CHAPTER 9 – WILDLIFE

Contents

9.1 INTRODUCTION / 134

9.2 EXTINCT, RARE OR ANOMALOUS / 136

9.3 DISTRIBUTION, HABITAT, NUMBERS, BIOMASS / 137
  Forest/Thicket Components/ 137
  Savanna and Grassland Components/ 137
  Aquatic Components / 137
  Rock Outcrop Components / 142
  Summary of Distribution Patterns / 143

9.4 FLOODPLAIN FLUCTUATIONS / 143
  Features / 144
  Fluctuations / 144
  Grassland and Grazing Succession / 145
  Dimensions of the Succession / 147
  Savanna Sequences / 147
  Daily Movements between Savanna and Floodplain / 149
  Grazing Succession: Summary and Comparisons / 150

9.5 FOOD, FEEDING, CONDITION / 153
  Food / 153
  Pasture Condition / 154
  Physical Condition of the Wild Ungulates / 157

9.6 MOVEMENT AND MIGRATION / 158

9.7 NATALITY, MORTALITY AND THE SEASONS / 160
  Natality / 160
  Mortality / 160
  Drought / 162
  Flooding & Wet Years / 162

9.8 ANIMAL FEEDING ASSOCIATIONS / 162
  'Beaters' / 163
  'Caterers' / 163
  'Socializers' / 163

9.9 ROLE OF ANIMALS IN GEOECOLOGICAL SUCCESSION / 166
  Geoecological effects / 166
  Utilization modification of plant communities / 167
  Dispersal of woody plant seeds by animals / 167
  Implications & An Appreciation / 170

REFERENCES / 171

CHAPTER 9 – WILDLIFE

9.1 INTRODUCTION

The term wildlife is used here mainly in relation to the larger indigenous mammals (Table 9.1), but some reference is also made to the avifauna in the context of diversity, seed dispersal, succession, seasonality and associations with mammals.

In Gorongosa a large faunal diversity matches landscape variety and the multiplicity of ecosystems, habitats and ecotones produced by the juxtaposition and overlap of different substrates as elucidated in the preceding chapters. The greatest abundance and diversity of larger mammals is concentrated in the Rift Valley, where buffalo are numerically dominant (now c 15000). The largest species spectrum is contributed by neotragids (5) followed by 3 each of cephalophids, tragelaphids and alcephalids (with tsessebe recently extinct from the region) (Table 9.1). A total of 27 ungulates (2 recently extinct locally) occur in the system, with 9 larger carnivores (Fig 9.1).

The spectacularly rich wildlife of the Rift Valley is a consequence of the mosaic evolution of forest, thicket, and savanna, abutted against a floodplain grassland ecosystem of high primary productivity on base saturated soils. Habitat and faunal diversity can also be gauged by the recorded occurrence of 800 species of birds in the montane to mangrove transect of the Gorongosa – Cheringoma area (vide checklists of Rosa Pinto 1968, Clancey 1971).

The larger fauna, which is associated with 4 major habitats: (a) forest/thicket (b) savanna/grassland (c) wetlands, and (d) rock outcrops, is composed of elements from 8 zoogeographic ranges of larger herbivores as derived from the distributional data in Dorst & Dandelot (1970).

(1) Widespread Savanna (eg. elephant, buffalo, warthog, oribi, black rhino, grey duiker)
(2) Widespread Forest (eg. tree dassie, bushpig, blue duiker, bushbuck)
(3) Widespread Wetlands (eg. hippo)
(4) Widespread Rock Outcrops (eg. klipspringer, rock dassie)
(5) Eastern and Southern Savannas (eg. wildebeest, Plains zebra, impala, Lichtenstein's hartebeest, sable, steenbok)
(6) Eastern Forest/Thick (eg. nyala, suni, Sharpe's grysbok, red duiker)
(7) Southern (tsessebe – recently extinct in area)
(8) Marine Indo-Pacific (estuarine and littoral) eg. dugong.

TABLE 9.1

LARGER MAMMAL SPECTRUM OF THE GORONGOSA ECOSYSTEM
(> 5 kg mass)

	HERBIVORES					
	GRAZER	MIXED	BROWSER	OMNIVORE	CARNIVORE	INSECTIVORE
PRIMATES						
Cercopithecids						
Chacma baboon *Papio ursinus*				x		
Samango monkey *Cercopithecus albigularis*				x		
Vervet monkey *Cercopithecus pygerythrus*				x		
PHOLIDOTE						
Manid						
Pangolin *Manis temmincki*						x
CARNIVORES						
Hyaenids						
Spotted hyaena *Crocuta crocuta*					x	
Felids						
*Cheetah *Acinonyx jubatus*					x	
Leopard *Panthera pardus*					x	
Lion *Panthera leo*					x	
Serval *Felis serval*					x	
Wildcat *Felis lybica*					x	
Canids						
Wild dog *Lycon pictus*					x	
Side-striped jackal *Canis adustus*				x		
Mustelids						
Clawless otter *Aonyx capensis*					x	
Spotted-necked otter *Lutra maculicollis*					x	
Honey-badger *Mellivora capensis*				x		
Viverrids						
Civet *Viverra civetta*				x		
TUBULIDENTATE						
Orycteropid						
Antbear *Orycteropus afer*						x
HERBIVORES						
Elephantids						
Elephant *Loxodonta africana*		x				
Equids						
Zebra *Equus burchelli*	x					
Rhinocerids						
*White rhino *Ceratotherium simum*	x					
Black rhino *Diceros bicornis*			x			
Suids						
Bushpig *Potamochoerus porcus*				x		
Warthog *Phacochoerus aethiopicus*	x					
Hippopotamids						
Hippo *Hippopotamus amphibius*	x					
Tragelaphids						
Kudu *Tragelaphus strepsiceros*			x			
Nyala *Tragelaphus angasi*		x				
Bushbuck *Tragelaphus scriptus*			x			
Hippotragids						
#Roan *Hippotragus equinus*						
Sable *Hippotragus niger*	x					
Reduncids						
Reedbuck *Redunca arundinum*	x					
Waterbuck *Kobus ellipsiprymnus*	x					
Alcephalids						
Lichtenstein's or Miombo hartebeest *Alcephalus lichtensteinii*	x					
#Tsessebe *Damaliscus lunatus*						
Wildebeest *Connochaetes taurinus*	x					
Antilopids						
Impala *Aepyceros melampus*		x				
Cephalophids						
Red duiker *Cephalophus natalensis*			x			
Blue duiker *Cephalophus monicola*			x			
Grey duiker *Sylvicapra grimmia*			x			
Neotragids						
Suni *Neotragus moschatus*			x			
Oribi *Ourebia ourebia*		x				
Klipspringer *Oreotragus oreotragus*			x			
Steenbuck *Raphicerus campestris*			x			
Sharpe's Grysbuck *Raphicerus sharpei*			x			
Bovinid						
Buffalo *Syncerus caffer*	x					
RODENTS						
Hystricids						
Porcupine *Hystrix africaeaustralis*				x		
Thryonomids						
Greater cane rat *Thryonomys swinderianus*	x					
Total	11	4	10	8	9	2(44)
Percent	25	9	23	18	20	

Recently extinct (between 1950 and 1970)
* Recently re-introduced

1973 Cheetah
1970 White rhino (extinct c. 1940 NW of Gorongosa Mt)

Of these the first, third and fifth groups contribute the greatest zoomass in the Gorongosa Ecosystem. The primates are represented by only two galagos, two monkeys and one baboon. In addition to the blue duiker another equatorial rain forest element, Fraser's flying squirrel ***Anomalurus derbianus***, occurs nearby in Zambezia District (Smithers & Tello 1976:136), and may well occur in the east of the system where it should be looked for in the ravine forests of the Cheringoma Plateau.

In a biome context only four of the seven major biomes (Tinley 1975) are represented by the larger mammals, these are: (1) Aquatic (eg. hippo), (2) Forest (eg. blue duiker, (3) Moist Savanna (eg. Lichtenstein's hartebeest, sable) and (4) Arid Savanna (eg. steenbok). The flora and avifauna however contribute elements representative of the remaining three biomes; Afro-temperate, Desert and Palaearctic Temperate (eg. Palaearctic bird migrants). Lechwe are confined to the floodplain systems of the Interior Continental Plateau; however another riverine ungulate, the sitatunga, may occur along the Zambeze in Mocambique (Smithers & Tello 1975:171–172).

