high. Other studies, however, indicate that the role of tannins as feeding deterents may not be easily generalized (Zucker 1983, Waterman 1983, Mole and Waterman in press).

Nevertheless, in the Ituri Forest, up to 50% or more of the foods available to ungulates on the forest floor were unripe fruits or parts of ripe fruits which showed evidence of being discarded by primates (Chapter 4). Many of these fruits were included in duiker diets and were apparently an exclusive resource for them. It is tempting to ascribe the ruminants ability to utilize these fruits to the detoxifiying and digestive capacity of foregut fermentation. Further investigation into this capacity may enlighten our understanding of trophic relationships between co-occurring frugivorous taxa. It may also help to explain the relative success and evolutionary radiation of the African forest ungulates.

Foliage as a Food Source

It has been suggested (Hladik 1978, Milton 1979) that foliage may be important in the diets of frugivorous primates as a source of protein which is lacking in fruits. While this may be true for many of the fruits consumed by primates, there is evidence that this is not the case for some of the important foods in the diets of the frugivorous ungulates.

In a survey of fruits, flowers and seeds available to duikers on the forest floor (Chapter 4), 19 ripe fruits, 21 unripe fruits and 5 flowers averaged 16.0 mg/g, 17.7 mg/g and 26.9 mg/g nitrogen respectively. Four species of frequently eaten seeds averaged 59.8 mg/g nitrogen, essentially equivalent to the average 60.0 mg/g contained in the 10 canopy foliage species tested in the trials. At least some seeds thus may be equivalent to foliage as a source of nitrogen. Seeds have an additional advantage over foliage in that they are often concentrated sources of readily digested energy (McKey et al. 1981, Waterman 1984).

The relative availability of nitrogen must also be taken into account in evaluating a food as a source of dietary protein. Many forest foliage species and some forest fruits available to ungulates are high in fiber. This would tend to reduce their digestibility and thus their value as a source of protein. Although many of the fruits eaten by duikers were lower in total nitrogen content than foliage, they were also relativley lower in fiber and thus probably more digestible. From the perspecitive of the animal, these may have been superior sources of dietary protein.

Blue and bay duiker differed in their patterns of foliage intake on the test diets. The bay duiker maintained a high fruit intake over a wide range of fruit preferences. *Ipomea* comprised more than 15% of the bay duiker's diet even when it had only less-preferred fruits as alternative foods. In the blue duiker in contrast, *I. batata* were presented fruits of apparent low nutritional quality, a pattern which was also documented in digestion trials (Chapter 2).

Diets dominated by foliage were correlated with low total dry matter intake. This may have been due to the low edible dry matter content of *I. batata* foliage relative to that of many fruits and seeds (Table 3-5). Since a lowered total intake could threaten an animals energy balance, especially in a species of small body size (Milton 1979, McKey et al. 1981), the availability of suitable fruits or seeds may be essential to the occupation of the forest understory by the duikers.

It is interesting that the only small ungulate folivore in this forest, *Neotragus batesi*, avoids the forest understory and is partial to clearings and treefalls where presumably higher light levels allow adequate supplies of high quality foliage to grow (Freer 1979, J. Hart, unpubl. obs.).

Intake, Diet Quality and Body Size in Duikers

Highest total dry matter intake was achieved by both duiker species on diets containing *Brachystegia laurentii* seeds. Relative to all other species of fruits and all foliage tested, *B. laurentii* seeds had both the highest edible dry matter density and protein to fiber plus tannin ratios.

The response of the two duiker species to lower quality diets varied. Like sheep on progressivly diluted concentrate diets (Baile and Forbes 1974), the bay duiker increased its total intake as the diet quiality was reduced. By varying total intake, it was able to maintain total dry matter intake at a constant level over all food combinations. Blue duiker did not show this same response to decreasing diet quality. This species was unable to increase intake on low quality diets.

Demment and Van Soest (1985) have proposed the hypothesis that different dietary fiber levels of plant food resources create a gradient of food quality which can be partitioned by animals of different body size as a function of their relative digestive capacity. Fiber levels alone were not the only correlate of food selectivity by duikers in captive trials. Dietary quality for duikers is likely to include relative levels of nutrients and other digestion inhibitors, as well as the edible dry matter content (see also Chapter 2). Nevertheless, the idea of size-partitioned resources based on food quality may be pertinent to an understanding of relations within the frugivorous ungulate guild.

While both blue and bay duiker preferred foods with high adjusted dry matter yield values, bay duiker had a greater capacity to broaden the diet to include lower quality items. Broadening of the diet would be expected to occur when food is scarce and the larger animals relatively large total needs would not likely be met by selective foraging for small, dispersed patches (see also Chapter 2 and 4). Based on the results of these trials, the smaller blue duiker is evidently more constrained to select high quality foods than the bay duiker. Its total food needs, however, are lower, and thus this species could be expected to be better able to meet these by being selective than would the bay duiker over periods of low food availability.

CONCLUSIONS

Two pairs of blue duiker and a bay duiker exhibited consistent preferences for fruits. Overall preferences for fruits in both species was better correlated with a measure of the edible dry matter content of the food multiplied by a ratio of protein to fiber or protein to fiber plus tannin content. Preferences for different foliage species were less apparent. Only small amounts of many foliage species were eaten. Overall, foliage is less preferred than many fruits and edible seeds.

Dry matter intake was highest on diets containing *Brachystegia laurentii* seeds. Dry matter intake in the bay duiker remained constant over diets including both high ranked and low-ranked fruits. In blue duiker in contrast, dietary dry matter intake declined in all three trials as the quality of the fruits presented was decreased. Blue duikers increased *Ipomea* foliage intake on low quality diets, but this did not compensate for a decline in fruit intake.

LITERATURE CITED

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APPENDIX

APPENDIX 3-A

Results of palatability trials[a] [b]

TRIAL A

Blue Duiker (Replicate R/D)

Species B:	B.l.	C.s.	D.p.	R.h.	P.p.	Preferred choice[c]	Preference rank
Species A:							
B.l.	---	>>	>>	>>	>>	4.0	1
C.s.		---	>=	>>	>>	2.5	2
D.p.			---	<=	>>	2.0	3
R.h.				---	>>	1.5	4
P.p.					---	0	5

Blue Duiker (Replicate E/K)

Species B:	B.l.	C.s.	D.p.	R.h.	P.p.	Preferred choice [c]	Preference rank
Species A:							
B.l.	---	>>	>>	>>	>>	4.0	1
C.s.		---	><	>>	>>	2.5	2.5
D.p.			---	>	>>	2.5	2.5
R.h.				---	>>	1.0	4
P.p.					---	0	5

Bay Duiker (Replicate M)

Species B:	B.l.	R.h.	D.p.	P.p.	C.s.	Preferred choice[c]	Preference rank
Species A:							
B.l.	---	>>	>>	>>	>>	4.0	1
R.h.		---	>	>	>>	3.0	2
D.p.			---	>=	>	1.5	3.5
P.p.				---	>	1.5	3.5
C.s.					---	0	5

Appendix 3-A continued

TRIAL B

Blue Duiker (Replicate E/K)

	Species B:					Preferred choice[a]	Preference rank
Species A:	I.w.	K.g.	M.u.	F.m.	K.t.		
I.w.	---	>>	>>	>	>>	4.0	1
K.g.		---	>>	><	>>	2.5	2
M.u.			---	=	>>	1.5	3.5
F.m.				---	>	1.5	3.5
K.t.					---	0	5

Bay Duiker (Replicate M)

	Species B:					Preferred choice[a]	Preference rank
Species A:	K.g.	I.w.	M.u.	F.m.	K.t.		
K.g.	---	>>	>	>	>	4.0	1
I.w.		---	>>	>	>	3.0	2
M.u.			---	>	>	2.0	3
F.m.				---	>	1.0	4
K.t.					---	0	5

Appendix 3-A continued

TRIAL C

Blue Duiker (Replicate E/K)

Species A: \ Species B:	M.r.	I.g.	K.g.	D.e.	C.m.	M.u.	Preferred choice*	Preference rank
M.r.	---	>>	>	>=	=	>>	4.0	1
I.g.		---	>	><	>>	>	3.5	2
K.g.			---	=	>>	>	2.5	4
D.e.				---	>>	>	3.0	3
C.m.					---	>	1.5	5
M.u.						---	0	6

Notes:

[a] For species abbreviations, see Table 3-2.

[b] Symbols: > , A eaten more than B; < , A eaten less than B; =, amount of A and B eaten differ by less than 10%. Each symbol records results of a single paired test.

[c] Number of paired combinations in which Species A is the preferred choice. Paired tests in which A = B, or replicate tests in which A> B and A< B are scored as o.5.

CHAPTER FOUR

Comparative Dietary Ecology in a Community of Frugivorous Ungulates

Studies of Central African forest faunas have established the predominance of frugivory among a diverse array of mammalian primary consumers (Gauteir-Hion et al. 1980, Emmons et al. 1983). Among these species are a group of seven co-occuring ruminants including six duikers (genus *Cepahalophus*) and the chevrotain (*Hyemoschus aquaticus*). These species are similar in gerneral form but span a more than ten-fold range in body size. Recent studies (Dubost 1979, 1984) have shown that these species differ in habitat, activity patterns and diets. Variations in dietary patterns have been difficult to interpret, however, since data on food availalbility and nutritional quality have been limited.

Among consumers exploiting clumped, particulate foods such as seeds or fruits, the location, identity and density of items within food patches have emerged as important variables affecting foraging and diet (Lewis 1980, Leighton and Leighton 1981, Schluter 1982). Differences in consumer body size have been shown to lead to differential use of food patches in primates (Terborgh 1983) and rodents (Price 1984, Harris, 1984).

Body size has also been shown to be a mechanism for dietary differention in communities of ruminants (Bell 1971, Hoffmann 1973, Owen-Smith 1980, Hanley 1980, Clutton-Brock and Harvey 1983, Demment and Van Soest 1985, Bunnell and Gillingham in press). The emphasis in these studies has been on the digestibility and availability of food in relation to total needs. Relative to smaller species, large animals are more mobile and have larger mouths and greater digestive capacity. Smaller animals, in contrast, have smaller total needs and can forage selectively where large animals can not. These size-linked differences have been seen to be important in allowing coexistence among potentially competing species.

Recent studies of captive duikers (see Chapters 2 and 3) found differences in digestibility and food selection in species of differing body size. In these experiments food availability was constant. It is likely that food distribution and abundance as well as food quality are important in determining dietary choice in free-ranging animals.

The purpose of this study was to investigate the relationship of frugivorous ungulates to their food resources and the potential importance of dietary differences as mechanisms of niche differentiation in the forest ungulate community. The species will be briefly described and basic data on food availability and general dietary composition presented. Three question will then be posed:

1. What are patterns of diet selection and how are these correlated with morphological and size differences in the animals? Attention will be focused on dimensions of the food which might affect

its quality and utility to different duiker species. Specific hypotheses relating diet selection to food patch size, food item size and food nutritional quality will be presented and tested.

2. What are the patterns of dietary convergence and divergence and are they correlated with differences in resource levels? This question examines dietary overlap in species of similar and differing habitats.

3. What are the patterns of ungulate distribution and abundance and how are they correlated with food abundance? Differences between different forest types will be discussed in relation to the abundance adn diversity of available foods.

STUDY SITE

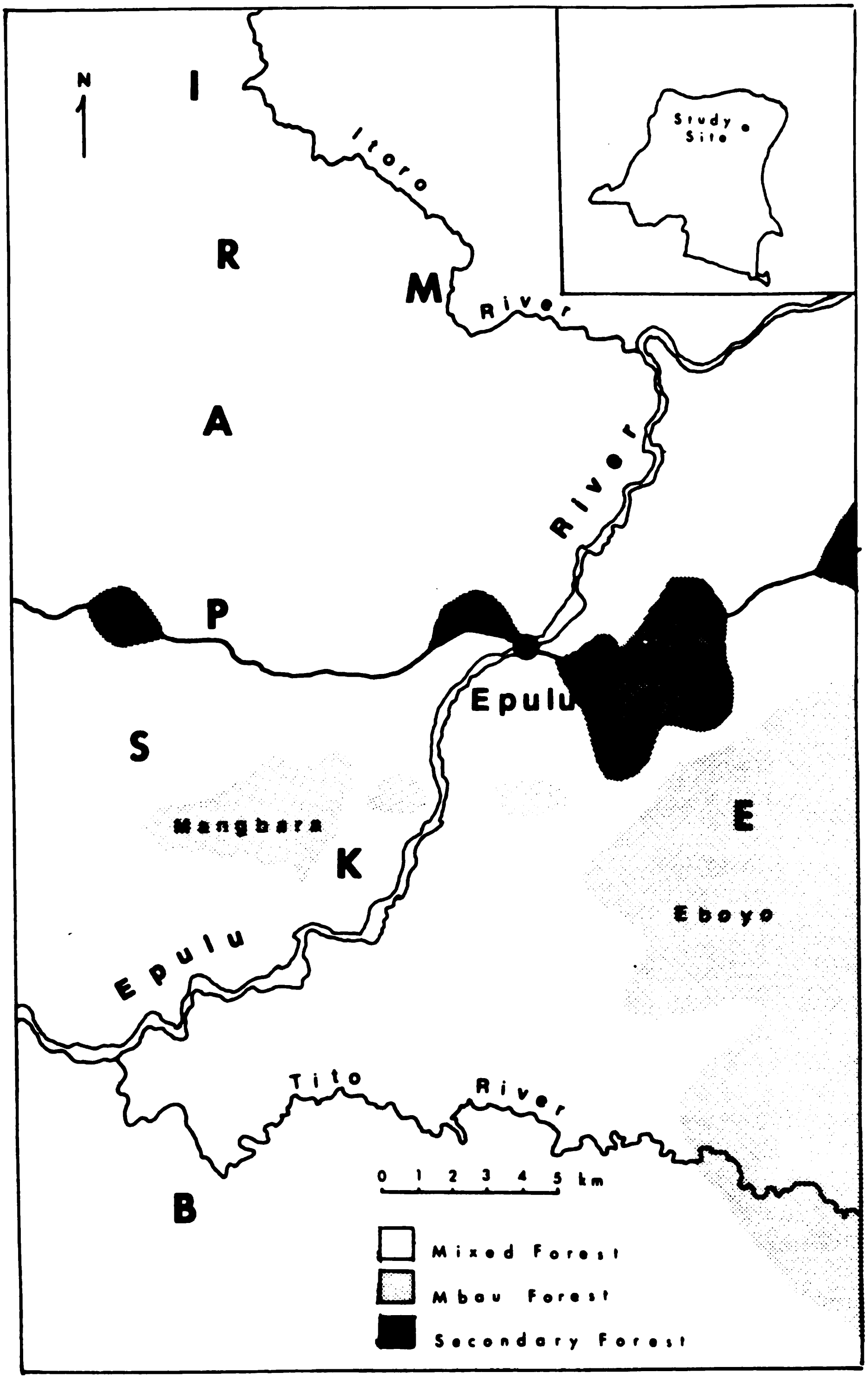
Data for this study were collected between June, 1981 and May, 1983 from an area of approximately 600 km^2 centered on the settlement of Epulu in the central Ituri Forest of Zaire, latitude $1^o25'$ N, longitude $28^o35'$ E, altitude 750 m (Figure 4-1).

Climate

The Ituri Forest lies in the equatorial zone. The climate is characterized by mean daily temperature range of 25^o to 27^o C with a variation of day length of less than one hour over the entire year (Walther 1973).

There are no long-term climatic rainfall data for the Ituri Forest area. Bultot (1971), summarizing records collected between 1939

Figure 4-1. The Epulu study area in the Ituri Forest of Zaire. Large letters locate the sampling sites reported in this study. Areas of each forest type greater than 1 km^2 only are shown. Mangbara and Eboyo are large areas of mbau forest.


N
I
R
A
P
S
K
M
E
B
Itoro
River
River
Epulu
Epulu
Mangbara
Eboyo
Tito
River
Study Site
0 1 2 3 4 5 km
Mixed Forest
Mbau Forest
Secondary Forest

and 1950 from stations in northeastern Zaire, estimated mean annual precipitation between 1700 and 1800 mm, with an annual dry season of less than forty days in the Ituri Forest area. Rainfall recorded for one year (October, 1980 to October, 1981) on the study area totaled 1802 mm.

