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Diets of Large Mammals in the Woodlands around Lake Kariba, Rhodesia

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Summary. Large mammals that formerly occupied the Kariba basin of the Middle Zambezi Valley have, since it was flooded, been forced to live in a restricted range of deciduous woodland habitats. Feeding records in a study area on the shore of Lake Kariba showed that most herbivore species were browsers, and that only the tree components of their diets varied significantly between vegetation types. The common species varied a proportion of their diets seasonally. However, each depended upon a small range of food staples which differed from those of other species and acted as food refuges for part of the year. Diets overlapped during the wet season because of diversification, and in the late dry season because of common use of a restricted range of plants remaining green. There was a good correlation between the ability of a species to avoid dietary overlap and its biomass in the study area. The chance of interspecific competition occurring increased in the late dry season when most of the species would formerly have migrated from the study area to the flood plain. Despite the enforced occupation of only part of their former annual range the more common herbivores maintained a considerable degree of ecological separation through utilisation of different foods.

Introduction

The flooding of part of the Middle Zambezi Valley to form Lake Kariba reduced the range of habitats that had formerly been available to herbivores. In particular it deprived them of the riverine habitats to which most species used to migrate at the height of the dry season in the unflooded valley.

Child and Wilson (1964), Gwynne and Bell (1968), Lamprey (1963), Talbot and Talbot (1962), Van Zyl (1965) and Weir and Davison (1965) have shown that ecological separation of large mammalian herbivores in Africa is mainly due to their differential occupation of habitat types and the selection of distinct diets. Seasonal migration may play an important part in ecological separation of species, and I have suggested (Jarman, in press) that this was so in the unflooded Zambezi valley.

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Flooding the valley has disrupted this seasonal migration, reducing the opportunity for this form of species separation.

This paper describes the diets utilised by herbivores in a study area in the deciduous woodlands on the shore of Lake Kariba. Variations in each species' diet in different vegetation types and in different seasons are discussed, and the similarity of diets between species is assessed. The extent to which species utilise distinct diets as one aspect of their ecological separation in the present restricted range of habitats available to them is explored.

The Study Area

The floor of the Middle Zambezi Valley is broad, and consists of a riverine flood plain and terraces of ancient alluvium; steep escarpments form the valley walls. Kariba dam was closed in December 1958. By late 1963 the riverine forest of evergreen trees (*Tamarindus* and *Trichilia* spp.), the flood plain grasslands and *Acacia albida* Del. savanna, and the ancient alluvial terraces whose vegetation resembled that of the escarpment hills, had been inundated along 240 km of the valley above Kariba, forming a lake of about 5500 km^2. The habitat range of the large mammals was thereby restricted to the unflooded deciduous woodlands of the escarpment hills that now form the lake shore. Nearly half the area of the valley was flooded.

The study area lies in the escarpment hills and is part of the Chete Game Reserve on the southern shore of Lake Kariba, between 17°08′ to 17°18′ S and 27°40′ to 27°54′ E. Its vegetation comprises a complex of deciduous woodlands, usually classified as *Colophospermum mopane* (Kirk ex Benth) woodlands and savanna (Rattray, 1961). *Combretum* woodland is found on ridge tops, and is dominated by *C. apiculatum* Sond., *C. elaeagnoides* Kloetzsch, and *C. celastroides* Welw. ex Laws, growing in that order of frequency. A low-canopied, dense woodland, dominated by *Meiostemon tetrandrus* (Exell) Exell and Stace, grows on deeper sandy soils. Faulting and erosion have produced a range of hillside types each supporting a characteristic tree flora beneath which creepers and succulents are common. At the base of slopes flat clay areas carry woodlands dominated by *Colophospermum mopane*, the mopani. Other vegetation types occur in the escarpment hills but do not fall within the area sampled in the study. These deciduous woodlands support very poor grass and herb growth, which commonly covers less than 20% of the ground, in contrast to the *Acacia albida* savanna and the grasslands of the flood plain.