Of the large faunal components the nyala has the smallest geographic range and is endemic chiefly to the Mocambique lowlands. Greater endemism in the Eastern Forest/Thicket Domain is exhibited by the flora and avifauna.

Until the arrival of the author at Gorongosa in August 1968, most of the faunal work in the region had been dedicated to building up collections for museum research, and the continued discovery of new records showed that much more field collecting was still required. These expeditions are summarised by Clancey (1971) for the avifauna and by Smithers & Tello (1976) for mammals. As a basis to the first stage ecological studies presented in this thesis, air surveys of the ecosystem and air counts of the large ungulates were completed twice a year at the height of the dry season (October) and in the wet season peak (February or March) for 5 consecutive years. However, due to pilot problems only 6 out of 10 were complete counts across the whole ecosystem. As wildlife conservation and the administration of natural parks and reserves was the responsibility of a Fauna Branch of the Veterinary Department in Mocambique, all disease aspects were left to veterinary staff. A detailed study of lion prey in Gorongosa was initiated including the collection and cataloging of all skulls and lower jaws recovered from kills. This study was taken over by Jose Tello, ex-chief warden of Gorongosa, now with the Ecological Studies Section of the Veterinary Institute in Maputo (Lourenco Marques).

9.2 EXTINCT, RARE OR ANOMALOUS

The tsessebe and roan antelope are recently extinct from the Gorongosa area, disappearing in the period between 1950 and 1970. Both species were recorded by Vaughan-Kirby (1899) and Vasse (1909) in the Midland, Rift Valley and Cheringoma sectors of the ecosystem and the latter author includes a photograph of a shot tsessebe on the Urema Plains. Up to my arrival in Gorongosa in 1968 persistent reports of several "black ***gondonga***" (***gondonga*** is the local tribal name for Lichtenstein's hartebeest) were received from the chief living in the Rift Valley savannas south of the park, between the Pungue River and the Rhodesia–Beira main road. During my time, several small herds were reported by professional hunters from the adjoining Lower Pungue–Buzi floodplain margins. In the summer of 1969/70 Dr. Donald Broadley from the Umtali Museum encountered a single roan male in the Inhamitanga area of the Cheringoma Plateau. Both these ungulates are threatened with extinction in Mocambique and tsessebe may already be extinct in the country.

White rhino occurred throughout Central Mocambique west of the Cheringoma Plateau until fairly recently. One of the last was shot northwest of Gorongosa Mountain in the Macossa area of the Midlands in 1935 (Sydney 1965:61, Fig 10). This species must have become extinct in the 1940's. The Macossa area is hill and valley terrain with 'sand rivers', similar to that of their last stronghold in Umfolozi, Zululand. Six white rhino were re-introduced to the Rift Valley sector of Gorongosa in midwinter of 1970 from Umfolosi Game Reserve.

Black rhino are recorded from all physiographic units in Gorongosa but the occurrence of only 3 to 5 individuals could be ascertained. It was estimated from reports by professional and tribal hunters plus our own field work that not more than 8 individuals occurred in the whole region.

Cheetah is another species recorded from the area, but was extinct from about 1950. Six were re-introduced to the northern sector of the park in 1973. No recent data is available on their status.

The steenbok which is abundant in the arid savannas of southern Africa is recorded from Central Mocambique only from the Macossa area (Smithers & Tello 1976: 122), and by the writer from one small area of the northern sector of the Rift Valley near the Lunga drainage in ***Acacia nilotica*** scrub on a sheet erosed site. The species was first recorded from the Gorongosa area by Vaughan-Kirby (1899: 289) who shot a steenbok 2 km south of the Nhandue River on the Rift floor, judged to be some 8 km SW of the Lunga site.

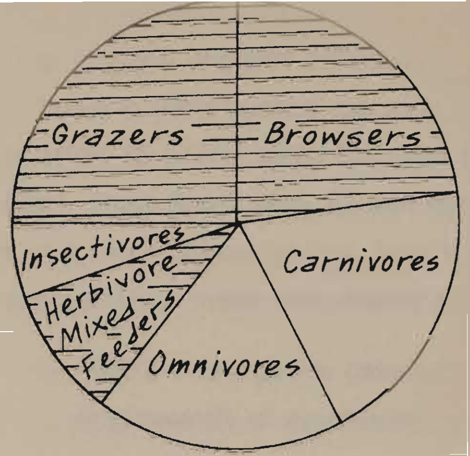


Fig 9.1 SPECIES COMPOSITION OF MAMMAL TROPHIC GROUPS. % of total ≥ 5 kg mass

▤ Herbivores

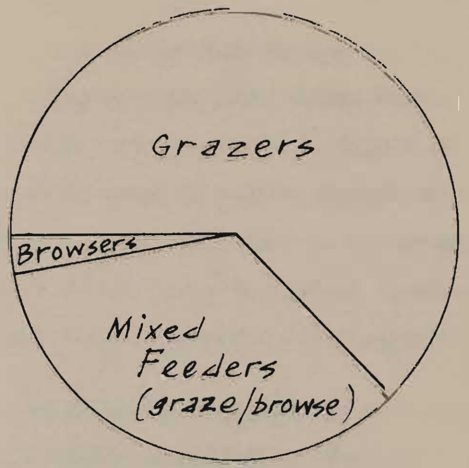


Fig 9.2 ZOOMASS CONTRIBUTION OF THE THREE LARGE HERBIVORE TROPHIC GROUPS IN THE RIFT VALLEY (UREMA TROUGH). Percent of total zoomass derived from air counts & rough estimates for purely browsing group.

The Zambeze Valley is roughly the line separating two races of the wildebeest, ***Connochaetes t. taurinus*** to the south and the Niassa or Johnston wildebeest, ***C. t. johnstoni,*** with white facial band, to the north. However, small populations of Niassa wildebeest occur amongst the nominate form in the Save Valley (Smithers & Tello 1976: 131–132).

Perhaps the most anomalous distributions pattern in Mocambique is that of giraffe. There are no records in historical times, or amongst old tribal hunters, of giraffe occurring north of the Save River environs. The Chegorongosa tribe, indeed, do not have a name for giraffe. Nor has the entire area of the Middle and Lower Zambeze Valley any historical record of their occurrence, despite expeditions such as those of Livingstone in 1856. The supposed record of giraffe near Tete noted by Du Plessis (1969:76–77) is a misinterpretation of a discussion on giraffe that Livingstone included whilst relating his traverse from Zumbo (Zambeze-Luangua confluence) to Tete. As a rinderpest outbreak in Kenya in 1960 resulted in the death of an estimated 70% of eland, buffalo and giraffe this virus disease is a likely suspect. However Livingstone's route from Zumbo was south of the river through ideal giraffe habitats interspersed with large areas of mopane, more than 30 years prior to the 1889–1896 rinderpest pandemic.

Ideal giraffe habitat, composed of arid savanna elements (acacia, mopane, ziziphus, combretum) occurs from the Save area up the Buzi Valley to the Urema Trough thence to the arid valley of the Lower and Middle Zambeze in Mocambique and to beyond the confluence of the Luangua River. Yet a totally isolated population of giraffe occurs in the lower Luangua Trough (Ansell 1960, map D) with a suitable habitat link all the way south to the Limpopo.

In Chapter 7 the antiquity of concentrated human activity in Central Mocambique for gold, ivory and slaves was traced back to at least 1400 BP, if not 2400 BP. The major access routes to the interior and the Monomatapo Empire were up the Zambeze Valley and its tributary the Luenha-Mazoe which rises in Rhodesia. Other routes followed the Pungue and Revue valleys and spurs adjacent to Sofala. Giraffe 'riems' and meat were a major resource in the history of Africa, and as the tribesmen of this region all used arrows tipped with ***Stophanthus kombe*** poison, it is possible that this great gap in giraffe distribution is a long standing human artifact.