Modern rainfall records from Angbalare (2 years), and Ngodingodi (3 years) at the northern border of the forest, 150 km NW of the study area (Bailey and Peacock in press), and from Beni (25 years) at the eastern border, 200 km SE of the study area (Bourlière and Verschuren 1960), show that monthly rainfall is locally variable. In general, however, the second half of December, through the month of Februray is the dry season for the region. The remainder of the year is wet, with irregular peaks in precipitation. This period can be divided into an early wet season of March through May, a mid-wet season of June through mid-August, and a late wet season from mid-August to mid-December.

Vegetation and Soils

Unbroken, mature forest on rolling to hilly uplands covered over 80% of the study area. Small areas of secondary forest and scattered swamp and riverine areas comprised the remainder. The upland forests were of two major types, mbau forest and mixed forest. Both forest types covered large areas in the Ituri Forest region and are considered to be climax forests for the area (LeBrun and Gilbert 1954).

In the mbau forest, a single tree species, *Gilbertiodendron* *dewevrei* (Caesalpiniaceae), accounted for 80% to 90% of the canopy. Canopy tree diversity was low, with an average of only 18 tree species greater than 10 cm diameter at breast height (dbh) on half-hectare plots (T. Hart 1985). *G. dewevrei* was well represented at all levels including the understory, which was heavily shaded and generally open. Most mbau forest on the study area were contained in two large stands, Mangbara and Eboyo, totaling together about 60 km^2.

Mixed forest was less uniform than the mbau forest and was significantly more diverse with an average of 65 tree species greater than 10 cm dbh on half-hectare plots (T. Hart 1985). *G. dewevrei* was absent from the mixed forest. The most important species was *Brachystegia laurentii* (Caesalpiniaceae). Other common species included *Cynometra alexandri* (Caesalpiniaceae), *Cleistanthus michelsonii* (Euphorbiaceae) and *Klainedoxa gabonensis* (Irvingiaceae). No species comprised over 35 % of the canopy, except in small localized stands. There were variations associated with shallow soils on slopes but there were no consistent tree associations. The understory was variably open or closed. Tangles of fallen lianes or other thickets occurred.

Both forest types occurred on a diversity of soil types, and were not separated by marked edaphic or topographic boundaries . Soils on the study area ranged from red clays to ochre sands. Soils were acidic and had very low cation exchange capacity (T. Hart 1985). Further description of both climax forest types and secondary forests on the study area can be found in T. Hart (1985).

The Caeslpiniaceous dominants of both forest types, *G.*

dewevrei and *B. laurentii*, flowered and fruited synchronously over large areas on an irregular basis (T. Hart 1985). Seeds of both species are large (mean 2.5 cm and 3.5 g wet weight for *B. laurentii*, 5.5 cm and 30.4 g wet weight for *G. dewevrei*). They are expelled from their pods and fall directly beneath upon ripening. During mast years, *G. dewevrei* produced flowers in March through May and seeds fell in October or November. *Brachystegia laurentii* flowers opened later, in the mid-wet season (May and June), while seed fall began in October and extended through the late wet season and even into the dry.

The Forest Ungulates and Their Status

Of the seven frugivorous ungulates of the central Ituri Forest (Table 4-1), two species, *Hyemoschus aquaticus* and *Cephalophus nigrifrons* are associated with water-side habitats in Gabon (Dubost 1978, Emmons et al. 1983) and were similarly found in areas of larger streams and swampy forest in the Ituri Forest (see below). The remaining species reportedly occupy broadly similar upland forest habitats (Dubost 1979, Emmons et al. 1983).

The upland duikers include one small species, the blue duiker *C. monticola*, 5 kg adult weight; two medium-sized species, *C. leucogaster* and *C. callipygus*, 17 kg and 19 kg adult weight respectively; a large species, *C. dorsalis*, 22 kg adult weight, and a very large species, *C. sylvicultor*, about 70 kg. The three species, *C. leucogaster*, *C. callipygus* and *C. dorsalis* will be referred to collectivley as the upland red duikers.

Table 4-1. The frugivorous ungulate fauna of the Ituri Forest, Zaire.[a]

Species	Vernacular	Adult weight (kg) [b] Mean	S.D.	n	Habitat	Activity pattern
Cephalophus monticola	blue duiker	4.7	0.6	59	upland forest	diurnal
Hyemoschus aquaticus	chevrotain	11.2	1.2	17	streams	nocturnal
Cephalophus nigrifrons	black-fronted d.	13.9	1.3	8	swamp forest	diurnal
Cephalophus leucogaster	Gabon duiker	16.7	1.0	19	upland forest	diurnal
Cephalophus callipygus	Peter's duiker	17.7	1.8	24	upland forest	diurnal
Cephalophus dorsalis	bay duiker	22.0	1.9	11	upland forest	nocturnal
Cephalophus sylvicultor	yellow-back d.	68.0			upland forest	diurnal & nocturnal

[a] Habitat and activity patterns from Emmons et al. (1983).

[b] Body weight is average of both sexes, the standard deviation is pooled from both sexes with total sample size shown by n. No adult body weight data for *C. sylvicultor* from study area. Figure shown is from Emmons et al. (1983) for this species in Gabon.

The community includes both distinctly nocturnal and diurnal species. One species, *C. sylvicultor*, is reportedly active both day and night (Emmons et al. 1983). Details on the biology of most species remain little known (Kingdon 1982). Accounts of the behavior and ecology of *C. monticola*, *C. dorsalis* and *H. aquaticus* are available in Dubost (1975, 1978, 1980 and 1983).

The major observed impacts on local duiker and chevrotain populations were hunting by nomadic Mbuti hunter-gatherers and conversion of forest to farmed bush and secondary forest by shifting cultivators. The latter was limited to a small area near the settlement. Although hunters ranged widely, remote forest areas were only infrequently hunted. Based on hunting returns and pellet counts, duiker populations may be higher in these areas than in continuously hunted areas near town (Koster and Hart in prep.). All data for this study were collected from more remote locations.

METHODS

Data on food availability, animal distributions and samples of animal gut contents for dietary analyses were collected by accompanying local hunters into the forest on drive hunts using dogs and nets. Working with the hunters allowed access to large areas of forest and samples of animals. The net hunt technique involved 10 to 30 hunters encircling areas of forest from 4 to 12 ha (mean 6 ha) with nets about 1.2 m in height and driving any animals within the circle into the nets. Nets were then coiled and quickly moved to a new site, usually less than 1 km distant. Five to seven drives were generally conducted in the same vicinity of forest in the course of one day.

Field data and gut contents were collected at nine sampling sites throughout the study area (Figure 4-1). These sites were visited during 13 sampling periods between June, 1981 and May, 1983. Each sampling period encompassed 3 to 9 daily hunts and 17 to 44 drives (Appendix 4-A).

Body weight and Cranial Morphology

Animals caught on net drives were weighed entire to the nearest 0.1 kg. Age (based on mandibular molar erruption) and reproductive condition were assessed. Fetal weights were subtracted from the body weight of gravid females.

Skulls of one to four individuals of six of seven species of frugivorous ungulates were collected from obliging hunters. Length of cranium was measured ventrally along the surface of the skull from the anterior edge of the occipital condyles to the tips of the premaxillary bones. Width of cranium was measured transversely on the ventral surface of the skull across the widest point of the zygomatic arches. Length of the mouth was measured longitudinally along the palatine and maxillary sutures from a transverse line connecting the posterior edge of the thrid molar, anteriorly to the tips of the premaxillary bones. Mouth width was measured transversely across the outer cusps of the tooth row at its widest point, usually the second molar.

Food Availability

The fallen fruits, seeds and flowers eaten by duikers and the chevrotain generally occurred in discrete patches on the forest floor, generally beneath parent trees. These food patches had well-defined boundaries and were readily identifiable against a background in which the item was absent.

The size, abundance and species composition of food patches were measured along transects 3 m wide which followed the perimeter of the net drive. Each time an item was encountered on the transect, an attempt was made to record the following basic data:

1. Items were identified to species. Unknowns were given a number and specimens were dried.

2. Fruits and seed were classified as ripe or unripe and the relative proportions of fruit flesh and seed were estimated. Note was made whether the patch occurred under a parent tree's crown, whether the patch contained items which had been bitten and dropped by arboreal vertebrates (mainly squirrels and primates) and whether aborted unripe fruits had insect or other damage.

3. Fruits, seeds and flowers were classified by the lengths of their longest axis into five size classes (Chapter 2): Class 1, 0.0 - 0.5 cm; Class 2, 0.5 - 1.0 cm; Class 3, 1.0 - 2.5 cm; Class 4, 2.5 - 5.0 cm; and Class 5, 5.0 - 10.0 cm. When a patch contained items of more than one size class, the proportion in each class was estimated visually.

4. Individual specimens of 40 species of commonly-encountered fruits, seeds and flowers were weighed to nearest gram (wet weight).

Weights of other species were estimated by visual comparison to known species of similar size.

5. The number of items on the ground along the transect was counted (or estimated when especially numerous) and expressed by square meter density.

6. Total patch area both on and off the transect was estimated by pacing the diameter or length of the patch and converting to areal measure by classifying patch shape as circular or rectangular.

This procedure was modified in specific instances. Where only an individual food item was found, it was classified as an isolate and arbitrarily assigned a patch area of 1 m^2.

Discrete patches could not be distinguished for flowers and released seeds of the Caesalpiniaceous dominants, *B. laurentii* and *G. dewevrei* during mast years. The occurrence and densities of these items were recorded at 30 pace (44 m) intervals along the transect. Each time seeds or flowers were encountered, the occurrence was equated with a single tree crown and the patch area was arbitraily assigned a value of 150 m^2, corresponding with crown dimensions of these species (T. Hart, 1985).

Partially-eaten fruits dropped by primates were often scattered at some distance from the parent tree. Identifications of patch boundaries were arbitrary in these cases. Discrete groups were counted as different patches, even though they may have been produced by the same tree or liane.

For each food patch, the weight (W) in grams was calculated as:

$$W = U \times D \times A$$

where

U = item unit weight (g)

D = average density (items/m^2) on transect

A = patch area (m^2).

Food patches were grouped into 4 size classes based on estimates of W: very small patches $W \leq 10$ g; small patches, W = 10 - 100 g; large patches, W = 101-1000 g; very large patches, $W > 1000$ g.

Weights of patches recorded on individual transects were summed for each sampling period. Patch species diversity for a sampling period was computed by the Shannon Index (H') (Brower and Zar 1977).

Note was kept of leafing phenology of the more common tree species (J. and T. Hart, unpublished data). The abundance and weights of patches of terrestrial fungi were noted qualitatively.

Diet

On net hunts, ruminoreticular contents (hereafter referred to as rumen contents) were removed from a sample of animals at the site of capture and stored in plastic bags. Rumen contents for animals dead less than four hours were washed through a 5 mm mesh screen and the larger food fragments retained in 10 % formalin for analysis. Duikers tend to swallow fruits and seeds whole and then to regurgitate and masticate (ruminate) them at a later time. Large fragments separated in the rumen contents evidently comprised the duikers' last meal. This fraction could be easily identified and its analysis was probably less biased by differential digestion of readily-fermented portions than smaller fractions (Dirschl 1962, Puglisi et al. 1978). Rumen contents from unweaned animals and contents in which the 5 mm fraction weighed less than 10 g and comprised less than 10% of the total contents were not included in the analyses.

Rumen contents were sorted by food type. Fruits, seeds and flowers were identified to species. Unknown items were assigned a number. Examples were dried and mounted on cards for later comparisons. For each species found in the gut, the total weight and item size class were determined. Patch weights of food species in the rumen were estimated when possible based on values obtained for the species from food transects or from visits made to fruit-bearing trees. It was found that within a given sampling period many species exhibited a characteristic patch weight, at least wihin the broad limits of the classes used in this study.

The contribution of each food species or food class to the total diet was evaluated by a percentage utility index (I_U) defined for each food *i* as:

$$I_U(i) = (p_i \times q_i) \times 100\%$$

where p_i equals the proportion of total rumens in the sample containing food item *i* and q_i equals the average proportional contribution of *i* to the total weight of contents in rumens in which it was recorded. Values for I_U ranged from zero in cases in which no rumen contained a given item to 100.0% where a single species comprised the total contents of all rumens.

Owaga (1978) has shown that the proportion of foliage measured in rumen contents may differ according to the screen size used to wash the sample. In order to test for this effect and to examine the frequency of smaller items in the gut such as insect parts, a fixed measured subsample of the total rumen contents was washed through a 2 mm mesh screen and the proportions of fragments by food type (fruit/seed, fungi, foliage, insect) were determined.

Diet overlap was measured by by Morisita's (I_M) index (Morisita 1959) and considered in light of discussions of Horn (1966) and Hurlburt (1978).

Nutritional Quality

Nutritional composition was determined for samples of 19 ripe fruits, 21 unripe fruits, four seeds and five flowers. These items included commonly-available potential foods collected from transects between October, 1982 and May, 1983.

For each food item, the nutritionally significant portion (Herrera 1981, see also Chapter 3), termed edible dry matter yield (Y), was determined as:

$$Y = (T - S) \times DM$$

where T is the total wet weight of the item (g), S is the weight of indigestible, regurgitated seeds (g) (if they occurred) and DM equals the dry weight of the assimilable portion determined by dessicating the sample at 100^2 C for 24 hours. Assays for condensed tannins (CT), acid detergent fiber (ADF) and crude protein (N) content were conducted for each sample by Dr. P.G. Waterman, following standard procedures described in Horowitz (1970), Goering and Van Soest (1970) and Oates et al. (1980). Levels of each component were expressed as mg/g fresh weight of the food.

An estimate of food nutritional quality (Y_Q), termed the adjusted dry matter yield, was calculated as:

$$Y_Q = Y \times [N / (ADF + CT)].$$

Y_Q is essentially an estimate of the edible dry matter portion of a food weighted by its relative levels of nutrient and refractory or digestion-inhibiting compounds. Y_Q was found to be positively correlated with food preference for two species of duiker in feeding experiments (Chapter 3).

The average nutritional value of all available food ($Y_{Q(T)}$) during a sample period was determined as:

$$Y_{Q(T)} = \sum Y_Q(i) \times p(i),$$

where $Y_Q(i)$ equals adjusted dry matter yield for food species i and $p(i)$ equals the proportion of total food biomass contributed by i as recorded on transects for the period. $Y_{Q(T)}$ values were calculated for five sample periods between July, 1982 and May, 1983. These values accounted for 81% to 98% of total foods recorded on transects for each period.

Diet Selectivity

Various indices have been proposed to measure an animal's differential utilization of foods in relation to their availability (Ivlev 1961, Manley et al. 1972, Petrides 1975, Cock 1978, Chesson 1983). Their use is limited, however, in tropical forests where high species diversity and scattered foods inhibit the accurate measurement of availability.

Johnson (1980) has proposed a rank index of the selective use of a resource which is calculated by subtracting a rank measure of the use of the resource from a rank measure of its availability. Values greater than zero indicate positive selection, those differences less than zero indicate avoidance. Resources for which rank availability and rank use are equal are utilized in proportion to their abundance and, by definition, are not used selectively. The Johnson index is relatively robust to the problem of irregular availability. It has the additional advantage that various measures of availability and utilization can be used, so long as they can be ranked.

The Johnson index was used in this study. The availability of a given food was calculated as its percentage contribution to the total weight of patches recorded on transects. Utilization of a given food was measured by it percentage occurrence (utility index value) from gut contents. Four ranked classes of use and availability were defined as:

Rank 1 = < 1.0 %

Rank 2 = 1.0 % to 5.0 %

Rank 3 = 5.1 % to 25.0 %

Rank 4 = > 25.0 %

Strong positive selection was defined as values of rank use minus rank availability of +3 and +2. Strong avoidance was defined similarly by values of -3 and -2. Weak selection was exhibited by values of +1 and -1. No selection was exhibited when rank use minus rank availability equaled zero.

Animal Abundance and Distribution

Total area of each drive hunt was estimated by assuming circular placement of the nets and pacing their perimeter to determine drive circumference then calculating drive area. Forest types of net drive areas were quantified by classifying forest type as mixed (including old secondary), mbau or swamp/riverine at 30 pace (44 m) intervals around the perimeter of the drive area. The identity of each animal captured on drives was recorded. The identities of animals flushed but not captured were ascertained by questioning hunters. Two independent confirmations of each sighting were sought whenever possible. Indices of animal density were calculated as the number of animals flushed per square kilometer of drive area summed over all drives at a sampling site or within a forest type.