The study area receives about 650 mm of rain each year between late November and April; rain is unusual outside this period. From the end of the rains until August there is a cold dry season, and from September to the start of the rains an increasingly hot dry season. Most food plants produce leaves and flowers after the rains begin, and growth ceases by late June: leaf fall continues until the next rains. Duration of leaf growth depends upon the duration and amount of rain falling. Some shrubs and trees, including *Diospyros quiloensis* (Hiern). F. White, *Boscia* and *Maerua* spp., retain green foliage in all seasons, and are referred to here as evergreen species.

The large mammal species recorded in the Middle Zambezi Valley are listed in Table 1; 23 of the 26 recorded species occurred in the deciduous woodlands of the study area. Jarman (in press) describes the seasonal pattern of distribution of herbivore populations in the unflooded valley where animals have access to the deciduous woodlands of the escarpment hills and ancient alluvial terraces as well as to the *Acacia albida* and evergreen woodlands and grasslands of the flood plain. Hippopotamus and waterbuck were found to utilise the rich grass cover of the flood plain throughout the year. Most other species moved into the deciduous woodlands during the rains, and retreated to lower catena levels and the flood plain during the dry season. Rhinoceros, however, made very littly use of the flood plain, continuing to feed in the deciduous woodlands throughout the dry season. Kudu made less use of the flood plain than did elephant, impala or buffalo, but more than did rhinoceros. The deciduous woodlands were thus found to be occupied most densely during their short productive period in the rains, after which most animals turned to the prolonged productivity of the flood plain.

Table 1. *Large mammals of the Middle Zambezi Valley. Those recorded in the study area marked* +

Vervet monkey	*Cercopithecus aethiops* L.	+
Baboon	*Papio ursinus* Kerr	+
Jackal	*Canis adustus* Sundevall	+
Wild dog	*Lycaon pictus* Temminck	+
Spotted hyaena	*Crocuta crocuta* Erxleben	+
Leopard	*Panthera pardus* L.	+
Lion	*Panthera leo* L.	+
Elephant	*Loxodonta africana* Blumenbach	+
Black rhinoceros	*Diceros bicornis* L.	+
Zebra	*Equus burchelli* Gray	+
Bush pig	*Potamochoerus porcus* L.	+
Warthog	*Phacochoerus aethiopicus* Pallas	+
Hippopotamus	*Hippopotamus amphibius* L.	+
Common duiker	*Sylvicapra grimmia* L.	+
Grysbok	*Raphicerus sharpei* Thomas	+
Klipspringer	*Oreotragus oreotragus* Zimmermann	+
Reedbuck	*Redunca arundinum* Boddaert	+
Waterbuck	*Kobus ellipsiprymnus* Ogilby	
Impala	*Aepyceros melampus* Lichtenstein	+
Roan antelope	*Hippotragus equinus* Desmarest	
Sable antelope	*Hippotragus niger* Harris	+
Bushbuck	*Tragelaphus scriptus* Pallas	+
Nyala	*Tragelaphus angasi* Gray	
Greater kudu	*Strepsiceros strepsiceros* Pallas	+
Eland	*Taurotragus oryx* Pallas	+
Buffalo	*Syncerus caffer* Sparrman	+

This pattern of habitat occupation has been disrupted by the flooding of the valley to form Lake Kariba. The flood plain and ancient alluvial terraces having been inundated, all herbivore species must now stay in the deciduous woodlands all year round.

During the filling of the lake animals ousted from the valley floor moved in front of the rising waters into the escarpment hills. This is clear from records of the recapture of marked animals (records of the Department of National Parks and Wildlife Management), and there were no indications of animals moving up or down stream into the unflooded parts of the Middle Zambezi Valley.

Later in the paper the extent of overlap of the diet has been related to the biomass of the species in the study area. The biomass figures were obtained from densities calculated from the transect records (Jarman, 1968), and mean individual weights taken from my own, or published, records. These published sources are quoted in Table 18.

Unless another test is specified, all statements of significance of difference are based upon Chi²-tests of 2×2 or $2\times n$ contingency tables, using the observed numbers of records and a probability level of $p<0.05$.