A similar anomalous gap in giraffe distribution existed in the vast thorn savanna area between Windhoek and Etosha in South West Africa even at the time of Shortridge's first expeditions in the 1920's (1934: map facing p. 612). Vedder's (1966) historical record shows that Damaraland (then known as Hereoland) was a major route for oxwagons, and the southern sector down to Windhoek was the main theatre for the 20 year war between the Nama and Herero which ended in 1820. In addition, perusal of the series of wall maps exhibited in the Windhoek museum, depicting the growth of

road and railway communications in the early 1900's radiating from Walvis Bay port and from the capital of Windhoek through Damaraland to Tsumeb, shows clearly that the Damaraland gap in many ungulate distribution patterns is probably a human artifact. The piles of bones at tribal hunters' camps in northern South West Africa and the Botswana border attest to giraffe being the most preferred prey, followed by eland (P. Stark ***pers. com***). These South West African hunters used bow and arrows, with or without the aid of a plant poison derived from the latex of ***Adenium boehmianum***, usually from horseback which made them doubly efficient.

In the early 1950's a few giraffe (about 6?) were introduced into Gorongosa National Park but were apparently all eventually taken by lions.

9.3 DISTRIBUTION, HABITAT, NUMBERS, BIOMASS

The salient feature of wild ungulate distribution in the ecosystem is their perennial concentration on the Rift Valley floor. In contrast, the adjacent miombo savanna and dambos of the Midlands and Cheringoma Plateau are extremely lightly stocked despite the presence of perennial water and the lack of human habitation over large areas. The miombo is however used more at certain seasons than at others by ungulates from the Rift floor.

The major ecosystem patterns (Fig 6.1) and field data show that the main distribution of forest and thicket species is in the northern sector of the Rift floor and along the Riftward slopes of the Cheringoma Plateau. Nyala, suni and Sharpe's grysbok are commonest in these sectors, whilst bushbuck and red duiker are more ubiquitous, occurring in the forest areas as well as through all thicket patches in the Rift Valley savannas. Bushbuck are also abundant in the dense palm scrub-thickets south of the Urema Plains. Blue duiker occur in the rain forest on Gorongosa Mountain and with suni and red duiker in the forests of the Cheringoma cuesta.

Savanna and grassland ungulates are concentrated along riverine zones, and especially on the floodplain grasslands on the Rift floor. Waterbuck is one species that maintains a high year-round linear concentration on the flood and ebb margins of the Urema Lake and other waters.

FOREST/THICKET COMPONENTS

Bushbuck and red duiker are the most abundant dense-cover species throughout the ecosystem. In this area the southern (***Tragelaphus s. sylvaticus***) and western (***T. s. scriptus***) races of the bushbuck overlap with interesting habitat separation. The southern race is most common in the forested areas whilst the western race is characteristic of the palm thickets.

Suni occur in the smaller isolated dry forests, on the duplex sand patches of the Rift floor, but only where the field and groundlayers are undamaged. In such areas suni typically occur within the forest precincts and red duiker occupy the forest margins and move out from one termitarium thicket to another. In the Zinave area of the Save River no red duiker occur and suni use all thicket habitats as do red duiker in Gorongosa (J.L.P.L. Tello *pers. com.*).

Kudu are uncommon but widely dispersed over the Rift floor and Midland valleys and hill areas. Nyala by contrast are confined to the dry forest and thickets of the Rift floor and to the Riftward foot slopes of the Cheringoma cuesta. They are most common from the centre of the park northwards. Bushpig are abundant throughout the system from the mountain summits to mangrove margins, and are only absent (at least in the day) from the largest grasslands of the Urema floodplains and those on the coast.

Unfortunately, no quantitative data is available for the forest and thicket ungulates but a rough estimate of their zoomass contribution is included in Fig. 9.2. These species are mainly browsers (bushbuck, suni, red duiker, blue duiker, Sharpe's grysbok). The nyala is ditrophic and can be classified a browser (Tello & Van Gelder 1975) as in the Save area, or a mixed feeder as in Zululand (J. Anderson *pers. com.*). Mixed feeders are species in which grass is included as a major component of their diet in addition to browse. The bushpig is omnivorous as is the forest samango monkey. This primate occurs in all forest areas of the system, and in the Rift Valley uses the tall riverine thickets as well as venturing out from larger forest areas to feed or pass through the archipelagos of termitaria thickets. The most important predator in closed habitats are leopard which abound throughout the entire Gorongosa-Cheringoma area.

SAVANNA AND GRASSLAND COMPONENTS

The large ungulate spectrum which inhabits both the savannas and the grasslands comprise 14 species of which the eight major species are listed in the biomass table (Table 9.2). The remainder include grey duiker, impala, oribi, reedbuck, warthog and white rhino. Grey duiker are confined to the miombo savannas and are absent on the Rift Valley floor at least within the bounds of the ecosystem. Impala are fairly common in the Rift Valley particularly in the southern sector at the junction of the Urema Plains with the marginal savannas. Oribi and reedbuck are abundant throughout the Rift Valley and sparse in the miombo-dambo terrain on either side. Warthog, though common and widespread on the Rift Valley floor, are nowhere abundant. A few occur in the adjacent miombo savannas particularly during the post-fire flush of grasses. After release in the southern sector of the park, the white rhino utilized both floodplain and savanna grasslands and were commonly observed on the ecotones between the two.

The most important predator in the open habitats of the ecosystem is lion, with an estimated population of about 200. Their greatest concentration is related to that of the large ungulates in the Rift Valley where prides of up to 30 individuals occur on the margins of the Urema Plains. Spotted hyaena are widespread but uncommon. Leopard, whilst being more commonly associated with closed habitats, are also found in any open terrain where tall grass patches or thicket clumps occur. They are the most ubiquitous of the carnivores, extending throughout the montane to mangrove transect. Wild dog, though rare, range through all the savannas and grassland areas except the mountain.

The major large ungulates, including elephant, are discussed individually in their order of biomass contribution (Table 9.2) but hippo are treated separately under a section on Aquatic Components. The zoomass contribution of the three large herbivore trophic groups is shown in Fig 9.2.

Elephant

Although grouped with open habitat species elephant range through and utilize almost every habitat listed in the montane to mangrove transect. Their greatest year-round density is however associated with the tall grass ***Acacia*** savannas and riverine areas of the Rift Valley. Here three main riverine-associated concentration areas are habitually used over both dry and wet season peak periods: (1) Nhandue riverine zone, (2) western Vundudzi – Mucodza – Mupuaze riverine zones (western central margin of Rift floor below the Rift sides), (3) Urema – Pungue riverine zone (Fig 9 3).

These three areas take the brunt of high density and biomass for most of the year, attaining figures of 3 elephant/km^2 (or 10 tonnes/km^2). Habitat diversity in the three areas is similar, comprising a mosaic of tall acacia and mixed tree savanna with a tall ***Panicum maximum*** (robust form) herb layer and well developed termitaria thickets (3/ha), interspersed with seasonal pans, and the riverine strips of the rivers noted above. Marshes are confined to the riverine meander belt margins, the largest being the Mucodza marsh near the western margin of the Rift. This spectrum provides an abundance and diversity of fruit, browse and grazing. With the advent of fire the grass stratum is totally eliminated for several months over extensive areas, and excessive use or damage to the other habitats is buffered by the availability of green pastures in marsh areas.