Reliability of net hunt results was verified in two ways. Indices of animal abundance from hunts were compared with densities derived from pellet group and track counts conducted in the same areas (Koster and Hart in prep.). Relative frequency of specific microhabitats sampled while accompanying net hunts was compared with similar counts made from randomly placed transects in the same area (J.

Hart and T. Hart,unpubl. obs.). These studies indicated that net hunt results were probably not strongly biased with regard to animal densities and specific habitat features.

It was noted, however, that hunters tended to prefer mixed forest to mbau and to avoid large swampy areas. These preferences did not create a sampling bias for ths study, however, since large swampy areas were uncommon, and the results of drives from mixed and mbau forest were analyzed separately.

Statistical Tests

Throughout this study standard parametric statistical techniques (Steel and Torrie 1982) were employed for all analyses where the required assumptions were met. Ranked data were analyzed by techniques described in Siegel (1956). Specific tests are identified with each analysis.

RESULTS

Cranial Morphology

Skulls of duikers are similar in general form. Crania of *C. nigrifrons* and *C. callipygus* can be differentiated only by the form of the horn sheath. The crania of *C. dorsalis* and *C. leucogaster* are distinctive in being more rounded, with foreshortened muzzles. The skull of *C. dorsalis* is especially robust with relatively large attachments for masticatory muscles, wider transverse of the mandibular condyle, and correspondingly heavier molars (Kingdon, 1982: 315-316). The crania of *C. monticola, C. nigrifrons, C. callipygus* and the chevrotain in contrast, are more finely structured with elongated muzzles and less massive teeth. The wide crania of *C. leucogaster* and *C. dorsalis* are associated with a broadened gapes and higher ratios of mouth width to length than in the other species (Figure 4-2).

Food Availability

The diversity and abundance of fallen fruits, seeds and flowers recorded along the transects in mixed forest varied seasonally over the two year study period. Abundance was greatest during the mid to late wet seasons. Peaks of diversity occurred during the mid wet seasons. During dry seasons and early wet seasons by comparison total fruit abundance and diversity were reduced (Figure 4-3). Many, but not all trees in the Ituri Forest followed the same general seasonal cycle. Flowering and fruit set occurred in the early wet season followed by fruit ripening and seed fall through the late wet season (J. and T. Hart, unpubl. obs.). This cycle is comparable to that reported in other tropical forests (Frankie et al., 1974, Terborgh 1983) including those of Zaire (Diterlein 1978).

On average, fruit comprised most of the food biomass and the majority of the patches recorded on the transects (Table 4-2). Ripe fruits dominated the transect finds, averaging 55% of the total weight and 32% of all patches. Unripe fruits averaged 21% of total weight and 36% of all patches. Fallen flowers and seeds comprised smaller percentages of the standing crop recorded.

Figure 4-2. Cranium size and mouth shape (width/length) in duikers and chevrotain. Values shown are mean and standard error. Number of skulls measured indicated below each species. Species abbreviations: C m, *Cephalophus monticola*; H a, *Hyemoschus aquaticus*; C n, *C. nigrifrons*; C l, *C. leucogaster*; C c *C. callipygus*; C d, *C. dorsalis*.

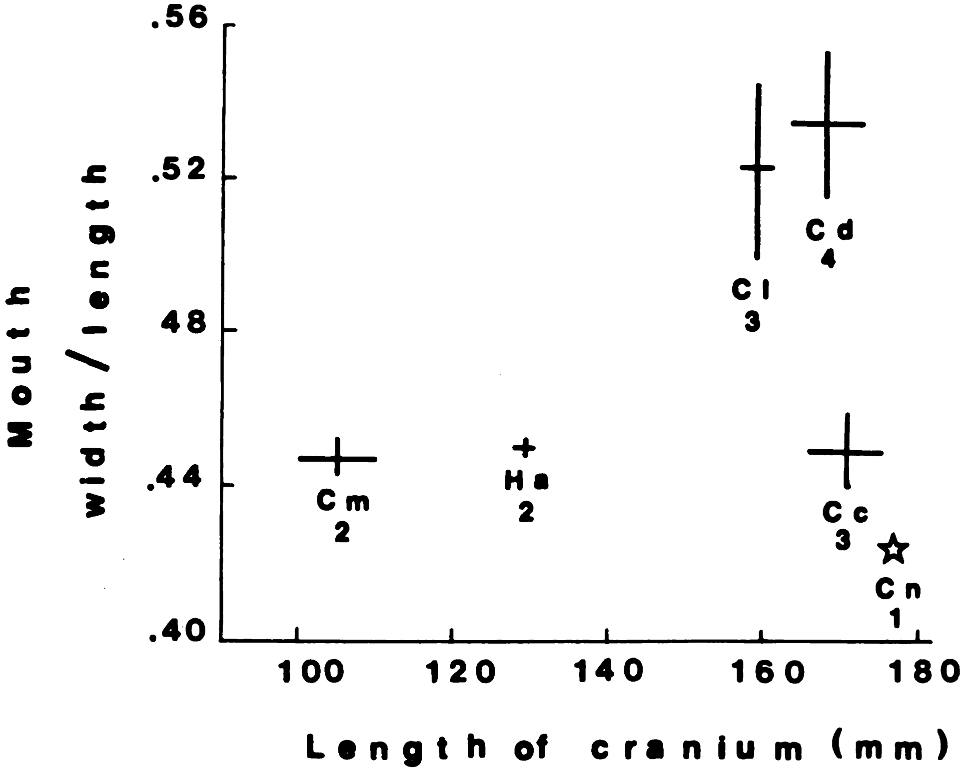
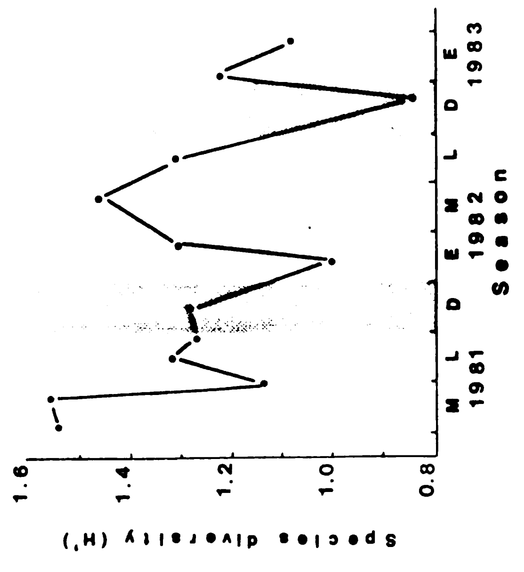
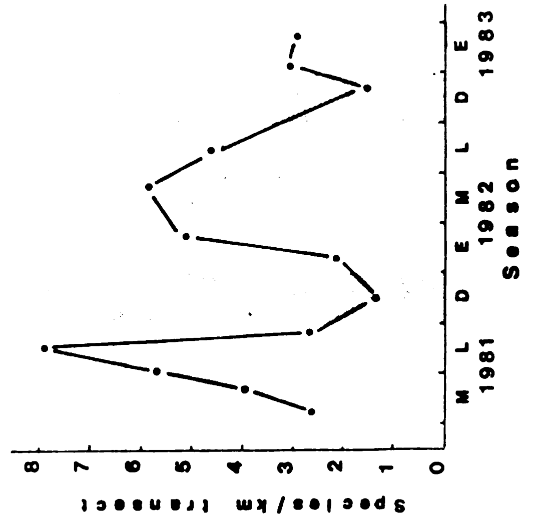

Mouth width/length
.56
.52
.48
.44
.40
100
120
140
160
180
Length of cranium (mm)
Cd
4
Cl
3
Cm
2
Ha
2
Cc
3
Cn
1

Figure 4-3. Diversity (Shannon index and number of species/km of transect) and collective abundance (kg/km of transect) of fruits, seeds and flowers on the forest floor. Ituri Forest, Zaire, July 1981 to May, 1983.


Species diversity (H')
1.6
1.4
1.2
1.0
0.8
M L D E M L D E
1981 1982 1983
Season


Species/km transect
8
7
6
5
4
3
2
1
0
M L D E M L D E
1981 1982 1983
Season

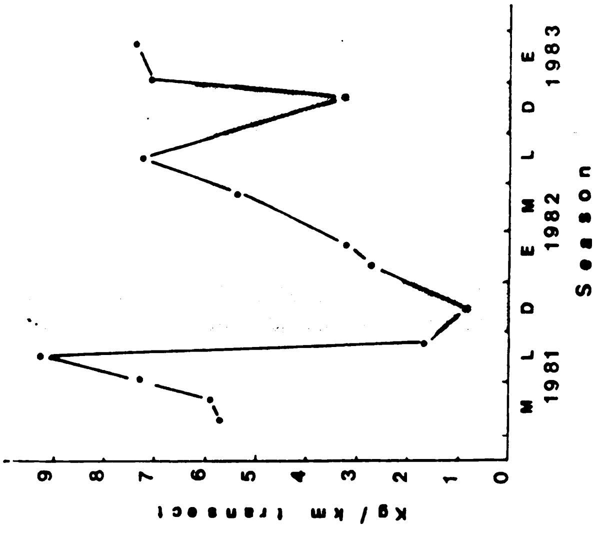

Kg/ km transect
9
8
7
6
5
4
3
2
1
0
M L D E M L D E
1981 1982 1983
Season

Table 4-2. Occurrence of fallen fruits, seeds and flowers on ground transects in mixed forest. Ituri Forest, Zaire, July, 1981 to May, 1983. Values are means (and standard deviations).

Season	Sample Periods	Percentages of transect weight				Percentages of patches			
		Ripe Fruit	Unripe Fruit	Seed	Flower	Ripe Fruit	Unripe Fruit	Seed	Flower
Dry	2	54.1 (50.0)	12.3 (3.2)	33.8 (46.9)	0.0 (0.0)	34.2 (30.7)	21.3 (8.0)	44.8 (38.4)	0.0 (0.0)
Early Wet	4	56.0 (26.3)	19.3 (16.8)	7.0 (8.1)	17.8 (15.4)	18.8 (5.9)	45.8 (9.8)	21.7 (22.3)	13.7 (12.9)
Mid-Wet	2	46.8 (31.7)	29.2 (11.4)	10.1 (8.6)	14.0 (11.7)	42.2 (2.1)	41.8 (8.6)	9.3 (4.0)	6.8 (6.9)
Late Wet	4	62.3 (27.0)	21.7 (24.1)	14.6 (20.2)	1.5 (3.0)	32.1 (9.5)	36.7 (10.0)	25.3 (11.8)	6.0 (12.0)
Average		54.8 (6.4)	20.6 (7.0)	16.4 (12.0)	8.3 (8.9)	31.8 (9.7)	36.4 (10.7)	25.3 (14.7)	6.6 (5.6)

These average trends concealed marked seasonal variability in the contribution of different food types to total food availability. High standard deviations associated with the percentage contributions of most food types, even within a given season (Table 4-2), reflect marked differences from one year to another. Much of this variation can be accounted for by the periodic occurrences of a few species. When these became available they comprised a large percentage of the the transect weight and in some cases the majority of food patches. Notable among these were the flowers and seeds of the synchronously fruiting Caesalpiniaceous dominants, *Brachystegia laurentii* in mixed forest and *Gilbertiodendron dewevrei* in mbau forest (see discussion below). Other common species which fruited gregariously on an irregular basis were several species of *Landolphia* which were available during the late wet season, 1982 and *Pancovia harmsiana* which fruited in 1982 but not 1981 or 1983. The ripe and unripe fruits of *Klainedoxa gabonensis* and *Cleistanthus michelsonii*, co-dominants in mixed forest (T. Hart 1985) were also periodically abundantly available.

Between 29% and 59% of all food patches recorded on transects contained items that had been bitten or showed other signs of having been handled and dropped by arboreal mammals. The damaged items included unripe fruits, ripe fruit parts and seeds, unripe pods and seeds of leguminous trees, partially eaten inflorescenses, and some foliage. Primates and large squirrels notably *Protxerus stangerii*, were responsible for most of this food rain from the canopy. Most of the unripe fruits which were dropped by primates were bitten once and rejected uneaten. Squirrel drops included the pulp and exocarp of full-sized, but unripe fruits, from which the seeds had been extracted. Ripe fruit drops mainly consisted of portions inedible to primates, such as rinds or capsules, discarded after the contents had been eaten.

Spontaneously-aborted fruits comprised a second major source of unripe fruit on the ground. Fruit abortion was especially prominent in the Irvigiaceae and Euphorbiaceae, but occurred in other families as well. Parent trees abort fruits for a variety of reasons (Stephensen 1981). In the present study, aborted fruits rarely showed evidence of insect damage. Some individual trees evidently aborted fruit over extended periods, as fruits under many crowns ranged in size up to more than half mature size.

On average, 52% of food patches recorded on transects over the year were of the smaller weight classes ($W < 100$ g). These smaller food patches, however, represented only 8% of the total weight of available food (Table 4-3). Very large food patches ($W > 1000$ g) were rare and widely dispersed. These largest patches, however, accounted for almost 58% of the total weight recorded.

The distribution of available food item sizes paralled that of food patch weights (Table 4-4). Small fruits, seeds and flowers (size classes 1 - 3) were numerically the most abundant, averaging 63% of all patches. Larger fruits (size classes 4 and 5), however, accounted for over 70% of the available weight.

On average, the size of an item and the weight class (W) in which it was recoreded were positively correlated ($r_S = 0.90$, $p <$

Table 4-3. Food patch weight (W) class of fruits, seeds and flowers collectively, recorded on transects in the Ituri Forest, Zaire, July 1981 to May, 1983. Values are means (and standard deviations). [a]

Season	Sample Periods	Percentages of transect weight				Percentages of patches			
		1	2	3	4	1	2	3	4
Dry	2	0.5	1.8	44.8	53.0	23.6	16.4	50.3	10.1
		(0.5)	(0.0)	(36.0)	(35.5)	(22.3)	(7.8)	(30.6)	(0.9)
Early Wet	4	0.5	5.2	32.2	62.2	25.3	28.7	33.3	12.4
		(0.4)	(5.6)	(34.1)	(31.9)	(14.3)	(26.1)	(25.0)	(15.8)
Mid-Wet	2	1.7	18.0	32.6	47.8	14.4	42.4	37.9	5.5
		(1.8)	(17.7)	(13.0)	(2.8)	(8.1)	(6.9)	(15.1)	(0.1)
Late Wet	4	0.4	5.1	27.5	67.3	16.0	40.9	30.4	12.8
		(0.2)	(4.8)	(19.6)	(19.3)	(16.9)	(19.2)	(25.2)	(6.4)
Average		0.8	7.5	34.3	57.6	19.8	32.1	38.0	10.2
		(0.6)	(7.2)	(7.4)	(8.8)	(5.4)	(12.1)	(8.8)	(3.4)

[a] Weight classes: 1, W < 10g; 2, W = 10g to 100g; 3, W = 101g to 1000g; 4, W > 1000g.

Table 4-4. Size classes of fruits, seeds and flowers collectively, recorded on transects in the Ituri Forest, Zaire, July 1981 to May, 1983. Values are means (and standard deviations) *.

		Percentages of transect weight					Percentages of patches				
Season	Sample Periods	1	2	3	4	5	1	2	3	4	5
Dry	2	9.8 (13.8)	0.6 (0.8)	5.8 (2.8)	45.9 (49.8)	34.3 (37.6)	14.8 (20.9)	12.6 (3.2)	36.8 (11.4)	17.2 (4.7)	17.0 (15.0)
Early Wet	4	2.5 (4.9)	15.6 (15.6)	20.5 (26.5)	15.5 (8.2)	46.2 (27.1)	3.6 (5.6)	22.6 (7.8)	44.9 (8.1)	34.1 (13.0)	5.5 (2.6)
Mid-Wet	1	8.4	19.9	6.4	21.0	44.2	3.3	12.5	32.6	24.5	27.2
Late Wet	4	1.2 (1.7)	3.4 (4.7)	21.6 (1.8)	52.1 (6.6)	22.0 (1.3)	1.5 (2.1)	15.7 (22.1)	37.0 (6.9)	31.7 (23.7)	14.0 (7.0)
Average		5.5 (4.3)	9.8 (9.3)	13.6 (8.6)	33.6 (18.1)	36.7 (11.1)	5.8 (6.4)	15.9 (4.7)	37.8 (5.1)	26.9 (7.6)	15.9 (9.0)

* Size class limits : 1, < 0.5; 2, 0.5 - 1.0; 3, 1.1 - 2.5; 4, 2.6 - 5.0; 5, 5.1 - 10.0 centimeters.