Results

Nearly a thousand separate patrols were made during the study. Visibility varied with stage of vegetation growth, and the set of transects sampled areas varying from 0.41 km² in the wet season to 0.83 km² in the late dry season. A patrol of the three transects sampled between 1.4 and 2.8% of the study area, and the accumulated sample area for the whole study period was 565 km². This was divided between the major vegetation types as follows:

Combretum woodland	43.0%
mopani woodland	35.4%
hillside woodland	12.0%
mixed woodland	7.3%
Meiostemon woodland	2.3%

The relative areas of these vegetation types, taken from a vegetation map (Jarman, 1968), in the study area were:

Combretum woodland	48.6%
mopani woodland	30.7%
hillside woodland	16.0%
Meiostemon woodland	4.7%

Mixed woodland was not mapped as such since it usually constituted the ecotone between *Combretum* woodland and one of the other three major types. Clearly the transects sampled an area representative of the vegetation types near this part of the lake shore.

Although the less numerous nocturnal or crepuscular herbivores may have been under-represented in the records, trial patrols at other times of day supported the assumption that, between 07.15 and 09.00 hrs, the common species were sampled in their feeding habitats. Feeding records were collected on 35 to 55% of the occasions on which common species were sighted during transect patrols.

The results were analysed for:

1. the role of grasses in the diet of each species,
2. variation between diets of each species in different vegetation types,

3. variation between diets of each species in different seasons,
4. the similarity of diets between species, expressed as overlap of diets, and
5. the relation between the extent of dietary overlap and species' biomasses in the study area.

1. The Role of Grasses in the Diet of Each Species

For most species the number of records accumulated during the study was low, and did not justify detailed analysis. However they are presented in Table 2, where the proportion of grass in the diet is used to place each herbivore species in a scale of relative dependence upon grazing or browsing. There is an obvious preponderance of browsers in the spectrum of herbivores. Hippopotamus and waterbuck were observed rarely in the study area and provided no feeding records. Both are grazers, and their absence and the preponderance of browsers among the herbivores, reflect the lack of grass cover in the escarpment woodland.

Table 2. *The proportion of grass recorded in the diet of herbivores during the study*

Species	Sample size	Grass records	% Grass
Rhinoceros	255	0	0
Kudu	408	6	1.5
Klipspringer	85	2	2.4
Elephant	906	39	4.3
Impala	817	38	4.6
Bushbuck	18	2	11.1
Bushpig	5	1	20.0
Duiker	9	2	22.2
Buffalo	78	36	46.2
Zebra	20	15	75.0
Warthog	109	109	100.0

2. Diets in Different Vegetation Types

Elephant, impala, kudu, rhinoceros and buffalo each provided records which have been analysed for variation in diets between vegetation types. The major vegetation types intergrade to some extent where they are contiguous, and feeding records from these intermediate zones have been omitted in analysis.

Elephant. The 891 records that could be assigned to vegetation types are shown in Table 3. In mopani woodland the eponymous species

Table 3. *The diets selected by elephant in the five major vegetation types.* C. elaeagnoides *and* C. mopane *differed significantly ($p \leq 0.05$) in their occurrence in the diets recorded from* Combretum *and mopani woodlands*

Food plant	*Combretum* woodland (%)	Mopani woodland (%)	Hillside vegetation (%)	Mixed woodland (%)	*Meiostemon* woodland (%)
Colophospermum mopane	32.2	63.8	58.8	53.1	9.1
Combretum elaeagnoides	30.1	9.6	12.3	14.8	20.5
Combretum apiculatum	13.7	10.2	13.2	4.9	27.3
Croton gratissimus	1.2	4.6	1.8	4.9	0
Strychnos innocua	4.6	3.7	2.6	2.5	4.5
Combretum celastroides	1.5	0.3	0	0	22.7
Erythroxylum zambesiacum	2.4	1.2	0	3.7	2.3
Boscia spp.	0.3	0	0.9	0	2.3
Diospyros quiloensis	1.0	0.6	0	0	0
Grasses	4.9	1.2	0.9	7.4	0
Meiostemon tetrandrus	0.6	0.3	0	0	4.5
Other species	7.6	4.3	9.6	8.6	6.8
Totals or records	329	323	114	81	44

Table 4. *The diet selected by elephant in three woodland types compared with the occurrence of tree species in those woodlands*

Species	Mopani woodland diet occurrence		*Combretum* woodland diet occurrence		*Meiostemon* woodland diet occurrence	
	%	%	%	%	%	%
Colophospermum mopane	63.8	70–95	32.2	5–20	53.1	1–10
Combretum spp.	20.1	5–25	45.3	60–85	70.5	3–20
Croton gratissimus	4.6	0–5	1.2	10–25	0	1–10
Meiostemon tetrandrus	0.3	0–10	0.6	5–10	4.5	70–90

dominates both the woodland and the diet, just as *Combretum* species do in their woodland. The only vegetation type in which *Meiostemon* formed more than 1% of the diet was *Meiostemon* woodland.