Unseasonal early thunder showers at the height of the dry season (Aug.–Oct.) cause an almost overnight emigration to the areas where rain has fallen. If grasslands are previously burnt and beginning to show a post-fire flush an unseasonal rain of more

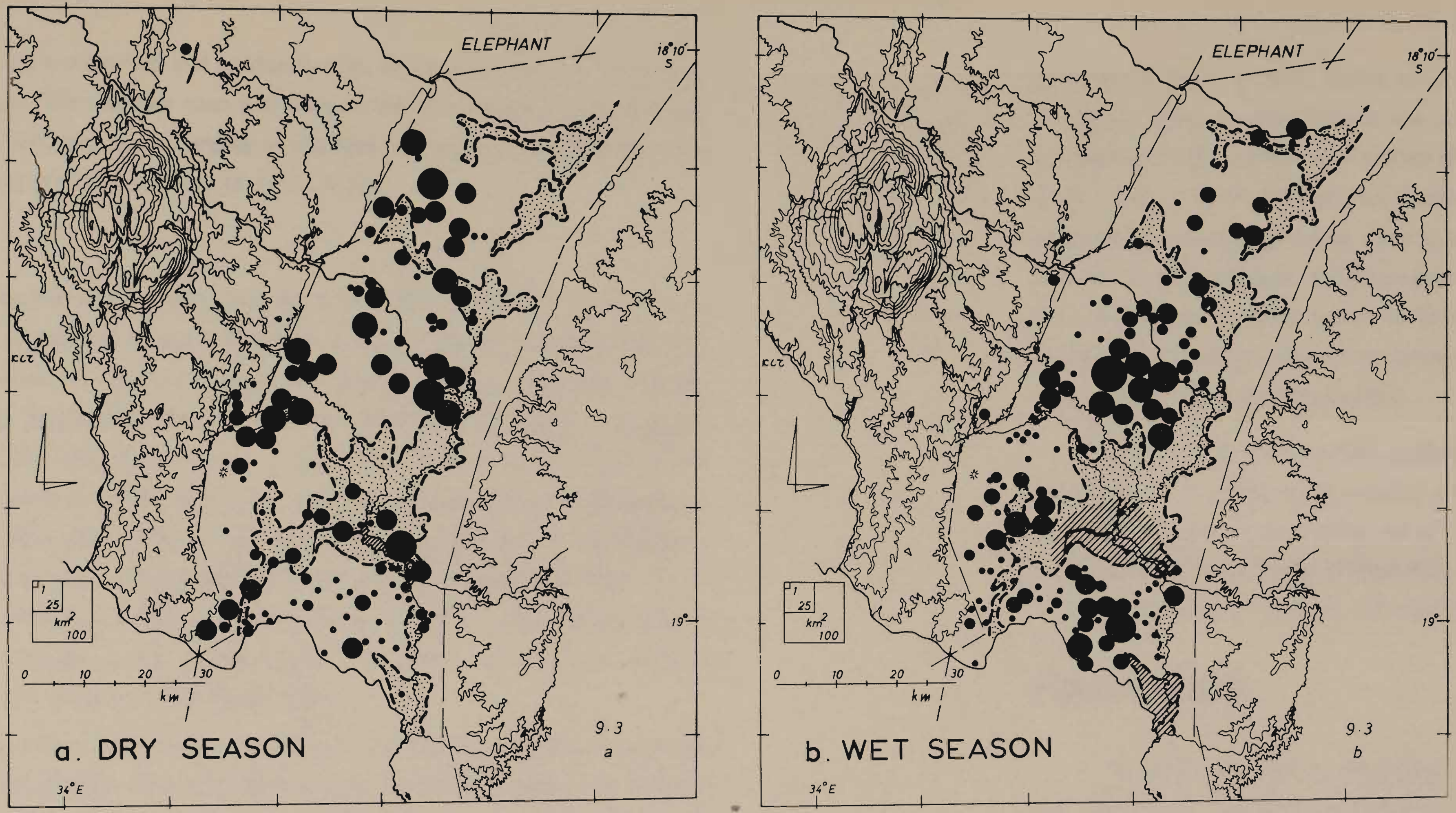


FIG 9.3 ELEPHANT – SEASONAL DISTRIBUTION & ABUNDANCE

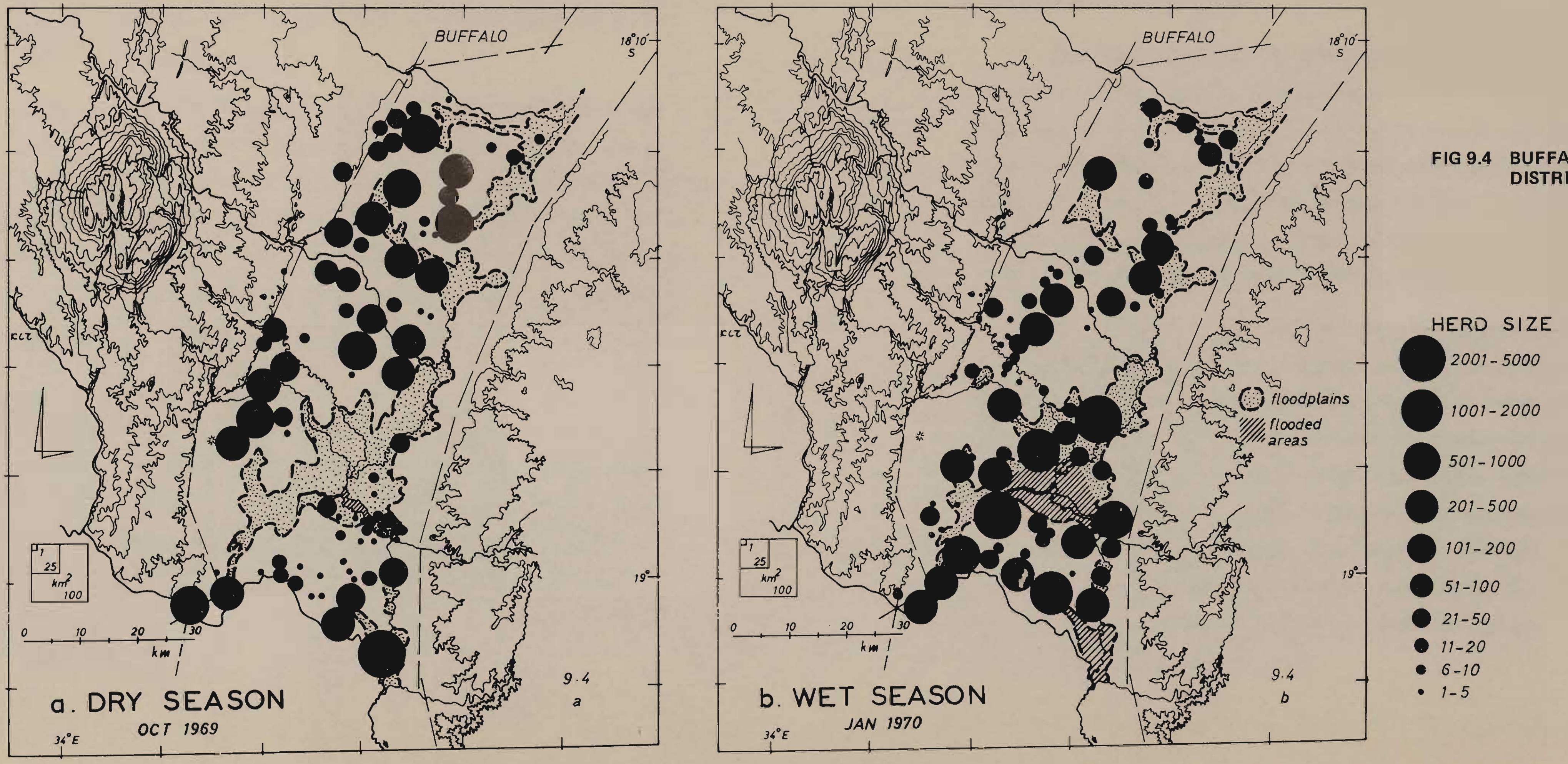


FIG 9.4 BUFFALO – SEASONAL DISTRIBUTION & ABUNDANCE

than 10 mm induces a magnified leaf production but wilting can follow if no further precipitation occurs. The elephant then withdraw to the riverine zones again or move into the adjacent hill miombo. Examples of elephant feeding in miombo and on the Rift floor are included in Figs 9.17a; 9.18; 9.19a; 9.20a.

Buffalo

The distribution and concentration areas of buffalo in the Rift Valley are remarkably similar to those of elephant (Fig 9.4). In the dry season there are three main areas of concentration:(a) Nhandue riverine zone and adjacent Nhamisangu floodplain grassland area, (b) Mucodza marsh area (western Vundudzi — Mucodza — Mupuaze riverine zones in the west central sector of the Rift), (c) Dingedinge marsh in the Urema — Pungue confluence area (Fig 9.4a). With the autumnal ebb of floodwaters a herd of nearly 2 000 buffalo become a permanent feature of the Goinha Plains (immediately north of the Urema Lake) which are ***Setaria*** floodplain grasslands (Plate). When these have dried out sufficiently (discoloured) to admit fire in about June or July, the large herd breaks up into smaller groups which graze in the wooded margins of the plains and up onto the Cheringoma Plateau.