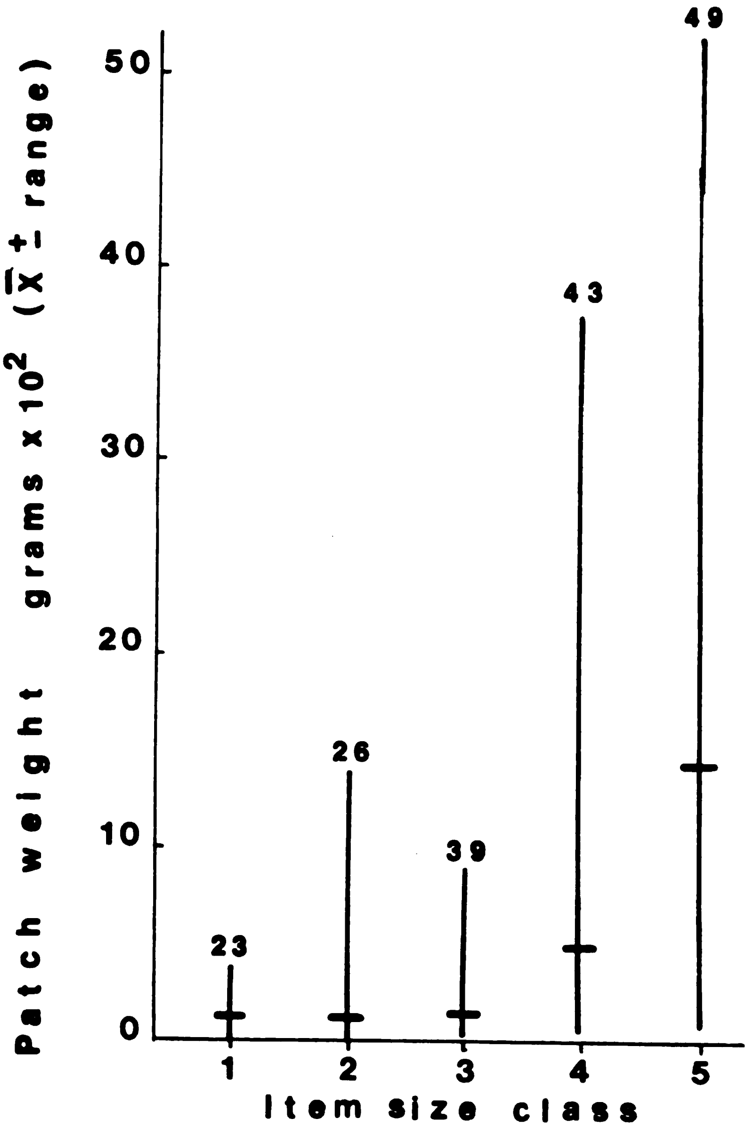
.10, n = 5). This relationship was variable, however, especially for larger items. In a survey of 174 recorded items (Figure 4-4), patch weights of most smaller-size classes were low, but ranged over 1000 g in some instances. For example, the bracts and unopened flowers of Bracystegia laurentii and *Gilbertiodendron dewevrei* (size classes 1 and 2) and the aborted unripe fruits of *Klainedoxa gabonensis, Irvingia grandifolia* and *I. wombolu* (size classes 2 -3) characteristically occurred in large, dense patches.

The relationship between the areal extent of a patch and its total biomass was less variable. Isolated items ranged in weight class depending upon the weight of the fruit. For example, certain of the larger unripe fruits (*Landolphia spp, Cola lateritia*) sometimes occurred as isolated items in small scattered patches, especially when they had been carried some distance and dropped by primates.

With the possible exception of primate drops and mast seed fall of the Caesalpiniaceous dominants, where contiguous crowns produce simultaneously, food patch areas were discrete and associated with the crown of a single tree. The largest patch area recorded was under 300 m^2, and most patches were less than 150 m^2. No patch of large area (> 90 m^2) recorded during the study had a patch weight of under 100 g.

In characterizing food patches, patch weight (W) provides a measure of the total food biomass available to be harvested. Patches of low weight (W < 100 g) contained small, scattered items of low unit weight or single isolated items of larger weight. Patches of larger total biomass contained larger itmes and/or smaller items in dense

Figure 4-4. Relationship between item size class and patch weight (W) for 174 fruits, flowers and seeds collected in the Ituri Forest, Zaire, July, 1981 to May, 1983.


Patch weight grams x 10^2 ($\bar{X}$ ± range)
0
10
20
30
40
50
23
26
39
43
49
1
2
3
4
5
Item size class

patches.

General Diet Composition

Dietary analyses were based on rumen contents from 175 animals collected during nine sampling periods from December, 1981 through May, 1983 (Table 4-5) Additional rumens collected between June and December, 1981 were analyzed for species poorly represented in this sample including *H. aquaticus* (8 rumens), *C. nigrifrons* (5 rumens) and *C. sylvicultor* (3 rumens). This brought the total collection to 191 rumens. Four duikers, including a small species, *C. monticola*, two medium-sized species, *C. leucogaster* and *C. callipygus* and a large species, *C. dorsalis* were sampled during every season and most sampling periods.

Between 240 and 250 species of fruits, flowers and seeds were recorded from the rumens of all seven ungulate species over the course of this study. The number of fruit, seed and flower species recorded per rumen varied from zero in rumens containing only foliage and/or fungi to over 23. In the majority of samples, however, the two most important food species accounted for 67% to 100% of the total sample weight.

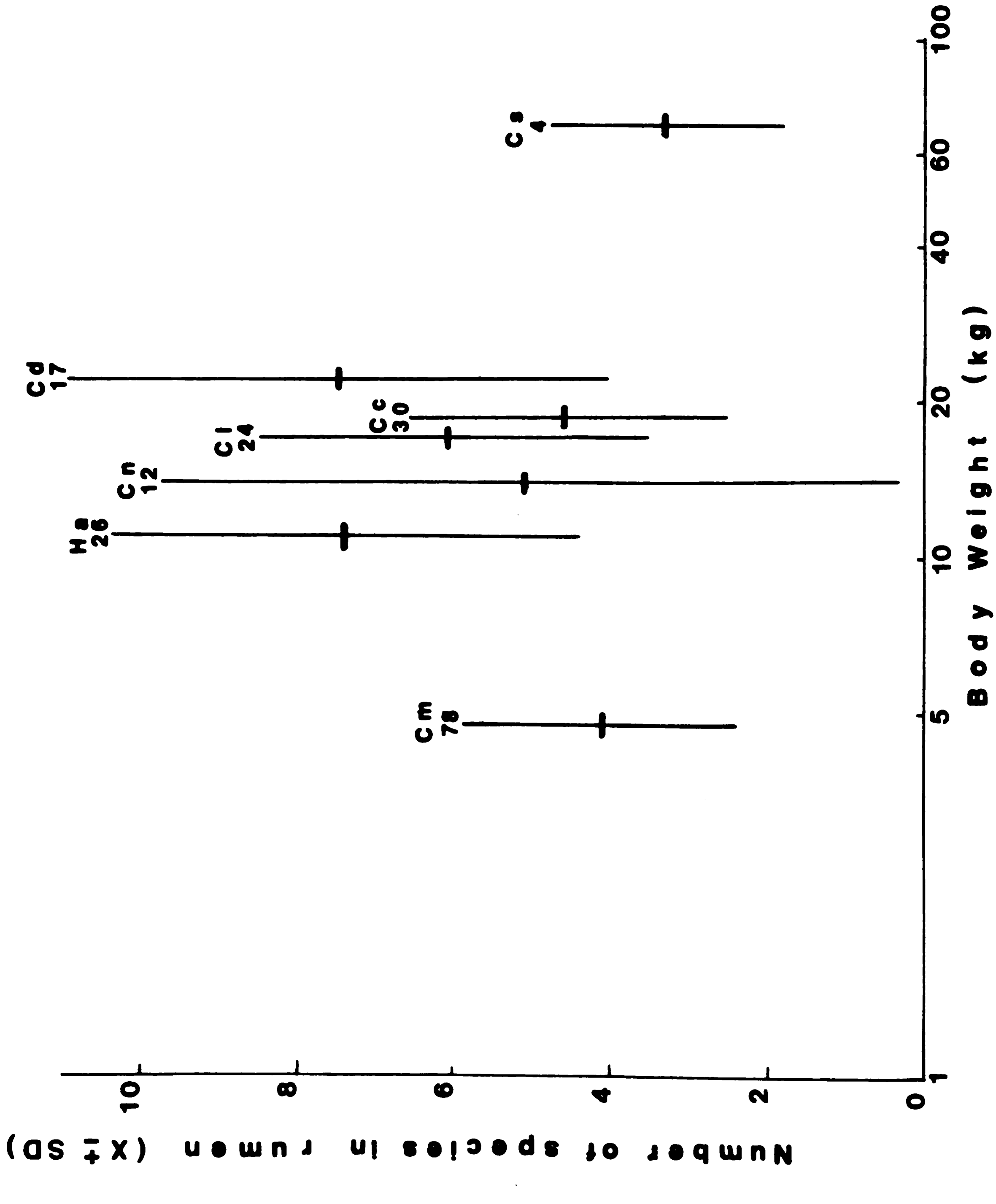
Averaged over all rumens examined during the entire study, there were no significant differences in dietary diversity (number of food species per rumen) between any of the seven ungulate species (Figure 4-5). Average dietary diversity was not correlated with body size ($r_S = 0.07$, $p > .05$, $n = 7$). The largest and smallest species exhibited the lowest average food diversity in the rumen,

Table 4-5. Rumen contents of frugivorous ungulates analyzed seasonally between December, 1981 and May, 1983. Ituri Forest, Zaire. [a]

Season	Location	*Cephalophus monticola*	*Hyemoschus aquaticus*	*Cephalophus nigrifrons*	*Cephalophus leucogaster*	*Cephalophus callipygus*	*Cephalophus dorsalis*	*Cephalophus sylvicultor*
Late Wet 81	M	10	3	4	4	4	2	1
Dry 82	B	13	3	0	4	12	3	0
Early Wet 82	A	8	0	1	4	2	1	0
Early Wet 82	K	9	3	0	2	0	0	0
Mid Wet 82	P	8	0	0	5	1	3	0
Late Wet 82	B	12	2	0	1	4	1	0
Dry 83	K	6	3	1	0	0	0	0
Dry/Early Wet 83	B	7	0	0	4	3	3	0
Early Wet 83	I	5	4	1	2	4	4	0
Totals		78	14	7	24	30	17	1

[a] Additional rumen contents sampled between June and December, 1981: *H. aquaticus* (8), *C. nigrifrons* (5), *C. sylvicultor* (3).

Figure 4-5. Numbers of fruits, seeds and flowers in rumens of six species of duiker and the chevrotain in the Ituri Forest, Zaire. Values shown are means and standard deviations averaged over 13 sampling periods, December, 1981 to May, 1983. Abbreviations: C m, *Cephalophus monticola*; H a, *Hyemoschus aquaticus*; C n, *C. nigrifrons;* *C l, C. leucogaster;* *C c, C. callipygus*; C d, *C. dorsalis*; C s, *C. sylvicultor*. Numbers of rumens sampled indicated below each species' abbreviation.


Number of species in rumen (X ± SD)
0
2
4
6
8
10
Body Weight (kg)
1
5
10
20
40
60
100
Cm
78
Ha
26
Cn
12
Cl
24
Cc
30
Cd
17
Cs
4

suggestive that the range of foods these species utilized was perhaps limited. Highest average diversity was found in the two nocturnal species, *H. aquaticus* (mean 7.4 species per rumen) and *C. dorsalis* (mean 7.5 species per rumen). The riparian species, *H. aquaticus* and especially *C. nigrifrons* showed the greatest variability in dietary diversity, indicating possible roles for activity pattern and habitat differences in determining diet. The two diurnal upland duikers of similar size, *C. leucogaster* (6.1 species per rumen) and *C. callipygus* (4.6 species per rumen) differed in average dietary diversity providing evidence that these otherwise similar species differed in foraging patterns.

Fruits and seeds comprised the bulk of of the diets of duikers and chevrotain throughout the year. Flowers and fungi comprised a variable small percentage of the total. Foliage was eaten in variable amounts but on average was low and sometimes absent (Table 4-6). Several authors (Gautier-Hion et al. 1980, Dubost 1984) have suggested that there is a relationship between body-size and insectivory in forest ungulates. Insect remains (mainly large ants) occurred in 62% of *C. monticola* rumens. They accounted for < 1% of the 2 mm sample in all but a few cases. In no sample did insect remains surpass 3.5%. Insect remains were only found in 20% of the rumens of larger animals, and then mostly in trace amounts. While some of these insects may have been ingested accidentally, this was probably not the case with all. In particular, ants killed by a fungal disease (and sometimes sprouting small gilled mushrooms) were ingested. These ants were found dead as solitary individuals in a characteristic pose, grasping low vegetation

Table 4-6. Percentage composition of large (≥ 5 mm) particles screened from rumen contents of adult and weaned-juvenile duikers and chevrotain. Ituri Forest, Zaire, 1981 to 1983. Values are grams wet weight, giving means, standard deviations (in parentheses) and ranges.

Species	Ripe fruit	Unripe fruit	Seed	Flowers	Fungi	Foliage
C. monticola n = 78	6.6 (7.8) 0 - 20	33.6 (32.0) 3 - 92	40.9 (31.9) 4 - 3	4.5 (5.5) 0 - 16	5.8 (0.4) 0 - 32	8.1 (12.6) 0 - 39
H. aquaticus n = 26	9.2 (4.7) 4 - 15	32.7 (28.0) 0 - 85	38.0 (32.2) 0 - 84	1.7 (3.4) 0 - 10	3.2 (6.2) 0 - 17	11.4 (16.2) 0 - 37
C. nigrifrons n = 12	10.7 (15.4) 0 - 46	24.0 (28.1) 0 - 73	46.4 (40.0) 0 - 100	0.3 (0.7) 0 - 2	0.4 (1.1) 0 - 3	29.0 (44.2) 0 - 100
C. leucogaster n = 24	18.1 (13.5) 3 - 42	46.2 (19.9) 1 - 72	21.1 (30.6) 0 - 80	7.7 (13.3) 0 - 38	0.7 (1.3) 0 - 4	6.2 (8.5) 0 - 24
C. callipygus n = 30	24.5 (12.5) 12 - 50	39.0 (21.6) 11 - 67	24.7 (29.5) 0 - 62	6.0 (11.5) 0 - 32	3.8 (7.2) 0 - 18	5.7 (6.2) 0 - 14
C. dorsalis n = 17	31.6 (21.9) 14 - 61	44.4 (25.3) 17 - 83	17.0 (29.0) 0 - 79	3.1 (3.5) 0 - 9	1.0 (2.3) 0 - 6	3.5 (5.5) 1 - 15
C. sylvicultor n = 4	96.7 (5.5) 90 - 100	4.3 (5.1) 0 - 10	0.0 (0.0) 0	0.0 (0.0) 0	0.0 (0.0) 0	3.0 (5.5) 0 - 6

in the understory. This is similar to the postures assumed by flies killed by *Entomophthora* fungi (T. Hart, pers comm). Why duikers should selectively ingest these ants was not clear. There was no further evidence for faunivory by any species except for the partial skeleton and flesh of a black mongoose *Crossarchus obscura* (probably scavenged) from an adult *C. dorsalis* rumen.

Most of the ripe fruits eaten by duikers belonged to species which are seemingly specialized for seed dispersal by large terrestrial mammals (van der Pijl 1972, Alexandre 1978). Many of these fruits were quite large or of low nutritional quality. Other ripe fruit on the forest floor included the less palatable rinds and capsules discarded by primates. Ripe fruits and fruit parts were more important in the diets of the larger animals than the smaller ones. The average percentage of ripe fruits in the diet was correlated with body size across all seven ungulate species ($r_S = 1.00$, $p < 0.001$, $n = 7$). Values ranged from 6.6% of wet weight contents in the diet of *C. monticola* (for which ripe fruit never averaged more than 20% of the diet in any sample period) to over 97% in that of *C. sylvicultor*.