Although diet varied with habitat to this extent, it is clear from Table 4 that in several features selected diets more closely resembled each other than they resembled the composition of the vegetation types in which they were recorded. Mixed woodlands and hillside have not been included because each is so varied in its composition. Many common trees in these two vegetation types, such as *Kirkia acuminata* Oliv., *Sterculia africana* (Lour). Fiori, *Terminalia* and *Commiphora* species, were relatively infrequent in the utilised diet, although each was recorded as eaten during the study.

Table 5. *The diet selected by rhinoceros in the five major vegetation types*

Food plant	*Combretum* woodland (%)	*C. mopane* woodland (%)	Hillside vegetation (%)	Mixed woodland (%)	*Meiostemon* woodland (%)
Meiostemon tetrandrus	9.7	20.0	15.9	5.9	27.6
Combretum celastroides	3.2	0	2.9	0	13.8
Holmskioldia spinescens	11.3	10.8	23.2	29.4	6.9
Euphorbia espinosa	3.2	4.6	5.8	5.9	17.2
Boscia species	38.7	36.9	24.6	35.3	3.4
Strychnos innocua	8.1	1.5	4.3	5.9	10.3
Diospyros quiloensis	12.9	7.7	4.3	5.9	10.3
Combretum elaeagnoides	0	1.5	8.7	0	3.4
Other species	12.9	16.9	10.1	11.8	6.9
Total of records	62	65	69	17	29

Rhinoceros. The 242 rhinoceros feeding records that could be assigned to vegetation types are shown in Table 5. Significant differences could not be found between diets in each vegetation type. Indeed there is a considerable similarity between the frequency of utilisation of many species in all vegetation types except *Meiostemon* woodland. The only eponymous species well represented in the diet from its vegetation type is *Meiostemon*. In the rhinoceros' diet, like the elephant's, *Combretum celastroides* is important in *Meiostemon* woodland.

Impala. Of the impala feeding records 782 could be assigned to vegetation types, and these are shown in Table 6. Impala were largely dependent upon the herb and shrub communities, and the similarity of these in each vegetation type is reflected in the insignificance of differences between the recorded diets.

Kudu. The 403 kudu feeding records that could be assigned to vegetation types are shown in Table 7. Kudu, although taking a high proportion of herbs and shrubs, utilise more tree species than do impala. Consequently three tree species, *Diospyros quiloensis*, *Combretum elaeagnoides*, and *Croton gratissimus* Burch., occurred at significantly different frequencies in the diets from the two major vegetation types (mopani and *Combretum* woodlands), while the most abundant herb, *Holmskioldia spinescens* (Klotzsch) Vatke, and the most frequent shrubs, *Boscia* spp., in the utilised diets differed insignificantly in occurrence.

Table 6. *The diet selected by impala in the five major vegetation types*

Food plant	*Combretum* woodland (%)	*C. mopane* woodland (%)	Hillside vegetation (%)	Mixed woodland (%)	*Meiostemon* woodland (%)
Disperma crenatum	62.7	50.6	46.5	44.4	50.0
Boscia species	4.4	11.1	8.5	0	0
Holmskioldia spinescens	14.3	18.9	19.7	27.8	0
Commiphora africana	2.7	7.2	7.0	3.7	0
Combretum elaeagnoides	1.7	1.1	4.2	5.6	0
Diospyros quiloensis	1.5	0.6	1.4	1.9	0
Adansonia digitata flower	1.7	0	0	0	0
Roots and bulbs	1.7	1.1	2.8	0	0
Grasses	2.7	4.4	8.5	3.7	0
Other species	6.5	5.1	1.4	13.0	50.0
Meiostemon tetrandrus	0.0	0.0	0.0	0.0	0.0
Total of records	475	180	71	54	2

The differences between the incidence of the following species in the diets selected in *Combretum* and *C. mopane* woodlands were significant at the indicated level: *Disperma crenatum* $p \leqq 0.005$; *Boscia* species $p \leqq 0.005$; *Commiphora africana* $p \leqq 0.010$.