In the wet season a similar concentration is maintained with two main shifts. The Mucodza Marsh concentration fades and a major wet season centre is on the converging delta of the Mucodza and Vundudzi at the head of the Urema Lake, and on the median height floodplain grasslands west (Sungue) and southwest (Nhauranga) between the Sungue and Pungue River (Fig 9.4b).

Between one and four herds containing more than a thousand animals normally occur in both the dry and wet seasons. In contrast between three and six herds of this dimension are recorded in the Marromeu sector of the Zambeze Delta grasslands (Tinley 1969b and unpubl. air counts). Thus in the main concentration areas buffalo biomass exceeds 1.600 tonnes/km^2 for the period in which herds up to 2 000 strong remain intact, moving and feeding through the median and tall grass pastures. The largest herds are all associated with marsh and riverine grasslands and move to adjacent sites in long columns.

Like elephant there is an immediate response by buffalo, in the dry season and first rains period, to any area where isolated thunderstorm rains have fallen. This is clearly portrayed by the spread of smaller herds into the waterless northern sector of the system between the Nhandue and Nhampaza Rivers after a thundershower; recorded by the air counts of November 1968 and October 1969. The exact limit of the isolated rain was demarcated by the limit of the herds, the adjacent unburnt and rainless area being quite devoid of large ungulates.

Buffalo are the most susceptible to starvation and high mortality when their

pastures are dried out early in the autumn by drought conditions, and especially when the annual event of uncontrolled fires sweep across the Rift floor. Elephant can turn to browse, and the other major species obtain sufficient nutrition from the remaining green zones of short microperrenial grasses (***Cynodon dactylon*** and ***Digitaria swazilandensis***) in waters-edge zones. Due to an excessive population hippo are the only exception to this amongst the short-grass feeders (see following section). Post-fire flush and wilted regrowth appear to be a main cause of excessive scouring in buffalo followed by death (possibly from prussic acid poisoning also known as ***'geilsiekte'*** — refer to section on mortality factors).

During midsummer whole buffalo herds often rest in pans and marshes from about 09h00 to 16h00 before moving out to graze for the night. However, in addition to ruminating, some local feeding takes place as the animals are lying amongst some of their important grass foods, ***Echinochloa stagnina*** and ***Vossia cuspidata***. Two examples of buffalo grazing are included in Fig 9.16A, B.

Wildebeest and Zebra

As short and medium height pastures form a mosaic, and the short grasslands are taller during the rains, the distribution and concentration areas of wildebeest and zebra are generally coincident.

The major dry season concentration area for both species are the Dingedinge floodplain marshes (slacks) at the Urema — Pungue confluence. Other concentration areas centre about the Mucodza marsh in the central western margin of the Rift floor (Vundudzi — Mucodza — Mupuaze riverine areas), and alternate between the Macoreia Plains and those of the converging delta at the head of the Urema Lake (Figs 9.5, 9,6). In some years the Nhandue riverine area (particularly where it enters the top end of the Macoreia Plain) and the adjacent Nhamisangu floodplain are important.

The wet season concentration patterns depend on the extent of flooding. Maximum spread of floods results in a linear concentration pattern in the abutting savannas, eg. in the ***Urochloa*** median savanna grasslands between the Urema Plains and the Pungue (eg. Jan. 1970). At this time zebra show separate concentrations on the Macoreia Plains, and on the margins of the Goinha Plains (Fig 9.6b). In the north other concentrations form in the lower Nhandue riverine zone and the grassland areas adjacent to the Lunga drainage and near the northern Nhamapaza River boundary. In wet seasons, with median to low flood, the main areas of concentration of both species is on the short grass plains south, west and northwest of the Urema Lake (including the converging delta area and Macoreia).