Patterns in edible seed consumption were in the opposite direction to those of ripe fruits. Average percentage seeds in diet of all seven species was negatively correlated with body size ($r_S = -0.93$, $p < 0.01$, $n = 7$). Seeds accounted for more than 5% of the diet of *C. monticola* during all nine sampling periods and accounted for over 40% of the diet in five samples. Edible seeds were also favored by the three red duiker species. Their importance in the diet, however, was limited to periods of mast seed fall of the

Caesalpiniaceous forest dominants or during periods when primates dropped or defecated seeds of *Landophia spp* and *Cola lateritia* in abundance. During the remainder of the year, seeds generally only occurred in small scattered patches and were not used by the larger animals.

Arcsine transformed percentage foliage was correlated in 2 mm and 5 mm screened samples from the same rumen ($R^2 = 0.85$, $p < 0.001$, $n = 46$). Foliage accounted for only a small proportion of the diet of all species, except during the dry seasons. Most of the foliage which could be identified in the rumens came from canopy trees. Much of this consisted of new leaves. Minor amounts of older, dead leaves and what appeared to be root fibers from the forest floor also were found. Foliage of the dominant understory species was unpalatable to *C. monticola* in feeding trials (Chapter 3) and was absent from the rumens of all species.

Foliage is apparently available year-round. Leaf flush in the evergreen canopy dominats, *Brachystegia laurentii* and *Gilbertiodendron dewevrei* occurred in all seasons. Leaf flush in most deciduous canopy species occurred in the late dry and early wet seasons. Use of foliage by the ungulates increased at this time, but foliagewas not a major componenet of the diet. Foliage was only preferred to lowest ranked fruits or seeds in palatability trials with two duiker species (Chapter 3) and apparently was not a favored food of free-ranging duikers either.

Food Selection

Although duiker diets were often diverse, many food specis contributed only a small percentage to the total diet. While some may have been nutritionally significant (Freeland and Janzen 1974, Oates 1977), preference levels for these species were difficult to ascertain because many were also rare in the environment. These species are not further considered here.

Data on food availability and use adequate to ascertain food selecion were available for 8 to 19 food species in each of nine sampling periods between December, 1981 and May, 1983 (Appendix 4-B). These species all had utility indices of at least 5% and/or comprised at least 5% of available food (total transect weight). This analysis of food selection focuses on four species of upland duikers for which data are adequate, including a small species, *C. monticola*, two medium-sized species, *C. leucogaster and C. callipygus* and a large species *C. dorsalis*.

The abundance of a potential food on the transects was not necessarily an indication of its importance in the diet (Table 4-7). During each sample period, between 40% and 83% of species comprising at least 5% of transect weight were avoided by upland duikers. There was no significant difference between duiker species in the percentages of foods avoided ($t = 0.73$, $p > 0.05$). All species fed selectivley. Many of the preferred foods were relatively uncommon.

An analysis of the characteristics of preferred and avoided foods permits an evaluation of specific dimensions of the food resources which are important to each of the ungulate species and along

Table 4-7. Selection by four upland duiker species for foods which were abundant on transects (> 5% total weight). Ituri Forest, Zaire, 1981 to 1983. [a].

Season & date	Food species	Food type[b]	Species[c]			
			C.m.	*C.l.*	*C.c.*	*C.d.*
Late Wet	*Klainedoxa gabonensis*	RF/UF	+	+	+	+
Dec, 81	*K. trillesii*	RF	-	-	-	-
	Uapaca guineensis	Fl	-	-	-	-
Dry	*K. trillesii*	RF	-	-	-	-
Jan, 82	*Albizia gummifera*	UF	-	-	-	-
	K. gabonensis	RF/UF	-	+	+	+
	Ficus sp 4	UF	+	+	+	+
Early wet	*K. gabonensis*	RF	-	-	+	+
Mar, 82	*Pacovia harmsiana*	UF/S	+	+	+	+
Early wet	*K. gabonensis*	RF	-	-		
May, 82	*Pancovia harmsiana*	S	+	-	NR	NR
	Cleistanthus michelsonii	UF	-	-		
	Celtis adolfi-friderici	RF	-	-		
	Gilbertiodendron dewevrei	Fl	-	-		
Mid wet	*Brachystegia laurentii*	Fl	-	-	-	-
Aug, 82	*Landolphia spp*	UF/S	-	+	+	+
	unknown "kokou"	RF	-	-	-	-
	Blighia welwitschii	RF/S	+	+	+	+
Late wet	*K. trillesii*	UF	-	-	-	-
Oct, 82	*G. dewevrei*	S	-	+	+	+
	B. laurentii	S	+	-	+	-
	Landolphia spp	RF/S	+	+	+	+
	B. laurentii	S	+	-	+	-
Dry	*K. gabonensis*	RF/UF	+	+		
Feb, 83	*K. trillesii*	RF	-	-	NR	NR
	G. dewevrei	Fl	-	-		
	B. laurentii	S	+	+		
D/E wet	*K. gabonensis*	RF	-	-	-	+
Feb-Mar,	*K. trillesii*	UF	-	+	-	-
83	*C. michelsonii*	UF	+	+	+	-
	Tarenna laurentii	UF	-	-	-	+
	G. dewevrei	Fl	-	-	+	-
Early wet	*K. gabonensis*	RF	-	-	-	+
May, 83	*B. laurentii*	Fl	-	-	-	-
	unknown "lipasa"	UF	+	-	+	+

[a] Selectivity: +, food selected or eaten in proportion to availability; -, foods avoided; NR, no data for duiker species.

[b] Food type: RF, ripe fruit; UF, unripe fruit; Fl, flowers; S, seeds.

[c] Upland duiker species: *C.m., C. monticola; C.l., C. leucogaster; C.c, C. callipygus; C.d., C. dorsalis.*

which animals' diets might be segregated. This analysis examines selection in relationship to the taxonomic identity of the food, food patch weight, item size and nutritional quality.

Taxonomic Identity

Six food species known to be eaten by duikers were available during more than one sampling period (Table 4-8). None of these species was a preferred food for duikers at all times it was available. Unripe *Klainedoxa gabonensis* fruits were selectively eaten by all species, ripe fruits of the same species were often avoided by the red duikers and were always avoided by *C. monticola* Flowers of *Gilbertiodendron dewevrei* and *Brachystegia laurentii* were less preferred than the ripe seeds. While consistency of duiker food preference was noted with captive animals during controlled feeding trials (Chapter 3) this was not the case in the field where abundance and relative availability of alternative foods may be a factor in determining preference. While no food was consistently preferred in the diet, a number of species, regularly recorded on transects were consistently avoided, even when abundantly available.

Food Patch Weight

Two hypotheses on the importance of food patch weight in food selection were examined for each duiker species:

1. Preferred food species occur equally in patches of both large and small weight.

2. Avoided food species occur equally in patches of both

Table 4-8 Changes in preference by four species of upland duikers for six food species available during more than one sampling period. Ituri Forest, Zaire, December, 1981 to May, 1983.

Species	Season	Food Type[a]	Selectivity[b]			
			C.m.	*C.l.*	*C.c.*	*C.d.*
Klainedoxa gabonensis	L 81	UF	++	++	++	++
	D 82	UF	+	++	++	++
	E 82	RF	-	-	++	-
	M 82	RF	-	-	-	++
	L 82	RF	-	-	-	-
	D 83	UF	++	++	no data	
	D/E 83	RF	-	++	-	-
	E 83	RF	-	-	+	+
Brachystegia laurentii	M 82	Fl	-	-	-	-
	L 82	S	++	-	+	-
	D 83	S	++	++	no data	
	D/E 83	S	+	-	+	-
	E 83	Fl	+	-	-	+
Gilbertiodendron dewevrei	E 82	Fl	-	-	no data	
	L 82	S	-	++	++	++
	D/E 83	Fl	+	-	+	-
Cleistanthus michelsonii	E 82	UF	-	-	no data	
	D/E 83	UF	++	+	++	-
Pancovia harmsiana	E 82	UF/S	++	++	++	++
	E 82	S	++	-	no data	
Ricinodendron heudelotii	L 81	RF	-	++	++	++
	M 82	RF	-	-	-	++
	L 82	RF	-	-	-	-

[a] Food type: UF, unripe fruit; RF, ripe fruit; S, seed; Fl, flower.

[b] Selection: ++, preferred; +, eaten in proportion to availability; -, avoided. Duiker species abbreviations: *C.m.*, *C. monticola*; *C.l.*, *C. leucogaster*; *C.c.*, *C. callipygus*; *C.d.*, *C. dorsalis*.

large and small weight.

There was no significant difference in patch weight of foods preferred by *C. monticola* (Table 4-9). Of 30 preferred food species in which patch weight was known, 13 (40%) occurred in large patches ($W > 100$ g) while 17 (57%) occurred in patches of $W < 100$ g. In contrast, significantly more preferred foods had large patch weights for *C. leucogaster* (21 of 27 foods) and *C. dorsalis* (18 of 24 foods). In diets of *C. callipygus* 21 of 30 preferred foods in which patch weight was known were large.
This was not significantly different than 15 which would be expected if theis species exhibited no selection for food patch weight ($X^2 =$ 2.40, $p > .10$, 2 df). Although most preferred foods of *C. callipygus* had large patch weights, at least some foods of small patches were also preferred during every sampling period.

In all four duiker species there was no significant trend in patch size of avoided food species (Table 4-9). Avoided foods included species which occurred in both large and small patches.

Food Item Size

The size distributions of preferred and avoided fruits, seeds and flowers (Figure 4-6) were examined with respect to two hypotheses:

1. The size distributions of preferred foods are equivalent across all duiker species.

2. Within duiker species, preferred and avoided foods are of equivalent size.

Species by species comparisons (Table 4-10) demonstrated

Table 4-9. Numbers of preferred and avoided food species of large patch weight ($W > 100$ g) and small patch weight ($W \le 100$ g) in diets of four species of upland duikers. Ituri Forest, Zaire, 1982-1983.

Duiker:	*monticola*	*leucogaster*	*callipygus*	*dorsalis*
Preferred foods [a]				
Large patch weight	13	27	21	24
Small patch weight	17	6	9	6
Total	30	37	30	30
X^2	0.53	6.68	2.40	5.40
P [c]	N.S.	<.01	N.S.	<.05
Avoided foods [b]				
Large patch weight	29	28	19	24
Small patch weight	16	21	15	16
Total	45	49	34	40
X^2	1.88	0.50	0.24	0.80
P [c]	N.S.	N.S.	N.S.	N.S.

[a] Numbers of preferred foods of unknown patch wieght: *monticola*, 5; *leucogaster*, 3; *callipygus*, 8; *dorsalis* 2.

[b] Numbers of avoided foods of unknown patch weight: *monticola*, 2; *leucogaster*, 2; *callipygus*, 1; *dorsalis*, 1.

[c] Probabilities of $p > .10$ are not significant (N.S.).

Figure 4-6. Size distributions of preferred (fine stipling) and avoided (coarse stipling) foods in diets of four species of upland duikers. Ituri Forest, Zaire, December, 1981 to May, 1983.

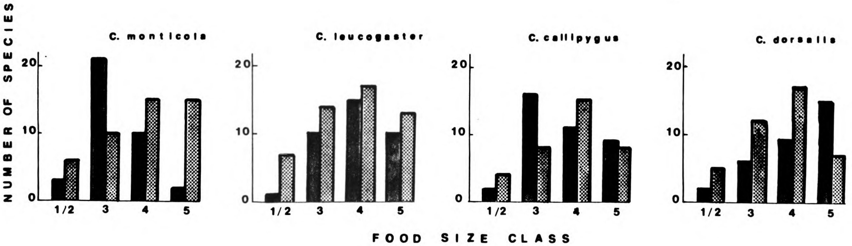

NUMBER OF SPECIES
C. monticola
C. leucogaster
C. callipygus
C. dorsalis
0
10
20
1/2
3
4
5
FOOD SIZE CLASS

Table 4-10. Chi square values for tests of A) equal food size distributions of preferred food species between diets of four species of upland duikers, and B) equal size distributions of preferred and avoided foods species within diets of each duiker spaces.

A) Between species[a]

Duiker:	*monticola*	*leucogaster*	*callipygus*	*dorsalis*
monticola	--	11.16 <.05	6.85 N.S.	16.82 <.001
leucogaster		--	2.36 N.S.	1.91 N.S.
callipygus			--	4.50 N.S.
dorsalis				--

B) Within species [a]

Duiker	*monticola*	*leucogaster*	*callipygus*	*dorsalis*
X^2	14.85	3.19	1.75	6.38
Probability	<.001	N.S.	N.S.	<.05

[a] Chi square values with 3 degrees of freedom. Probabilities of $p > .10$ are not significant (N.S.).

significant differences in size distributions of preferred foods only between *C. monticola* and the two red duikers *C. leucogaster* and *C. dorsalis*. Sizes of preferred foods were not significanlty different between *C. monticola* and *C. callipygus* or between the three red duiker species.

Within species comparisons demonstrated that the sizes of preferred and avoided food species were significantly different in diets of *C. monticola* and *C. dorsalis* but not in diets of *C. callipygus* or *C. leucogaster*. Preferred food species were under-represented in the largest size class in the diet of *C. monticola* while avoided food species were over represented. In *C. dorsalis* the reverse trend was apparent. Most preferred foods were of large size while relatively few avoided species were of this class (Figure 4-6).

Patterns of food size selection revealed that both mouth size and shape contributed to the distribution of food sizes an animal will ingest. Overall, larger animals with larger mouths can ingest larger foods. This restricts *C. monticola* to smaller food sizes. Two species, *C. monticola* and *C. callipygus* of differing body size but similar narrow mouth shape included small-sized items among the foods they selected. *Cephalophus callipygus*, the largest of these two species also included a larger proportion of large food sizes in its diet as well. Species with relatively broad mouths, *C. leucogaster* and *C. dorsalis* preferred larger foods and avoided smaller food items. The largest of these two species, *C. dorsalis* selectively fed on fruits of the largest size class. Many of these, including the ripe fruits of *Klainedoxa gabonensis*, and *Irvingia grandifolia* were tough and fibrous. Their inclusion in the diet was associated with this species' relatively heavy jaw musculature (Kingdon 1982) as well its broad mouth.

Food Nutritional Quality

Palatability trials with captive *C. montiocla* and *C. dorsalis* (Chapter 3) deomonstrated taht preferred foods generally had high values of adjusted dry matter yield (Y_Q). Selection for food nutritonal quality (Y_Q) in free-ranging animals was investigated according to two hypotheses:

1. Adjusted dry matter yield (Y_Q) of selected foods is greater than avoided foods.

2. Values of Y_Q of preferred foods are greater than the average available value ($Y_{Q(T)}$).

The adjusted dry matter yield of available foods ($Y_{Q(T)}$) varied widely over the five sampling periods in which it was measured (Figure 4-7). Food values of Y_Q analyzed on a seasonal basis revealed that in diets of *C. monticola*, preferred foods had significantly higher values than avoided foods (U test, $p < .10$) in four of the five sampling periods (Table 4-11). Values of preferred and avoided foods were not singinificantly different only during the early wet season of 1983. Average food value ($Y_{Q(T)}$) at this time was low and high quality foods were rare.

The three upland red duikers species were not as consistently selective for foods with high Y_Q values as was *C. monticola*

Figure 4-7. Adjusted dry matter yield (Y_Q) of selected (closed circles) and avoided (open circles) food species in diets of four species of upland duikers in comparison with average adjusted dry matter yield ($Y_{Q(T)}$) of apparently available fruits, seeds and flowers on transects (connected squares). Ituri Forest, Zaire, October, 1982 to May, 1983.