Table 7. *The diet selected by Kudu in the five major vegetation types*

Food plant	*Combretum* woodland (%)	*C. mopane* woodland (%)	Hillside vegetation (%)	Mixed woodland (%)	*Meiostemon* woodland (%)
Croton gratissimus	41.0	58.0	46.2	41.2	23.8
Combretum apiculatum	2.6	0.6	7.7	0	0
Holmskioldia spinescens	7.7	12.4	2.6	5.9	4.8
Diospyros quiloensis	14.7	5.9	12.8	23.5	19.0
Boscia species	3.8	6.5	12.8	0	14.3
Combretum elaeagnoides	9.0	2.4	5.2	11.8	14.3
Meiostemon tetrandrus	1.9	1.2	2.6	0	9.5
Combretum celastroides	2.6	2.4	5.2	0	0
Strychnos innocua	1.9	2.4	0	0	4.8
Grasses	1.3	1.8	0	11.8	0
Other species	13.5	6.5	5.2	5.9	14.3
Total of records	156	169	39	17	22

The difference between the incidence of the following species in the diets selected in *Combretum* and *C. mopane* woodlands were significant at the level indicated: *Croton gratissimus* $p \leqq 0.005$; *Diospyros quiloensis* $p \leqq 0.010$; *Combretum elaeagnoides* $p \leqq 0.025$.

Table 8. *The composition of the recorded diet of elephant throughout the year, and in each of three seasons*

Food plants	All year (%)	Seasons Wet (%)	Early dry (%)	Late dry (%)
Colophospermum mopane	47.7	39.5	55.6	49.7
Combretum elaeagnoides	17.9	20.3	14.9	17.6
Combretum apiculatum	12.1	13.2	12.3	10.5
Other trees	15.0	12.3	15.8	19.1
Evergreen herbs and shrubs	1.8	0	1.4	3.1
Other herbs and shrubs	1.2	3.7	0	0
Grasses	4.3	11.0	0	0
Total of records	906	354	268	284
Total of species	37	27	17	23

Table 9. *Proportion of the recorded diet of elephant formed by grasses and herbs in the months of the wet season*

	December (%)	January (%)	February (%)	March (%)	April (%)	May (%)
Grasses	0	2.5	8.3	21.4	8.2	0
Herbs	0	2.5	2.3	4.7	2.3	0

3. *Seasonal Diets*

Elephant. Table 8 shows that the majority of elephant feeding records were of tree species, of which mopani formed over half. Seasonal variation in the utilised diet was obvious, although certain species predominated throughout the year. The utilisation of grasses and non-evergreen herbs and shrubs was confined to the wet season, and a more detailed analysis of their contribution to the diet is given in Table 9.

The parts of trees utilised by elephant varied during the year. In the wet season they ate leaves and twigs, which continued to form the bulk of their diet in the early dry season. In June elephant began to eat branches and to strip bark from mopani. At the same time fruits of some *Commiphora* species and *Sclerocarya caffra* Sond. were found in faeces. As trees lost leaves the amount of woody tissue in the diet increased. From mid-August until the end of the dry season elephant broke down and ate the soft sap-filled wood of *Adansonia digitata* L. and *Sterculia*. These were either pushed over or eaten through until felled after which the branches were eaten in preference to the trunk. *Afzelia quanzensis* Welw., *Kirkia*, and *Commiphora karibensis* Wild were also pushed over and eaten in this season and barking was recorded on mopani and

Afzelia. Some trees which came into leaf before the rains broke, such as *Kirkia* and *Afzelia*, were heavily used at the very end of the dry season as well as in the wet season. Of 25 tree species recorded as eaten by elephant, 15 were recorded in the wet season, 16 in the early dry, and 21 in the late dry season. The use of three of these was confined to the wet season, none to the early dry, and six to the late dry season.

In contrast to other herbivores elephant ate few evergreen trees or shrubs.