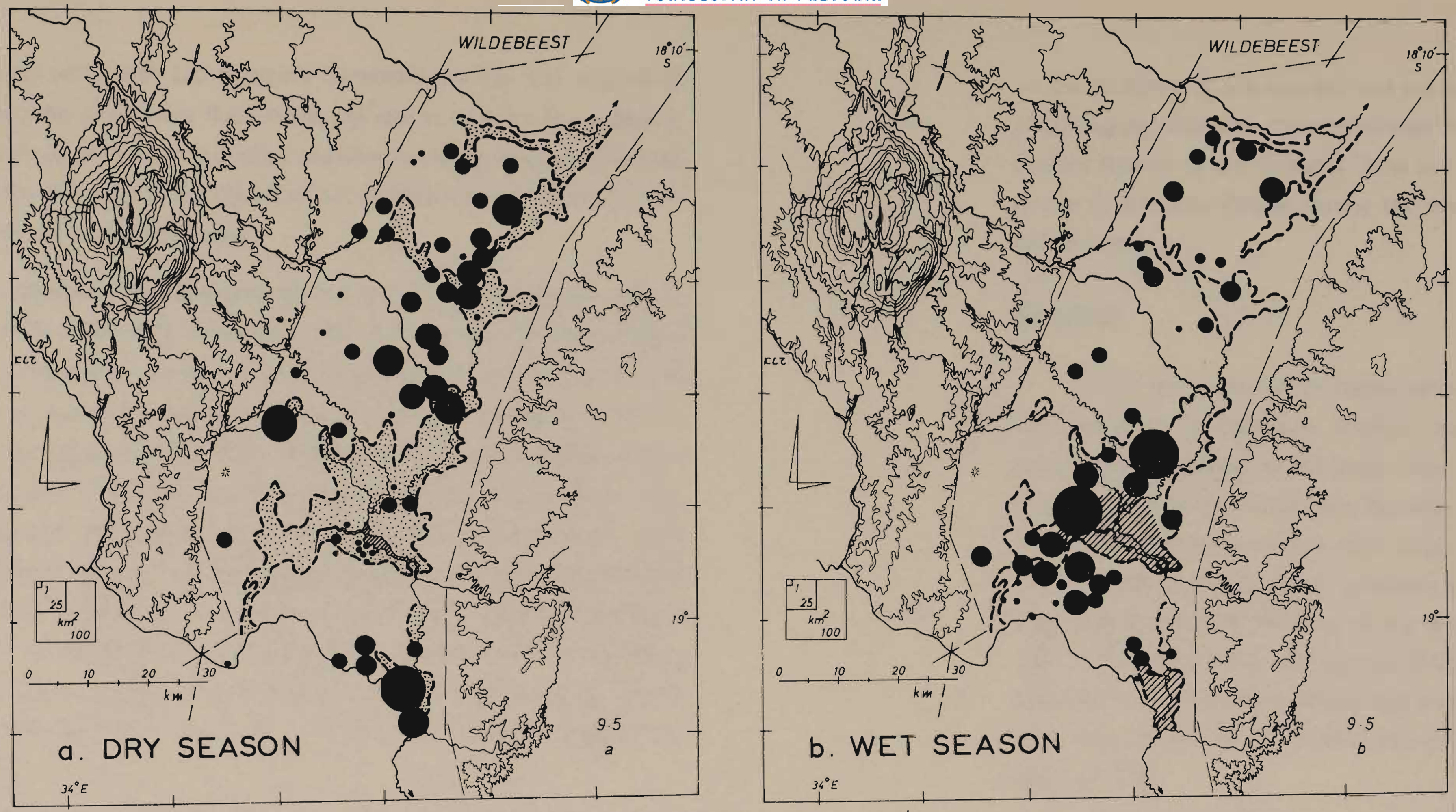


FIG 9.5 WILDEBEEST – SEASONAL DISTRIBUTION & ABUNDANCE

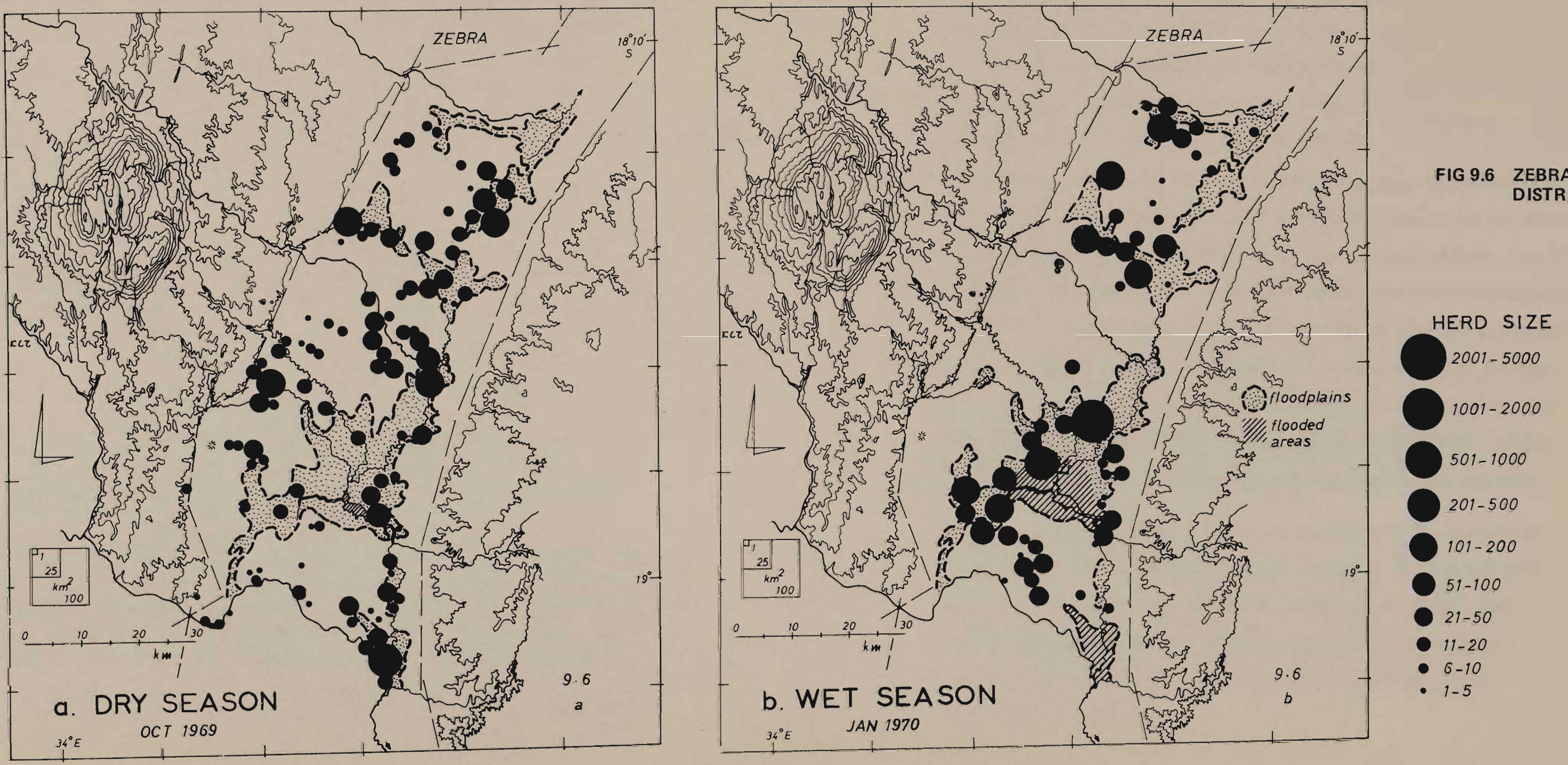


FIG 9.6 ZEBRA – SEASONAL DISTRIBUTION & ABUNDANCE

Wildebeest and zebra with Lichtenstein's hartebeest are the first large herbivores to invade new areas of post-fire flush in the dry season, and like the species already dealt with, show an immediate migratory response to the occurrence of isolated, unseasonal rain. If the rain was too little to provide an adequate grass flush and surface water, the herds return to the riverine zones.

In numbers wildebeest have increased from about 3 000 in November 1968 to 7 000 in October 1972 (Table 9.2). In October 1969 the least number were counted (2391) followed by a large influx in the dry 1969/70 summer to give the highest count of 7 060 animals in January 1970. Although inaccuracies are an inevitable artifact of total counts, these changes in number reflect immigration into the park and emigration from the remainder of the Rift Valley sector between the park and the Zambeze Valley, which is much drier and with rare surface water. Small localized herds, or no wildebeest, occur south of the Pungue or in the Midlands. In the summer rain months wildebeest densities attain 4,3 tonnes/km^2, and at the height of the dry season a quarter of this, 1,5 tonnes/km^2. Like waterbuck, wildebeest form concentrations of more than a hundred animals at the two seasonal extremes, on marshland green zones in the dry season, and on the rains and/or flood-ebb flush of the short floodplain grasslands in summer and autumn.

No wildebeest occur in the Zambeze Delta or on the Riftward slopes of the Cheringoma cuesta, nor is there any historical record of their having done so. Wildebeest migrations thus appear to be confined mainly to lengthwise movements along the Rift Valley. In the past they moved southward to the vast floodplain grasslands of the Pungue -- Buzi confluence area, but now mostly northward to Dimba Marsh and possibly nortwest up the Nhandue and other Midland valleys.

Zebra numbers in the five year period increased from about 1 196 (Nov 1968) to 3 331 (October 1972). A regular pattern of greater numbers in the wet season and less in the dry season featured in every pair of dry-wet season counts. Certainly their merging more easily with the substrate in the dry season would have been a contributory factor to lower numbers being counted at this time. However this concentration pattern contrasts with that of waterbuck which show greater numbers in the dry season and lowest in the rains, although they are the most difficult species of all to count from the air in the dry season without the aid of oblique (early or late) sunlight.

In the rains period, zebra biomass attains 2 tonnes/km^2, and a third of this in the dry season, 0,6 tonnes/km^2. Unlike wildebeest and waterbuck, zebra only form large aggregarions of more than a hundred animals on the rain season pastures. In the dry season, concentrations in riverine and marshland areas seldom exceed groups of thirty animals. Zebra also move into post-fire flush areas of miombo and dambos on the adjacent plateaux in the late dry season, particularly if good unseasonal rains occur on the Midlands. It is suspected, but not known for certain, that there is a movement of zebra groups between the approximate thousand strong population of the Marromeu Buffalo Reserve in the Zambeze Delta and those on the Rift Valley, along the dambos of the Cheringoma Plateau during the dry season, particularly in the post-fire flush period in August.

Waterbuck

With the exception of hippo, which are tied to open waters, waterbuck have the most restricted dispersion of all the ungulates in the system. The major part of the population is confined to the green zone pastures which expand and contract with flood and ebb of the Urema Lake. Equally high concentrations of waterbuck are found at both seasonal extremes in a zone around the Urema Lake, especially in the converging delta area of the Mucodza, Vundudzi and Mucombeze streams (Fig 9.7). This area supported the greatest densities in the dry season peak of 1968 and following rains peak in February 1969, and again in October 1969 (Fig 9.7a). Very few waterbuck occurred in the Dingedinge marsh area until the 1969 dry season when large numbers were recorded for the first time in the dry season peaks of that year (Oct 1969) and again in 1972.

During the rains and flood period there is a shift of concentration to the Macoreia ***tando*** (Feb. 1969) or to eitherside of the Mucombeze drainage on the Macoreia and Goinha ***tandos*** (Jan. 1970) and along the Sungue branch of the Urema Lake. (Seasonally flooded or waterlogged grass plains or drainage lines are known locally as ***tandos***). There is also an outward radiation of herds from the Urema concentration area to the northern chain of ***tandos*** of Lunga, Nhamisangu and Tengane (Fig 9.7b). Some herds move along the Rift Valley drainage as far as Dimba Marsh, 120 km north of the Urema and 40 km south of the Zambeze River. The Dimba Marsh area has a flood and ebb regime similar to the Urema, but since the advent of Kariba Dam is totally reliant on summer rains. Had this marsh fallen within a protected zone instead of forming part of the open hunting concession area it would probably have been a centre of a major concentration area. However, during dry years the waters dry up altogether and this would force waterbuck and species such as buffalo, wildebeest, and zebra to move south to the Urema or to parts of the Zambeze River less settled by people.