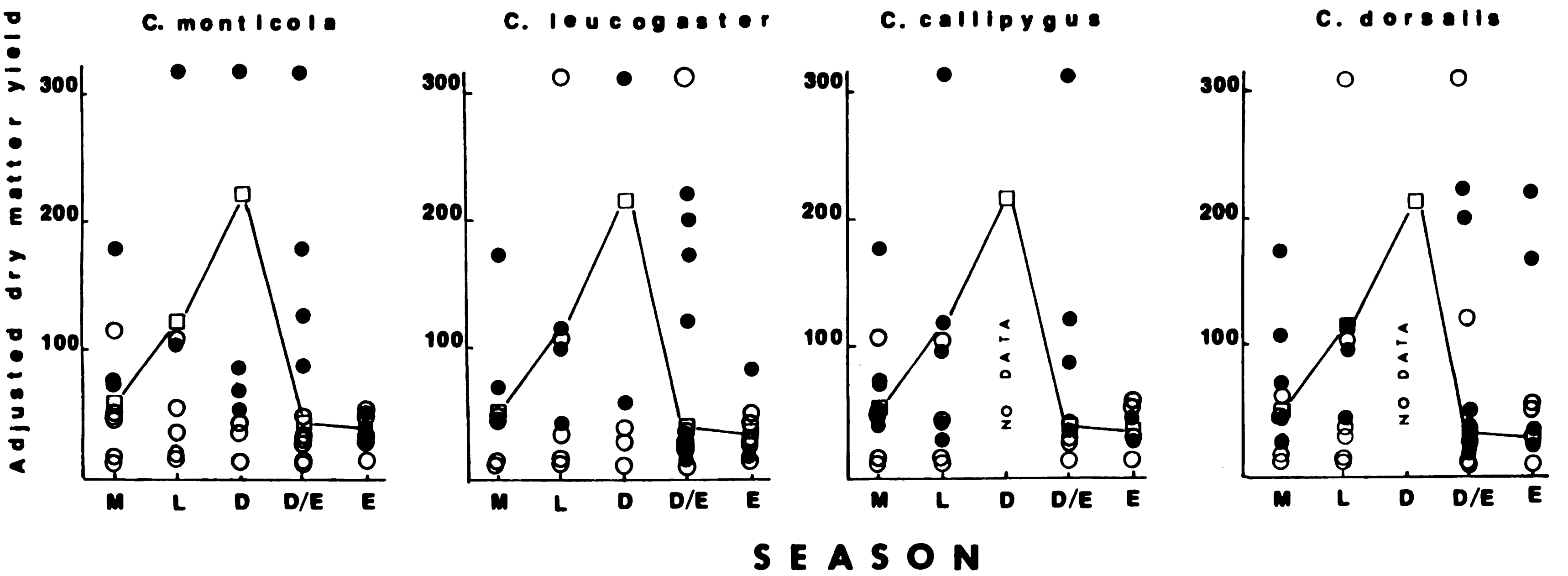

C. monticola
C. leucogaster
C. callipygus
C. dorsalis
Adjusted dry matter yield
300
200
100
M
L
D
D/E
E
NO DATA
NO DATA
SEASON

Table 4-11. A) Mann Whitney U probabilities associated with tests that adjusted dry matter yield (Y_o) values of preferred foods are greater than avoided foods in diets of four species of upland duikers during five sample periods. B) Numbers of preferred food species with Y_o values greater than and less than average values for available foods summed over five sample periods. Ituri Forest, Zaire, July 1982 to May, 1983. [a]

A) Preferred > Avoided

Duiker	Mid Wet 1982	Late Wet 1982	Dry 1983	Dry/Early Wet 1983	Early Wet 1983
C. monticola	<.05	<.10	<.01	<.01	N.S.
C. leucogaster	<.05	N.S.	<.10	N.S	N.S.
C. callipygus	N.S.	<.10	no data	<.05	N.S.
C. dorsalis	<.10	N.S.	no data	N.S.	N.S.

B) Preferred > Average

	C. monticola	*C. leucogaster*	*C. callipygus*	*C. dorsalis*
> Average	11	9	8	11
< Average	5	8	8	7
X^2	2.25	0.03	0.00	0.88
Probability	N.S.	N.S.	N.S.	N.S.

---

[a] Data are values for food items shown in Figure 4-9.
N.S. , difference not significant, $p > .10$.

(Figure 4-7). Preferred foods included species with high values, but also species with low values. Values of Y_Q were significantly higher than avoided foods in only two of five sampling periods for *C. leucogaster*, two of four samples for *C. callipygus* and only one of four samples for *C. dorsalis* (Table 4-11 A).

Summed over all five sample periods, values of Y_Q of preferred foods were not significantly greater than average available food value ($Y_{Q(T)}$) in any duiker species (Table 4-11 B). An examination of the trends on a sample by sample basis, however (Figure 4-7), reveals differences between the species in preferences for foods of high Y_Q values. During periods when high quality foods were abundant and average nutritonal value of available foods was high (late wet season, 1982 and dry season, 1983, during *Bracystegia laurentii* seed-fall), selected foods of all duikers included species of below average value. During periods when average food values were lower (mid wet season, 1982 and early wet season, 1983) Y_Q values of preferred foods in diets of *C. monticola* were singificantly greater than average available values (10 of 11 food species. $X^2 = 7.36$, $p < .05$). The upland red duikers, *C. leucogaster, C. callipygus* and *C. dorsalis* selected foods of less than average value during these same three sample periods. Four of 14 preferred foods in diet of *C. leucogaster* had Y_Q values less than average. Three of seven preferred foods in diet of *C. callipygus* and four of seven in diets of *C. dorsalis* were similarly below average quality (X^2 values 2.58, 0.14, 0.14 for each species respecitively, $p >> .10$).

Diet Overlap

Dietary overlap (I_M) between the three species of upland red duikers, *C. leucogaster, C. callipygus* and *C. dorsalis* ranged from zero to over 0.90 (mean 0.55) over seven sample periods for which there were adequate data (Figure 4-8 A). The diets of all three species converged during four sample periods and exhibited marked divergence during three periods. Dietary overlap between the three red duiker species and *C. monticola* ranged from zero to 0.60 (mean 0.43) over this same period (Figure 4-8 B). Rank values of I_M for diets of *C. callipygus* and *C. monticola* were significantly higher (mean 0.55) than between *C. leucogaster* and *C. monticola* (mean 0.39) or between *C. dorsalis* and *C. monticola* (mean 0.32) (Friedman 2-way ANOVA, $p < 0.001$). There were, however, no periods of marked dietary convergence. Overall, dietary overlap between *C. monticola* and the red duikers was never as high as between the three red duikers species.

During periods of dietary convergence, the dominant foods in the diets of the red duikers were both high quality and abundantly available (Table 4-12). Among the shared food species at this time were species with high values of Y_Q as well as fruits which had high preference ranks in feeding trials with captives (Chapter 3). Most of these foods comprised at least 4 % of total food transect weight and up to 28% of total patches recorded.

By comparison, during periods of dietary divergence, high quality foods were scarce, although total food diversity was high. This

Figure 4-8. Values of Morisita's (I_M) index for dietary overlap between: A) three species of upland red duikers, *C. leucogaster* (l), *C. callipygus* (c) and *C. dorsalis* (d) and B) three species of upland red duikers and *C. monticola* (m), for seven sample periods. Ituri Forest, Zaire, December, 1981 to May, 1983.

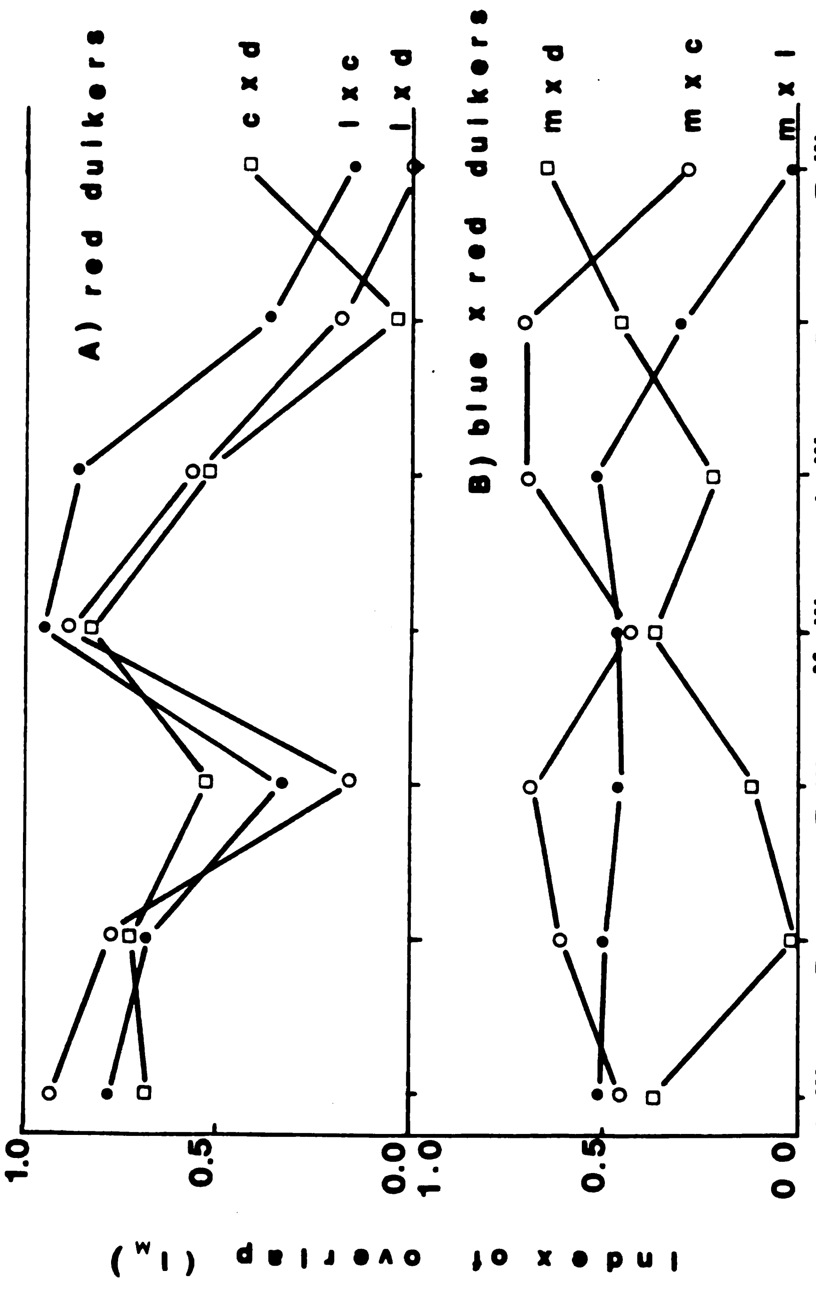

A) red duikers
c x d
l x c
l x d
B) blue x red duikers
m x d
m x c
m x l
Index of overlap (I_M)
1.0
0.5
0.0
1.0
0.5
0.0
LW
1981
Dry
1982
EW
MW
LW
Dry
1983
EW

Table 4-12. Quality and abundance of dominant foods ($I_u > 5\%$) shared in the diets of at least two of three species of duikers, *C. leucogaster, C. callipygus* and *C. dorsalis* during periods of high dietary overlap. Ituri Forest, Zaire, December 1981 to May, 1983.

Season	Species	Food Quality	Abundance on transect	
			% weight	% patches
Late Wet 1981	*Klainedoxa gabonensis* unripe fruit	preferred in trials high Y_o	51.2	10.4
	Ricinodendron heudelotii ripe fruit	preferred in trials high Y_o	not recorded	
Dry 1981	*Klainedoxa gabonensis* unripe fruit	preferred in trials high Y_o	not recorded	
	fungi	low quality ? low dry matter yield	abundant	
	foliage	low quality most not preferred in trials	not measured	
Mid Wet	*Landolphia spp* unripe fruit & seeds	high Y_o	35.7	7.3
	Croton mubanga ripe fruit	high Y_o	not recorded	
	Blighia welwitschii ripe fruits & seeds	high Y_o	4.3	1.2
Late Wet 1982	*Gilbertiodendron dewevrei* ripe seeds	high Y_o	6.7	1.2
	Landolphia spp ripe fruit & seeds	high Y_o	10.5	27.6

is evident by examining the range of foods selected by each of the duikers which were not found in the diets of the other species. (Table 4-13). Most of the domianant foods ($I_U > 5\%$) eaten by each species during these periods were unique to the diet and not shared with the other two species. The only exception to this trend being the *C. callipygus* diet during the early wet season of 1982. Characterisitics of these unique foods indicated that each species appeared to adopt differing foraging and feeding behaviors. *C. leucogaster* evidently was highly mobile. It appeared to attend primates and its diets were dominated by widely dispersed foods which occurred in ephemeral patches such as flowers and soft figs (*Ficus*). Diets of *C. callipygus* were broadened during these periods to include increased percentages of scattered food patches of smaller patch weight. This indicates that this species may have had restricted movements and made increasing use of foods which were ignored at other seasons. The diet of the largest red duiker, *C. dorsalis* consistently included very large and in some cases low quality fruits including ripe fruits of *Klainedoxa gabonensis, Irvingia grandifolia* and *I. wombolu* These fruits were difficult for smaller species to handle.

An apparent exception to this trend occurred during the dry season sample of 1982 (Table 4-12). Unripe fruits of *K. gabonensis* occurred in all diets but the fruits were rare in the forest. Foliage and fungi were dominant in the diets, but both were of apparent low quality (see discussion). A further feature of food availability during this period was that both total availability and food diversity

Table 4-13. Numbers and characteristics of dominant food species (I_u > 5%) unique to diets of each of three duikers, *C. leucogaster, C. callipygus* and *C. dorsalis* during periods of dietary divergence. Ituri Forest, Zaire, March, 1982 to May, 1983.

Sample	Duiker	Number dominant foods	Number unique foods	Characteristics
Early Wet 1982	*leucogaster*	6	3	primate drops
	callipygus	2	0	None
	dorsalis	5	2	large hard fruits
Dry/ Early Wet 1983	*leucogaster*	7	4	primate drops, low Y_o, 2 spp soft *Ficus*
	callipygus	4	2	primate drops, small size
	dorsalis	7	5	large, hard, low quality
Early Wet 1983	*leucogaster*	2	2	flowers, aborted fruits
	callipygus	5	4	small patch, hard *Ficus*
	dorsalis	4	3	large, tough fruits/capsules

were lower than during any other sample period recorded (Figure 4-4).

Dietary overlap between the riverine species and upland duikers was variable but often high (Table 4-14). Values of I_M ranged from 0.50 to 0.97 (mean 0.70) for *H. aquaticus* and *C. monticola* and from 0.00 and 0.77 (mean 0.46) between *H. aquaticus* and the three red duikers species. Dietary overlap between *C.nigrifrons* and upland red duikers ranged from 0.01 to 0.22 (mean 0.22) and between 0.06 and 0.95 (mean 0.50) with *C. monticola*. Overlap values for diets of the two riverine species were comparable to those between riverine and upland species. Periods of high overlap in the riverine species paralled those in upland duikers and occurred mainly during periods of food abundance in upland forests. Diets diverged during periods when these foods were absent (Table 4-14). These patterns demonstrate that neither *C. nigrifrons* nor *H. aquaticus* were confined to riparian habitats for foraging. Instead it appears that these habitats were a refuge, at least for *C. nigrifrons*, during periods of potential competiton with upland species. This was less clearly the case for *H. aquaticus*. Dietary overlap between *H. aquaticus* and *C. monticola* was consistently high over all sample periods it was measured. *H. aquaticus* forages in upland forests at night and apparently only retreats to the water-side for shelter during the day (see also Dubost 1978). Although data on diet and behavior of *H. aquaticus* were limited, it was neither as active nor as selective a feeder as *C. monticola* (J. Hart, unpubl. obs., see also

Table 4-14. Values for Morisita's (I_M) index for dietary overlap between two riverine species, *N. aquaticus* and *C. nigrifrons*, and between two riverine species and upland duikers. Ituri Forest Zaire, 1981 -1983.[a]

			N. aquaticus		*C. nigrifrons*	
Date	Available food[b]	Riverine species	blue duiker	upland red duikers	Blue duiker	Upland red duikers
Jun, 81		0.04	0.63	0.33	0.06	0.01
Sep, 81	Fruit	0.52	0.50	--	0.82	--
Oct, 81	Mast	--	0.72	0.62	--	--
Dec, 81	Fruit	0.92	0.97	0.55	0.95	0.61
Jan, 82		--	0.83	0.77	--	--
Mar, 82		--	--	--	0.31	0.26
May, 82	Fruit	--	0.78	0.00	--	--
Oct, 82	Mast	--	0.72	0.62	--	--
Feb, 83	Mast	0.52	0.50	--	0.82	--
May, 83		0.04	0.63	0.33	0.06	0.01
Average		0.41	0.70	0.46	0.50	0.22

[a] No value shown (--) indicates one or both species absent and comparison could not be made. Overlap value for red duikers is average for *C. leucogaster, C. callipygus* and *C. dorsalis*.