Rhinoceros. The occurrence of the eight most commonly recorded rhinoceros food plants is shown in Table 10. There is a clear change of diet from wet and early dry seasons to late dry season; the shrubs *Holmskioldia* and *Euphorbia espinosa* Pax and the small tree *Meiostemon*, strongly represented in the wet season records, are replaced by the evergreen tree *Diospyros quiloensis* and evergreen shrubs of the genus *Boscia* in the late dry season. Of the 29 recorded food species, 12 were recorded only in the wet season; apart from the trees mopani and *Lonchocarpus* sp. these were all herbs or shrubs. Three species, the early-leafing shrub *Commiphora africana* (A. Rich.). Engl., the evergreen shrub *Boscia salicifolia* Oliv., and *Combretum apiculatum*, occurred in the late dry season records only.

Table 10. *The composition of the recorded diet of rhinoceros throughout the year, and in each of three season*

Food plants	All year (%)	Seasons		
		Wet (%)	Early dry (%)	Late dry (%)
Meiostemon tetrandrus	18.7	30.0	23.7	3.4
Holmskioldia spinescens	14.8	22.0	13.6	7.9
Euphorbia espinosa	6.7	10.0	10.6	0
Strychnos innocua	5.1	5.0	4.5	5.6
Combretum celastroides	3.1	4.0	3.0	2.0
Combretum elaeagnoides	3.1	3.0	3.0	3.4
Diospyros quiloensis	8.2	4.0	3.0	16.9
Boscia spp.	26.9	4.0	30.1	50.6
Total of records	255	101	66	88
Total of species	29	23	13	14

Impala. Table 11 shows that *Disperma crenatum* (Lindau) Milne-Redh., the most common food plant recorded for impala, was most frequent in the diet during the early dry season when impala's diet contained fewest species. Like elephant, impala took a wide range of grasses and herbs during the wet season, but were dependent upon a small range of herbs and shrubs in the early dry season. The role of grasses in the wet season diet is shown in Table 12. The shrub *C. africana* was conspicuous in the diet of the late dry season as it comes into leaf before all the other small deciduous plants; impala continued to use it in the early wet season. Evergreen shrubs of the genus *Boscia* were important in the late dry season diet, but not the evergreen tree *Diospyros quiloensis*. The fallen flowers of *Adansonia* were eaten in November and December and the fallen seeds of mopani throughout the year.

Table 11. *The composition of the recorded diet of impala throughout the year and in the three seasons*

Food plants	All year (%)	Seasons		
		Wet (%)	Early dry (%)	Late dry (%)
Disperma crenatum	55.8	48.4	72.8	53.5
Holmskioldia spinescens	16.3	28.3	6.8	5.7
Grasses	4.6	9.0	0.5	0
Combretum elaeagnoides	1.9	1.6	2.1	2.0
Roots and bulbs	1.5	0.3	1.0	3.7
Commiphora africana	4.3	4.1	0	8.2
Diospyros quiloensis	1.6	0.3	2.6	2.9
Boscia spp.	5.7	0	7.3	13.0
Total of records	817	373	194	250
Total of species	41	28	15	18
Species confined to that season		15	5	4

Table 12. *Proportion of the recorded diet of impala that was formed by grasses during the months of the wet season*

	December (%)	January (%)	February (%)	March (%)	April (%)	May (%)
Grasses	0	1.1	4.8	20.2	10.2	0

Kudu. Croton gratissimus was by far the most important of the 30 species recorded as being eaten by kudu, and it occupied a place in the diet similar to that of *Disperma* for impala or mopani for elephant. Like those two species, *Croton* was at its least important during the wet season, as can be seen in Table 13. Again a greater array of species was recorded in the wet season than in the dry. The semi-evergreen herb *Courbonia glauca* (Klotzsch) Briq. was eaten in the early and late dry seasons, and *C. africana* at the end of the late dry season. While elephant and impala showed little seasonal variation in their use of *Combretum* species, kudu confined their use of three *Combretum* species to the wet and early dry seasons only, *C. elaeagnoides* being taken in all seasons.