As noted above, waterbuck numbers in the system are greatest during the dry season when there are lowest zebra numbers. Air counts showed an increase of waterbuck from 1 856 (Nov. 1968) to 3 382 (Oct. 1972), with the highest total of 3 557 animals recorded in Feb. 1969 (Table 9.2). In the summer rains season densities attain biomasses between 1 and 2 tonnes/km^2 and the dry season concentrations only slightly less, 0,8 tonnes/km^2.

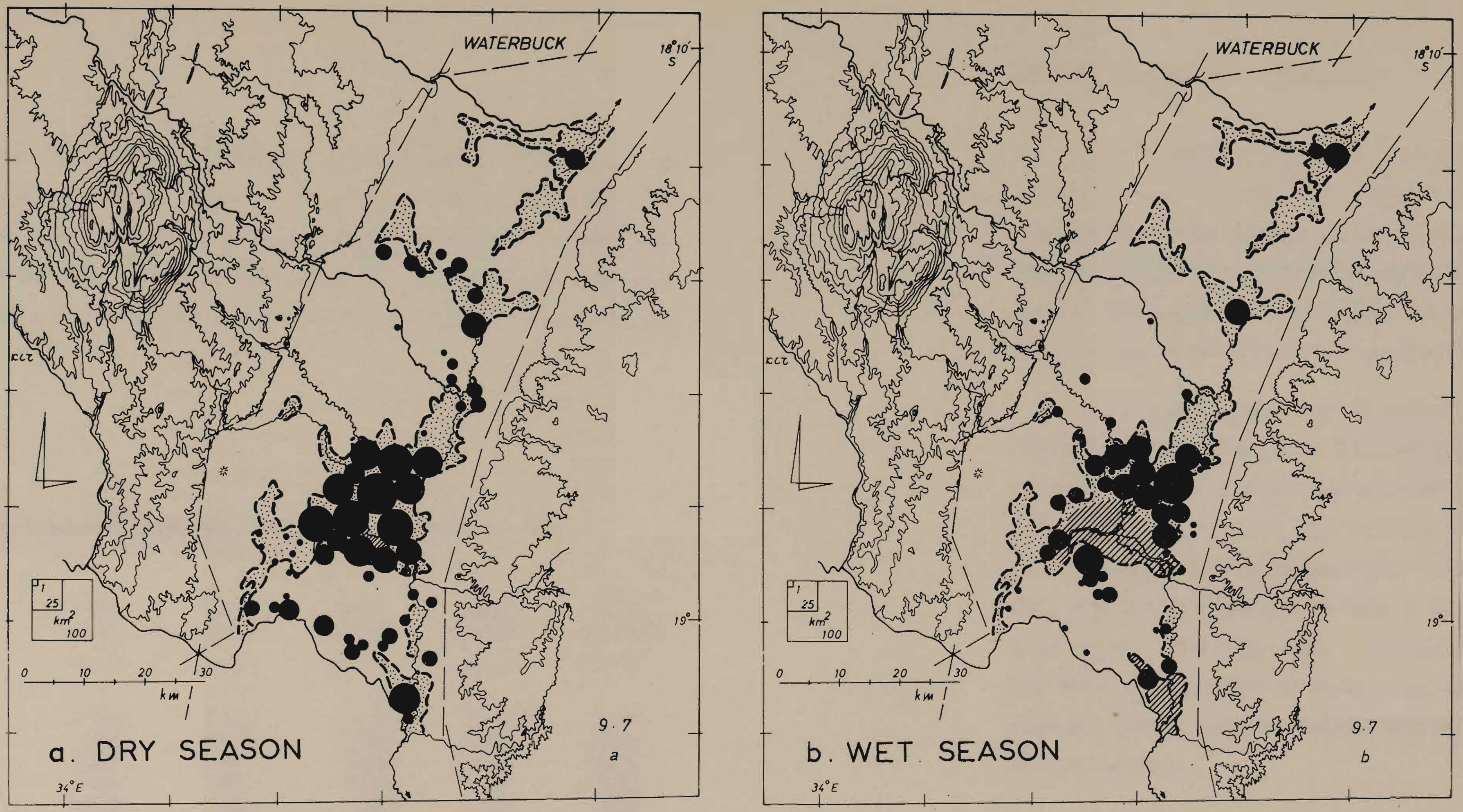


FIG 9.7 WATERBUCK – SEASONAL DISTRIBUTION & ABUNDANCE

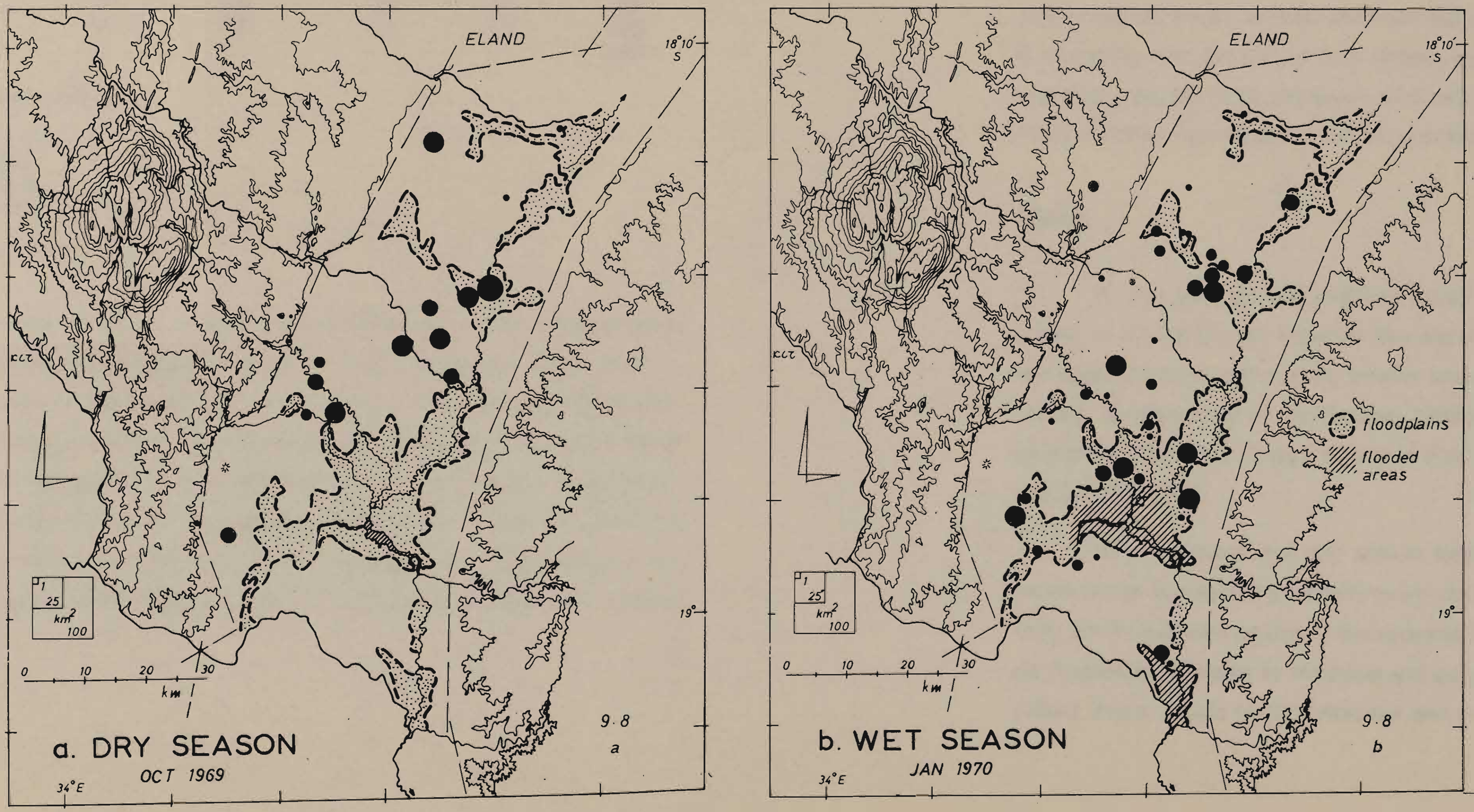
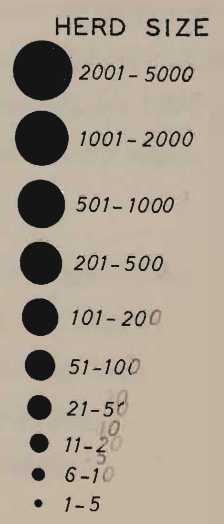


FIG 9.8 ELAND – SEASONAL DISTRIBUTION & ABUNDANCE



Eland

Like sable and Lichtenstein's hartebeest, eland are found mainly down the central and western part of the Rift floor in the savannas and their ***tando*** grassland ecotones. Eland show large seasonal change in numbers, the most occurring in the summer rains period, and the least in the dry season when they are suspected to be north and northwest of the park in the dry Midland valleys such as those of the Macossa area (Fig. 9.8).