[b] Periods of abundant high quality food in upland forest: fruit, ripe or unripe fruit; mast, Caesalpineaceous mast seed fall.

Dubost 1978, 1975).

Patterns in Abundance of Frugivorous Ungulates

Ungulate Distributions

Four species, *C. monticola*, and the upland red duikers *C. leucogaster, C. callipygus* and *C. dorsalis*, were recorded at all nine sample sites and accounted for the largest percentage of total animals flushed (Table 4-15). The smallest species, *C. monticola* was the most abundant, averaging 52% to 65% of total observations with 14.9 animals flushed/km^2. The upland red duikers, *C. leucogaster, C. callipygus* and *C. dorsalis*, accounted for most of the remaining observations and together averaged 7.4 animals flushed/km^2. Two riverine species, *C. nigrifrons* and *H. aquaticus* were encountered on drives in the vicinity of streams. *Cephalophus sylvicultor* was irregularly and less frequently recorded in upland forest. Excluding the riverine species, average abundance and body weight were significantly and negatively correlated ($R = -0.92$, $p < .01$, $n = 5$).

Two red duiker species of similar body size, *C. leucogaster* and *C. callipygus* varied in aspects of their social behavior and in their distributions. Average group size (number of animals flushed together) in *C. callipygus* was 1.3 with 24 % of flushes including more than one animal. Group size in the similarly-sized *C. leucogaster* was 1.1, with only 12.5 % of flushes containing more than one animal.

Table 4-15. A) Numbers flushed/ km², and B) percentages of duikers and chevrotains flushed on drive hunts at nine sites in the Ituri Forest, Zaire, 1981 to 1983.

	Site[a]										
Species	K	R	E	M	B	A	P	S	I	Mean	Standard deviation
	A) Abundance (number flushed/ km²)										
C. monticola	15.6	13.5	11.9	10.3	17.5	11.9	13.7	15.7	24.2	14.9	4.14
H. aquaiticus	2.7	0.6	N.R.	1.7	0.6	N.R	0.3	0.8	5.5	1.4	1.78
C. nigrifrons	0.5	0.2	N.R	1.7	N.R.	1.1	0.3	N.R.	1.4	0.6	0.65
C. leucogaster	4.4	2.5	4.0	2.6	1.2	3.4	2.7	2.4	1.4	2.7	1.07
C. callipygus	2.0	2.9	0.8	2.1	6.2	4.0	0.6	6.3	4.1	3.2	2.10
C. dorsalis	1.5	1.9	3.2	0.4	0.8	1.1	2.1	2.4	1.2	1.5	0.73
C. sylvicultor	1.0	1.2	N.R.	0.9	0.6	N.R.	0.9	1.6	N.R	0.7	0.58
Total flushes per km²	27.7	22.8	19.9	19.7	26.9	21.5	20.6	29.2	37.8	25.1	5.90
Total flushes	168	120	25	46	128	33	72	38	33	663	
Total area sampled km²	6.06	5.26	1.26	2.33	4.76	1.54	3.58	1.30	0.87	26.96	
	B) Percentage total animals flushed										
C. monticola	57.1	60.8	60.0	52.2	64.1	54.5	65.3	52.6	60.6	63.0	5.1
H. aquaticus	9.5	2.5	N.R.	8.7	2.3	N.R.	1.4	2.6	12.1	5.6	4.4
C. nigrifrons	1.8	0.8	N.R.	8.7	N.R.	6.1	1.4	N.R.	3.0	3.6	3.1
C. leucogaster	15.5	10.0	20.0	13.0	4.7	15.2	13.9	7.9	3.0	12.3	5.8
C. callipygus	7.1	12.5	4.0	10.9	23.4	21.2	2.8	21.1	9.1	13.3	7.9
C. dorsalis	5.4	7.5	16.0	2.2	3.1	3.0	11.1	7.9	9.1	7.7	4.5
C. sylvicultor	3.6	5.8	N.R.	4.3	2.3	N.R.	4.2	5.3	N.R	4.6	1.3

[a] For location of sites, see Figure 4-1. N.R. indicates no individuals recorded in sample.

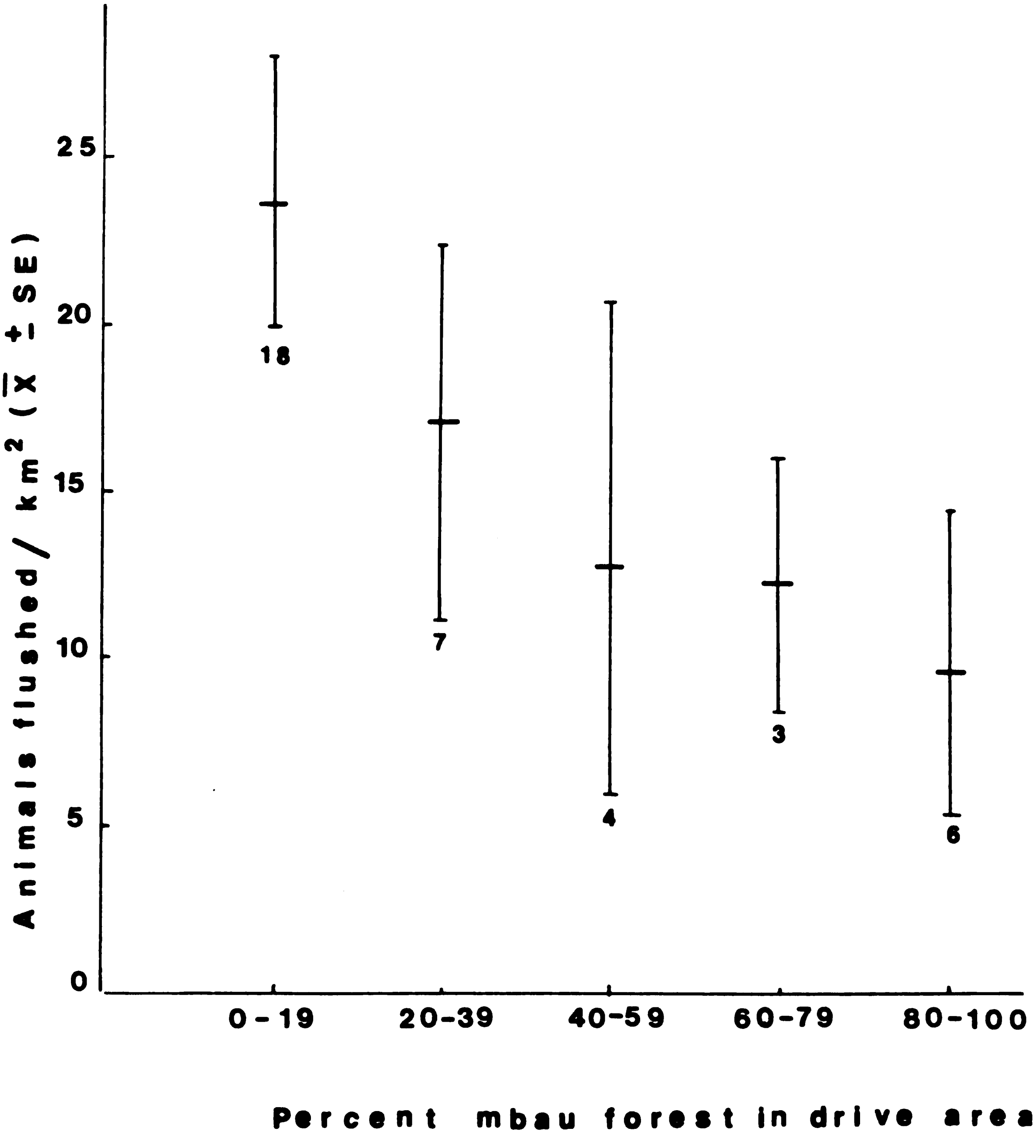
C. callipygus appeared to occur in pairs or as family parties. These assemblages were irregularly distributed over the study area. Indices of abundance for *C. callipygus* varied from $0.6/km^2$ at site P, to $6.3/km^2$, at site S. No differences were noted in the mixed forest composition at locations where this species was present and where it was absent. Averaged over all nine sampling sites, the abundances of *C. callipygus* and *C. leucogaster* were not significantly different (2.7 and 3.2 animals flushed $/km^2$, $t = 0.87$, $p >> 0.10$ $n = 9$). On a site by site basis, however, the relative abundance of the two species was negatively correlated ($R = -0.66$, $p = 0.05$, $n = 9$).

Ungulate Abundance and Patterns in Food Abundance

There were few discernible trends in total upland duiker abundance between sites in mixed forest of comparable hunting hisotry. Differences in abundance between the two mature forest types on the study area, mixed forest and the mbau forest were apparent. At two sites, K and E, where drive samples included both forest types, the average abundance of all upland species combined was negatively correlated with the percentage mbau forest in the drive area (Figure 4-9; $r_S = -0.96$, $p <.01$, $n = 5$).

Overall patterns of food abundance in borth forest types were affected by the irregular cycles of synchronous flowering and seed-fall of the Caesalpiniaceous dominants of each forest type *Brachystegia*

Figure 4-9. Average ungulate abundance (± SE) on drive areas of differing percentage mbau forest cover at two sites, K and E. Ituri Forest, Zaire. Sample sizes indicated for each percentage class.


Animals flushed/ km^2 ($\bar{X}$ ± SE)
25
20
15
10
5
0
18
7
4
3
6
0-19
20-39
40-59
60-79
80-100
Percent mbau forest in drive area

laurentii in mixed forest and *Gilbertiodendron dewevrei* in mbau forest. Most *B. laurentii* were inactive over the study area in 1981 but fruited synchronously and widely in 1982. Abundant seed-fall in the late wet season of 1982 extended into the succeeding dry season. This contributed to a nearly three-fold difference in dry season food abundance in mixed forest in 1983 than in the non-mast dry season of 1982 (Figure 4-3).

Flowering and seed-fall of *G. dewevrei* in the two major stands of mbau forest on the study area were not synchronized. Simultaneous flowering occurred in the Eboyo mbau forest in 1981 but not in 1982. Flowering and seed production occurred in Mangbara in 1982 but not to any large extent in 1981.

The flowering and fruiting of the caesalpiniaceous dominants created pulses of abundant food resources (Table 4-16). This was especially evident in the mbau forest where fallen fruits of other species were scarce. Total food abundance recorded on transects varied from no foods recorded on 0.7 km of transect druing the dry season of 1983, to almost 70 kg/km recorded during the *G. dewevrei* seed-fall of 1981 at Eboyo. High transect weights were also recorded during periods of *G. dewevrei* flowering and seed ripening when fallen flower bracts and unripe seeds dropped by foraging primates were common. Despite peaks in apparent food abundnace, however, overall food diversity in mbau forest was consistently low, corresponding with the low tree species diversity in this forest type.

In the mixed forest, the seasons of mast seed-fall of *B. laurentii* were also periods of greatest food availability. Levels of

Table 4-16. Species diversity and total weights recorded on transects in mixed and mbau forests during the seasonal fruiting cycle of Caesalpiniaeceous trees in the Ituri Forest, Zaire, July 1981 to May, 1983. Dominant trees: *Gilbertiodendron dewevrei* in mbau forest, *Brachystegia laurentii* in mixed forest.

Condition of dominant tree species	Mbau forest				Mixed forest			
	Date	km transect	Diversity[a]	Abundance kg/km	Date	km transect	Diversity[a]	Abundance kg/km
Flowering	May, 82	3.01	0.79	25.81	May, 82	6.99	1.08	5.29
Seed ripening	Sep, 81	1.21	0.82	5.85	Aug, 82	11.82	1.46	5.39
Seed fall	Oct, 81	4.17	0.45	69.71	Oct, 82	10.14	1.31	7.29
Inactive (dry season)	Feb, 83	0.70	0.00	0.00	Jan, 82	14.58	1.28	0.79

[a] Shannon diversity index (Zar and Brower 1979).

food biomass recorded on transects, however, did not reach levels recorded in mbau forest during periods of *G. dewevrei* seed-fall. This was offset by a decreased disparity in food abundance between mast and non-mast seasons. The seasonally more equitable food availability in mixed forest corresponds with the lower dominance of *B. laurentii* in mixed forest and the higher representation of other fruit bearing species in the canopy. Overall, mixed and mbau forest did not differ in the weight of fallen fruits, seeds and flowers on transects. The diversity of these potential foods, however, was significnatly greater in mixed forest than in mbau forest ($t = 7.59$, $p < .001$, $n = 5$).

DISCUSSION

Food Selection in Upland Duikers

Dubost's (1984: 311) conclusion that duikers were unselective polyphagic foragers and that there "appears to be no major determining factor for the trophic differentiation of these frugivorous ruminants." is not supported by the results of this study. Although the taxonomic diversity in the diets of all ungulates for which there were adequate data was high, at least four species studied in depth exhibited marked patterns of selection along other dimensions of their food. In this study, food patch weight, food item size and food nutritional quality were differntially selected by animals of differing body size and mouth morphology. The small species preferred foods of high nutritional quality and smaller item size but selected equally foods of both large and small food patch weight. Two medium-sized species and a large species selected foods over a range of relative nutritional quality. One of the middle-sized species with a broad mouth preferred foods of both large size and generally large patch weight. The other medium-sized species had a narrow mouth and included both large and small food items and a greater proportion of foods from smaller food patches in its diet. Among the species selected by the largest species were a number of the largest and toughest fruits.

Differences in selectivity of the duikers were evident even when all species fed on the same food species. Fruits with embedded seeds were typically found in fallen *Blighia welwitchii, Cola lateritia* and *Landolphia spp.* and were eaten by all upland duiker species. Whereas the larger species, *C. dorsalis* characteristically ate both fruit and seed together, the smallest species, *C. monticola* and the narrow-mouthed medium species *C. callipygus* selected seeds from the fruits and left the capsules and rinds. In the case of *Landolphia spp.* and perhaps *C. laterita* as well, the selectivity of *C. monticola* apparently extended to finding and eating dispersed seeds defecated by primates, perhaps even eating them from their droppings.

Selection for different parts of the same food species has parallels in ungulate communities of more open environments. Smaller species are reported to select for specific plant parts while larger species are restricted to foraging on large, but sometimes low quality swards (Bell 1971, Owen-Smith 1980, Bunnell and Gillingham in press). Differences in foraging and diet reflect differing constraints associated with the body size of the animal (Demment and Van Soest 1985). Small animals are required by higher relative metabolic needs to forage on more readily digested, nutrient-rich foods. Larger species, though having lower relative needs and hence a greater capacity to digest poor quality food, are nevertheless constrained by large total food needs which may not be met searching for small, dispersed food items.

The relationship between body size and the relative ability to exploit diffuse versus concentrated food patches has emerged as a common theme in the study of a number of size-distributed guilds of consumers, including seed eating heteromyid rodents (Brown 1975, Price 1984; Harris 1984) and frugivorous primates (Terborgh 1983). As Terborgh has shown, large species may be unable to effectively exploit small, scattered food patches, thus providing for an exclusive resource for smaller species.

The results of the present study support this theory in demonstrating that the larger duikers preferred food patches with high food weights and avoided patches with low food weight. One problem with the patch use analysis reported here, however, is that patch weight is a composite value incorporating measures of both food item density and areal extent. Qualitatively very different food patches thus can have the same total weight.

Both Lewis (1980) and Schluter (1982) have suggested that the relative value of a food patch to a consumer is a function of the rate of resource harvest from the patch. Patch value then is a function not only of the value of the individual items, but how easily they can be found and ingested. With the ungulates, food nutritonal quality is potentially an important determinant of food patch value. Large dense patches of fruits may be potentially easily harvested, but their value is decreased or completely negated if th fruits are unpalatable or poorly digested (Chapter 2 and 3).

While fruits and seeds available to the ungulates are patchily distributed on the forest floor, it remains to be demonstrated what dimensions of these patches animals attend to. In the case of the diurnal speices at least at some seasons, the animals may not select specific food patches but rather acccompany mobile "patches" of primates which generate food patches for the duikers as they move through the canopy.

Diet Overlap and Community Structure

Species specific differences in food choice can not be related directly to species diversity in this ungulate community. Patterns of dietary convergence and divergence, however, do indicate that competiton for food was possible during periods when high quality food was scarce and a diversity of alternative foods was low.