To test this assertion, the rank orders of the five species in the biomass sequence (Table 18) and in the table of overlap upon their diet by the other four species combined (Table 16) were tested for correlation. Using the method described by Siegel (1956), the Spearman Rank Correlation Coefficient was calculated as 0.9, and the Kendall Rank Correlation Coefficient as 0.8. In each case the null hypothesis, that overlap and biomass were unrelated, is rejected with a probability, $P < 0.05$.

As an extension of this hypothesis, the overlap in selected diet between pairs of species (Table 17) should be related to their relative biomasses. The overlap between two species high in the biomass sequence should be low and that between two species low in the sequence should be high. The overlap between the diet of any one species and the diets of the other four separately should be ranked in the inverse order to their ranking in the biomass sequence. If the overlap between pairs of species is plotted against the product of their biomasses, regression analysis can be applied to the resulting curve to determine whether the two values are correlated. Doing this and using the formula given by Simpson *et al.* (1960, p. 240), the Pearson coefficient of correlation, $r = -0.719$, indicating a negative correlation significant at the level, $p \leq 0.02$. This again supports the hypothesis that the ability to avoid overlap in diet was related to the ability to sustain a higher or lower biomass, although no causal relationship can be demonstrated.

Discussion

Throughout the paper diets are not described as selected because too few data were collected to allow direct comparison between food eaten and food available. Except for elephant which were able to utilise trees out of the reach of other herbivores, the major species fed from a comparable range of heights of plants. Since their diets differed when feeding in the same area, it is resonable to suppose that these herbivores were, in fact, selecting their diets to some extent.

The sparseness of grasses in the plant communities of the study area was reflected in the predominance of browsing among the herbivores. Even grazers such as buffalo and zebra took more browse than has been reported in other studies; for instance, Lamprey (1963) reported buffalo taking 93.6% and zebra 92.6% grass. *Hippopotamus* and waterbuck, both grazers, were rare in the study area, presumably for lack of suitable grassland feeding habitat since both had been common in that part of the valley before flooding.

Vegetation types were distinguished by their distinctive tree communities rather than by their more similar herb communities. Consequently dietary differences between vegetation types were greatest for herbivores which ate many trees, such as elephant, and least for those which ate herbs, like impala. The contrast between the short period of food abundance in the wet season and the depleted food resources of the late dry season influenced the diets of the common herbivores. All of them augmented their diets in the wet season, using the ephemeral productivity of grasses and herbs, and taking temporarily palatable plants that later disappeared from their diets. In the early dry season herbivores reverted to their food staples, showing least variety in their diets. In the late dry season they again expanded their diets to include evergreen plants and the few deciduous trees and shrubs which produced leaves and flowers before the rains. This sequential use of foods obviously made most complete use of the resources. The staples upon which each of the five most numerous herbivores depended were different, and by this diversification of dependence the community made greater use of resources than would have been possible if all diets had been similar.

Dependence upon different food staples was the basis for the ecological separation through diets of the five most common herbivores. Separation was not absolute, diets of pairs of species showing varying degrees of similarity in different seasons, measured here as overlap between diets. In general overlap was greatest during the period of augmentation of diets in the wet season, least during the reversion to food staples in the early dry season, and increased again in the late dry season as herbivores turned to the few evergreen and early-leafing species for food. It is probable that the extensive overlap in the wet season did not indicate extensive competition for the abundant and, to some extent, replenishable resources, since species were able to revert to much more distinct diets as soon as the productive period was past. These distinct diets were as readily available in the wet season as in the early dry season, and the fact that species did not use them strongly suggests that they were under no competitive pressure to do so. This is clearly a situation in which species are retreating to food refuges, in the sense of Reynoldson (1966) and Reynoldson and Davies (1970), at a time of diminished food resources, thereby reducing the possibility of competition.

However, the increasing similarity of diets in the late dry season probably did indicate increasing competition, although without figures for consumption and availability this can not be demonstrated. At this stage the seasonal distribution of herbivores in the unflooded valley must be recalled. I have shown (Jarman, in press) that in the unflooded valley most herbivore species dispersed into the deciduous woodlands during the wet season, remaining there for varying proportions of the early dry season. In those seasons they occupied deciduous woodlands like those sampled in this study. However in the late dry season in the unflooded valley most species migrated to the flood plain and riverine habitats, taking advantage of the prolonged productivity and water resources of those habitats. This the animals in the flooded valley can no longer do. So while the low competition between species in the deciduous woodlands in the wet and early dry seasons represents the natural, pre-flooding, situation, the increased competition in the late dry season represents an artificial situation arising because animals are no longer able to migrate to the lower catena levels.

Rhinoceros, unlike the other common species, used not to migrate to the flood plain in the unflooded valley, but remained in deciduous woodlands all year. Unlike the other species in the study which continued to use the same food staple in the late dry as in the wet and early dry seasons, rhinoceros changed their food staples, eating a range of herbs, shrubs and small trees in the wet season, and depending on evergreen trees and shrubs in the late dry season. In the unflooded valley they had enjoyed exclusive use of these evergreen plants in the late dry season, but during the study these were heavily used by other, more numerous species. This pattern of food use, appropriate to the rhinoceros' life in the unflooded valley, exposed the species to considerable competition for its dry season food staple in the conditions of the study.

General Conclusions

Three aspects of ecological separation through diets can be seen here.

a) There was dietary augmentation during the wet season, probably without much competition, which conserved the resources of food staples.

b) Species placed much dependence upon food staples which were distinct from those of other species, and may be considered as food refuges. These were most obviously effective during the early dry season.

c) In the unnatural circumstances of occupation of the deciduous woodlands throughout the late dry season, species accepted a range of specifically dry season foods.

Rhinoceros, the only natural occupant of the area at that season, placed most dependence upon these foods, and as a consequence its diet was extensively overlapped by those of the other, more numerous species.

During the period of the study the five most plentiful herbivore species used diets which reduced the chances of interspecific competition for food in the wet and early dry seasons, but in the late dry season the use by all five species of a common set of plants must have increased the chances of competition. If it occurred, this competition would have fallen most heavily upon rhinoceros.

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References

Bubenik, A. B.: Le rhythme nycthéméral et le régime journalier des ongulés sauvages. Problèmes théoriques. Rhythme d'activité du chevreuil. Mammalia 24, 1–66 (1960).

Child, G., Wilson, V. J.: Observations on ecology and behaviour of roan and sable in three tsetse control areas. Arnoldia 1 (16), 1–8 (1964).

Gwynne, M. D., Bell, R. H. V.: Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature (Lond.) 220 (5165), 390–393 (1968).

Harker, K. W., Taylor, J. I., Rollinson, D. H. L.: Studies on the habits of Zebu cattle. 1. Preliminary observations on grazing habits. J. agric. Sci. 44, 193–198 (1954).

Horn, A. S.: Measurement of "overlap" in comparative ecological studies. Amer. Naturalist 100, 419–424 (1966).

Hughes, G. P., Reid, D.: Studies on the behaviour of cattle and sheep in relation to the utilization of grass. J. agric. Sci. 41, 350–366 (1951).

Jarman, P. J.: The effects of the creation of Lake Kariba upon the terrestrial ecology of the Middle Zambezi Valley, with particular reference to the large mammals. Ph.D. thesis, Manchester University (1968).

— Seasonal distribution of large mammal populations in the unflooded Middle Zambezi Valley. J. appl. Ecol. (in press).

Lamprey, H. F.: Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. E. Afr. Wildl. J. 1, 63–92 (1963).

— Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and Masai steppe in Tanganyika. E. Afr. Wildl. J. 2, 1–46 (1964).

Laws, R. M.: Age criteria for the African elephant, *Loxodonta a. africana*. E. Afr. Wildl. J. 4, 1–37 (1966).

Rattray, J. M.: Vegetation of Southern Rhodesia. Kirkia 2, 68–93 (1961).

Reynoldson, T. B.: The distribution and abundance of lake-dwelling triclads—towards a hypothesis. Adv. ecol. Res. 3, 1–71 (1966).

— Davies, R. W.: Food niche and co-existence in lake-dwelling triclads. J. anim. Ecol. 39 (3), 599–617 (1970).

Siegel, S.: Nonparametric statistics for the behavioural sciences. New York-Toronto-London: McGraw-Hill 1956.

Simpson, G. G., Roe, A., Lewontin, R. C.: Quantitative zoology. Revised ed. New York: Harcourt, Brace & Co. 1960.