Recent studies of primary consumers in tropical forests have demonstrated that diets of different species may converge on abundant resources and diverge during periods when these foods are scarce Heithaus et al. 1975, Emmons 1980, Gautier-Hion 1980, Terborgh 1983, see also Fleming 1979). In this study diets converged when high quality foods such as the seeds of *B. laurentii*, the fruits and seeds of *Landolphia ssp* or the unripe fruits of *K. gabonensis* were abundantly available. Competition for food during these periods was unlikely as these high quality foods were evidently available in surplus and were recorded on the fruit transects.

Dietary divergence occurred during periods when high quality foods preferred by all species were absent but a diversity of other foods remained available. During these periods, species-specific patterns of foraging and food choice were most evident. In addition to the differences in body size and mouth morphology investigated in this study, there was evidence for other factors differentiating the ungulates. Two species utilized restricted water-side habitats. Differences in activity pattern may have also played a role as diets of nocturnal species were on average more diverse than those of diurnal species. There was also evidence for spatial segregation without apparent habitat separation in two species of similar body size. This latter case suggests some form of direct interspecific interference (see Terborgh 1971, Terborgh and Weske 1975 Diamond 1975 and Noon 1981 for descriptions and discussions of this phenomenon in birds). Other than this case, it was not clear that the other species were actively competing during periods when diets diverged, as the food resources available to some species were not available to other species for reasons related to the constraints of body size, relative mobility and perhaps habitat and activity pattern.

Periods during which both high quality foods were scarce and total food diversity was low were periods when competiton was most likely. During the course of this study, the combination of low food abundance and low food diversity was most likely to occur during dry season which were not preceeded by *B. laurentii* seed fall.

These conditions apparently obtained during the dry season of 1982. During this period fruit levels on transects were very low. The diets of the three upland duiker species all contained unripe fruits of *K. gabonensis* as well as foliage and fungi. The diets of *C. monticola* contained few fruits but were dominated by foliage and fungi.

Both foliage and fungi were generally not preferred foods of any ungulate species. Both were available year round but rarely comprised more than 5% of the diet. Foliage was only eaten in quanitiy by duikers in feeding trials when offered with low qulaity fruits (Chapter 3). A number of fungi, known to be eaten in the wild were rejected by captive duikers when offered with more preferred unripe *Klainedoxa gabonensis* fruits (J. Hart, unpubl obs.).

Fogel and Trappe (1978) and Blair et al. (1984) report fungi as important in the diets of a number of mammals including ungulates. The authors argued that fungi may contain appreciable levels of protein and digestible carbohydrates on a dry weight basis and they may represent a high quality food source. The evidence from the diets of the forest ungulates does not support this view, however. Although fungi may be nutritous on a dry matter basis, they routinely average 70% and even up to 90% water (Fogel and Trappe 1978). As a result, their edible dry matter yield is low. Results of this study (see also Chapter 3) indicate that dry matter yield is an importannt component of food quality for ungulates. Favored foods contain concentrated sources of nutrients. Low rumen content weights and low kidney fat levels, recorded during the period when fungi dominated *C. monticola* diets is further evidence that this diet was suboptimal.

There is circumstantial evidence that the blue duiker's limited diet during the 1982 dry season was due in part to competiton with red duikers. Unripe *K. gabonensis* fruits were preferred foods of blue duikers and were eaten freely during other sample periods when they were abundant (late wet season, 1981). Captive blue duiker selected unripe *K. gabonensis* fruits during palatability trials (Chapter 3). Fruits of *K. gabonensis* were not recorded on transects during the dry season, however. Their occurrence in most red duiker rumens indicated that the larger animals were better able than the blue duiker to find and exploit the evidently limited quantities which were available. Because both the diversity and abundance of remaining foods was low at this time, all duikers, and the blue duiker in particular, were forced to broaden their intake to include foods which were otherwise generally ignored.

The particular configuration of low abundance of favored foods and low diversity and abundance of alternatives was recorded only once in over two years observations in mixed forests on the study area. This combination, however, may characterize food availability more frequently and for longer periods in mbau forest and may be an important reason why upland duiker densities are overall lower in this forest type. The evidence from the diet studies indicated that low food diversity may not be a problem to foraging duikers during periods when favored food were abundant. Limited food diversity, however, may preclude divergence of diets during periods when high quality foods are not available.

Are Forest Ungulates Food-limited?

Reduced abundance of upland duikers in mbau forest demonstrates the potential importance of food availabilty as a determinant of duiker abundance in mixed forest as well. If duikers are food limited, this presents the apparent paradox that many species of fallen fruits are not eaten (see results above) and rot on the forest floor.

Two hypotheses can be presented to account for the apparently uneaten food. One is that duiker densities are controlled by periodic bottlenecks in food availability and populations can not track fluctuating resource levels. This hypothesis has been developed to explain patterns of species co-occurrence in some temperate avian communities (Wiens 1977, 1984). It has not, however, been used to examine tropical forest communities (see however Leigh et al. 1982).

A second hypothesis is that all that was recorded as potential food on the transects was not in fact really available to the ungulates. Fruits, seeds and flowers vary in nutritional quality and may contain appreciable levels of toxins and digestion inhibitors. A number of fruits collected from the forest floor were not preferred by captive duikers in palatability trials (Chapter 3) Furthermore, even the most preferred species were not eaten to the exclusion of other foods. While the ruminants with foregut fermentation can eat many foods which were unpalatable or unused by other frugiovres in the forest, notably primates, this capacity is not unlimited.

Further more careful stuides determining what can and cannot be eaten and factors determining inclusion of a potential food in the diet will be needed before we can evaluate these two hypotheses.

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APPENDICES

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APPENDIX 4-A

Locations and seasonal distributions of drive hunts which were accompanied to sample food availability and collect rumen contents. Ituri Forest, Zaire, 1981 to 1983.

Sample number	Map Location[a]	Date	Season[b]	Days	Drives	Total transect (km)	Forest types
1	K	Jun 81	M	4	21	12.3	mbau, mixed
2	R	Jul 81	M	9	44	25.4	mixed
3	K	Sep 81	L	4	28	8.2	mbau, mixed
4	E	Oct 81	L	4	22	8.3	mbau, mixed
5	M	Dec 81	L	4	19	11.5	mixed
6	B	Jan 82	D	5	23	14.6	mixed
7	A	Mar 82	E	4	24	9.8	mixed
8	K	May 82	E	5	34	10.0	mbau, mixed
9	P	Aug 82	M	5	25	11.8	mixed
10	B	Oct 82	L	5	21	10.1	mixed
11	K	Feb 83	D	5	31	8.5	mbau, mixed
12	S	Feb-Mar 83	D/E	5	32	5.7	mixed
13	I	May 83	E	3	17	5.0	mixed

[a] Locations shown on Figure 4-1.

[b] Season abbreviations: D, dry season; E, early wet season; M, mid wet season; L., late wet season.

APPENDIX 4-B

Characterisitcs of selected and avoided food species in diets of four species of upland duikers during nine sampling periods between December, 1981 and May, 1983, Ituri Forest, Zaire. [a]

Species	Food type	Y_o	Patch Weight	Item Size	Selection			
					C.m.	C.l.	C.c.	C.d.
			December, 1981					
Klainedoxa gabonensis	UF	62	L	2-4	+	+	+	-
K. gabonensis	RF	33	L	5	-	-	-	+
Ricinodendron heudelotii	RF	112	L	4		+	+	+
Alstonia boonei	UF		S	5		+	+	
Thonningia sanguinea	Fl	53	S	4		+	+	
Ficus 196	RF	33	L	3	-	-	+	-
Croton mubanga	R/UF	73	S	3	+	+	+	
Unknown 192	UF			3			+	
Uapaca guineensis	Fl		L	3	-	-	-	-
U. guineensis	UF	10	S	3	-	-	-	-
Amanjenje	R/UF			3	-	-	-	-
Unknown 205	S		S	3	+			
Annonaceae sp 1	S	100	S	3	+			
			January, 1982					
Celtis adolfi-fridericii	RF	236	S	3				+
Klainedoxa gabonensis	UF	62	S	4		+	+	+
Klainedoxa trillesii	RF	13	L	4	-	-	-	-
Foliage			S		+	+	+	+
Fungi			S	2-4	+		+	+
Thonningia sanguinea	Fl	59	S	4	+		+	
Anthocleista schweinfurthii	UF			4	+			
Ficus 220	R/UF	41	L	5			+	
Unknown 219	UF			3		+		
Combretum sp	UF		S	4	-	-	-	-
Albizzia gummifera	UF		S	5	-	-	-	-
Canthium sp	S		S	4		-		-

Appendix 4-B. Continued

Species	Food type	Y_o	Patch Weight	Item Size	Selection			
					C.m.	C.l.	C.c.	C.d.
March, 1982								
Klainedoxa gabonensis	UF	43	L	5	-	-	+	+
Irvingia wombolu	UF	61	L	5				+
Ricinodendron heudelotii	UF	94	L	4		+		
Ficus 4	RF	41	L	5				+
Blighia welwitschii	UF/S	178	L	4		+		
Musanga cercropioides	UF	30	L	5		+		+
Tarenna laurentii	UF	44	L	5		+		
Pancovia harmsiana	UF/S		S	3	+	+	+	+
Drypetes sp	Fl		S	2		-		
Kokou	UF	13	S	4	-	-	-	-
Uapaca guineensis	UF	10	S	3	-	-	-	-
Celtis adolfi-fridericii	UF		S	2	-	-	-	-
May, 1982								
Pancovia harmsiana	S		S	3	+	-	no	data
Klainedoxa gabonensis	RF	33	L	5	-	-	"	"
Cleistanthus michelsonii	UF	42	L	3	-	-	"	"
Celtis adolfi-fridericii	R/UF		L	3	-	-	"	"
Gilbertiodendron dewevrei	Fl	32	L	2	-	-	"	"
Unknown Sapindaceae	RF/S			4	+		"	"
Unknown 242	RF/S			3	+		"	"
Ricinodendron heudelotii	UF	92	L	4		+	"	"
Irvingia wombolu	UF	67	L	4		+	"	"
Diospyros crassiflora	Fl	86	L	4		+	"	"

Appendix 4-B. Continued

Species	Food type	Y_o	Patch Weight	Item Size	Selection			
					C.m.	C.l.	C.c.	C.d.
			August 1982					
Croton mubanga	RF	73	S	3	+	+	+	+
Cola lateritia	S	72	S	3	+		+	
C. lateritia	RF	40	S-L	4			+	
Blighia welwitschii	RF/S	178	L	3	+	+	+	+
Klainedoxa gabonensis	RF	33	L	5				+
Brachystegia laurentii	UF		S	4	+	-	-	-
B. laurentii	Fl	50	S	2	-	-	-	-
Landolphia spp	UF/S	48	L	5	-	+	+	+
Ricinodendron heudelotii	RF	112	L	4	-		-	+
Unknown 271	UF			3	+			
Kokou	RF	13	S	4	-	-	-	-
Koroso	UF		S	4		-	-	-
Uapaca guineensis	RF	10	L	3	-	-	-	-
Pancovia harmsiana	S		S	3	+			
Dasylepsis seretii	UF		S	3		-	-	-
Tarenna laurentii	UF	44	L	5	-	-	-	-
Nauclea xanthoxylon	UF			3				+
			October, 1982					
Bracystegia laurentii	S	317	L	3	+	-	+	-
Gilbertiodendron dewevrei	S	120	L	5		+	+	+
Landolphia spp	S	101	L	3	+	+	+	
Landolphia spp	RF	47	L	5	-	+	+	-
Irvingia wombolu	UF	67	L	5				+
Klainedoxa trillesii	RF	13	L	4	-	-	-	-
Klainedoxa gabonensis	RF	33	L	5	-	-	-	-
Combretum sp	UF		S	5	-	-	-	-
Kokou	RF	13	S	4	-	-	-	-
Duboscia viridifolia	RF		L	4	-	-	-	-
Canarium schweinfurthii	UF	32		3			+	
Ricinodendron heudelotii	RF	112	L	4	-	-	-	-
Unknown 6	RF			3			+	
Chrsophyllum sp	RF		L	4	-	-		-
Unknown 272	S		S	3	+			
Unknown 195	RF/S			3			+	

Appendix 4-B. Continued

Species	Food type	Y_o	Patch Weight	Item Size	Selection C.m.	C.l.	C.c.	C.d.
February, 1983								
Brachystegia laurentii	S	317	L	3	+	+	no	data
Klainedoxa gabonensis	UF	62	L	3	+	+		"
K. gabonensis	RF	33	L	5	-	-	"	"
Klainedoxa trillesii	RF	13	L	4	-	-	"	"
Annonaceae sp 1	S	90	S	3	+		"	"
Donella pruniformis	RF	45	L	5	+		"	"
Tarenna laurentii	UF	41	L	5	-	-	"	"
Musanga cecropioides	UF	33	L	5	-	-	"	"
February, March, 1983								
Bracyhstegia laurentii	S	317	S	3	+	-	+	-
B. laurentii	Fl	50	S	2				+
Cleistanthus michelsonii	UF	124	L	3	+	+	+	-
Klainedoxa gabonensis	RF	33	L	5	-	-	-	+
Klainedoxa trillesii	UF	16	L	4	-	+		-
Chlorophora excelsa	UF	200	L	4		+		+
Blighia welwitschii	UF/S	178	L	4	+	+		
Irvingia grandifolia	UF	231	L	4		+		+
Ricinodendron heudelotii	UF	92	L	4			+	
Gilbertiodendron dewevrei	Fl	32	L	2	-	-	+	-
Tetracarpidium conophorum	UF			4				+
Tarenna laurentii	UF	44	L	5	-	-	-	+
Diospyros crassiflora	Fl	86	L	2	+			
Uapaca guineensis	UF	10	L	3	-	-	-	-
Ficus 2	RF	30	S	2	-	-	-	-
Syzgium staudtii	RF/S			3	+			
Ficus 4	RF	44	L	4		+		
Ficus 3	RF	33		3		+		
Musanga cecropioides	UF	30	L	5				+

Appendix 4-B. Continued

Species	Food type	Y_o	Patch Weight	Item Size	Selection			
					C.m.	C.l.	C.c.	C.d.
			May, 1983					
Dacryoides edulis	UF	55	S	3	+			
Anthocleista schweinfurthii	UF			4			+	
Cola lateritia	UF	40	L	4	+			
Lipasa	UF/S	31	L	4	+	-	+	+
Phyllanthus pynaertii	UF	16	L	4		+		
Klainedoxa gabonensis	RF	33	L	5	-	-	-	+
Ficus 4	UF	41	L	4			+	
Irvingia grandifolia	UF	231	L	4				+
Blighia welwitschii	UF	178	L	4				+
Brachystegia laurentii	Fl	50	L	2	-	-	-	-
Grewia oligoneura	UF	45	L	3	-	-	-	-
Kokou	UF	13	S	4	-	-	-	-
Canthium sp	S		S	4	+			
Unknown 234	UF			3	+			
Diospyros crassiflora	Fl	86	L	2		+		
Unknown 279	UR			3			+	
Canarium	UF	32	L	4	-	-	-	-
schweinfurthii	UF	32	L	4	-	-	-	-
Unknown Sapotaceae	UF		L	4	-	-	-	-
Diospyros sp	RF			4			+	
Unknown legume	S		S	4	+			

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* Notes and abbreviations.
Food type: UF, unripe fruit; RF, ripe fruit; S, ripe/unripe seed; Fl, flower.

Y_o equals adjusted dry matter yield:

$$Y_o = Y \quad N/(ADF + CT)$$

where Y = edible dry matter density
N = nitrogen content (mg/g wet weight)
ADF = acid detergent fiber content (mg/g wet weight)
CT = condensed tannin content (mg/g wet weight).

Where no values are shown, Y_o was not determined.

Appendix 4-B. Continued

Notes and abbreviations continued.

Patch weight: S, small food patch weight (W < 100 g); L, large food patch weight (W ≥ 100 g). Where no symbol is shown, food patch weight was not known.

Item size: 2, < 1.0; 3, 1.0 - 2.5; 4, 2.5 - 5.0; 5, 5.0 - 10.0 centimeters.

Selection: Duiker species symbols: C.m., *C. monticola*; C.l., *C. leucogaster*; C.c., *C. callipygus*; C.d., *C. dorsalis.*

+ indicates selected food species; - indicates avoided food species; no symbol indicates use in proporiton to availability and/or food rare in forest and minor in diet, selection could not be assessed.