TABLE 9.2

TOTAL NUMBERS OF THE MAJOR LARGE HERBIVORES RECORDED IN SIX TOTAL AIR COUNTS ACROSS THE GORONGOSA ECOSYSTEM.

	DRY SEASON[1]	WET SEASON[1]	DRY SEASON[2]	WET SEASON[2]	WET SEASON[3]	DRY SEASON[4]
	Nov. 68	Feb. 69	Oct. 69	Jan. 70	Mar. 71	Oct. 72
Elephant	1.555	1.634	2.072	2.185	1.401 (?)	2.542
Buffalo	10.928	11.214	11.168	11.756	12.953	13.295
Wildebeest	3.020	2.989	2.734	7.060	5.618	6.427
Waterbuck	1.930	1.604	3.557	2.223	2.697	3.362
Zebra	1.196	2.899	2.391	3.583	2.938	3.331
Eland	134	226	342	429	356	126
Sable	436	84	628	361	352	483
Hartebeest	87	352	472	839	603	344
Hippo	2.972	–	–	–	–	3.483

Author's co-observers in the air counts:

1. J.L.P.L. Tello
2. F.C. Costa
3. S.J. Liversidge
4. T.P. Dutton

The largest herds (up to 90 animals) were encountered in the dry season but herds up to 50 strong are recorded at other seasons. In two dry season periods the majority of eland occurred in the lower Nhandue – Lunga – Nhamisangu ***tando*** area, below the Bunga inselbergs near the Vundudzi River, and across to the Mucodza Marsh area (Fig 9.8a). In the wet season large numbers remained in the Lunga – Nhamisangu ***tando*** area and the remainder were in the savannas south of the Nhandue River to the Sungue ***tando*** west of the Urema Lake (Fig 9.8b). The largest herds contribute a biomass of over 40 tonnes/ha when feeding in a group, or spread over some five hectares when spread out.

Sable and Lichtenstein's Hartebeest

The largest numbers of sable occur on the Rift Valley floor in the dry season and the least in the wet season (Table 9.2 / Fig 9.9). Sable and Lichtenstein's hartebeest utilize similar habitats, preferring ecotones of savanna with dambos and floodplain grasslands. They also feed on the same grass species and the same parts of grasses. Unlike sable however, the hartebeest are inveterate followers of burnt grassland, feeding on toasted basal parts and the first post-fire flush.

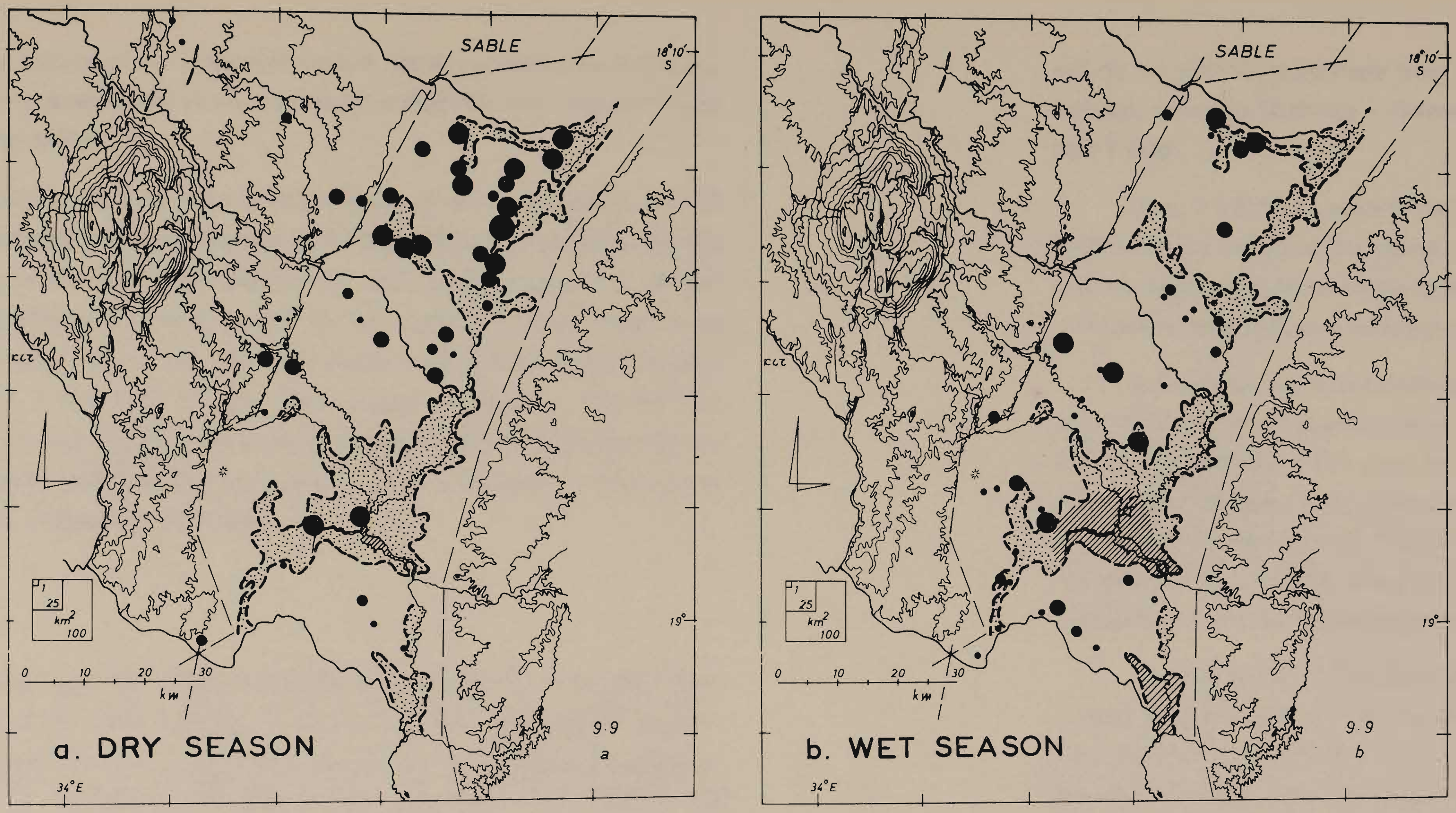
In the wet season there is a lateral upward movement of sable from the Rift into the miombo savannas of the Midlands and the Cheringoma Plateau. About the same time there is a downward movement of Lichtenstein's hartebeest from the uplands onto the Rift Valley floor resulting in a maximum of their numbers in the wet season opposite to that of sable (Fig. 9.10). In the dry season the hartebeest move back into the miombo and dambos of the uplands on either side of the Rift and the sable return to the Rift Valley – and opposing altidudinal migration similar to transhumance. Unfortunately no quantitative data from the uplands is available, but these opposing density patterns and movements are confirmed by tribal hunters from the miombo uplands.

Although two herd sizes, 11 and 30, are most frequent amongst sable, groups containing up to 83 animals are recorded (October 1972), giving a biomass of some 6 tonnes/ha over the period they remain together. Lichtenstein's hartebeest also have two high frequent herd size peaks of 6 and 12 but occasionally large gatherings of up to 72 animals occur (October 1972), providing about 3 tonnes/ha.

Impala

A first attempt was made to count impala from the air in February 1969 resulting in a total of 908. However this was discontinued as it proved too distracting for the observers to search out the smaller animal whilst nine larger species were being recorded. Subsequently in the October 1969 and January 1970 counts only distribution of impala was noted. It was estimated that the impala population was between 1 500 and 2 000 in 1972.

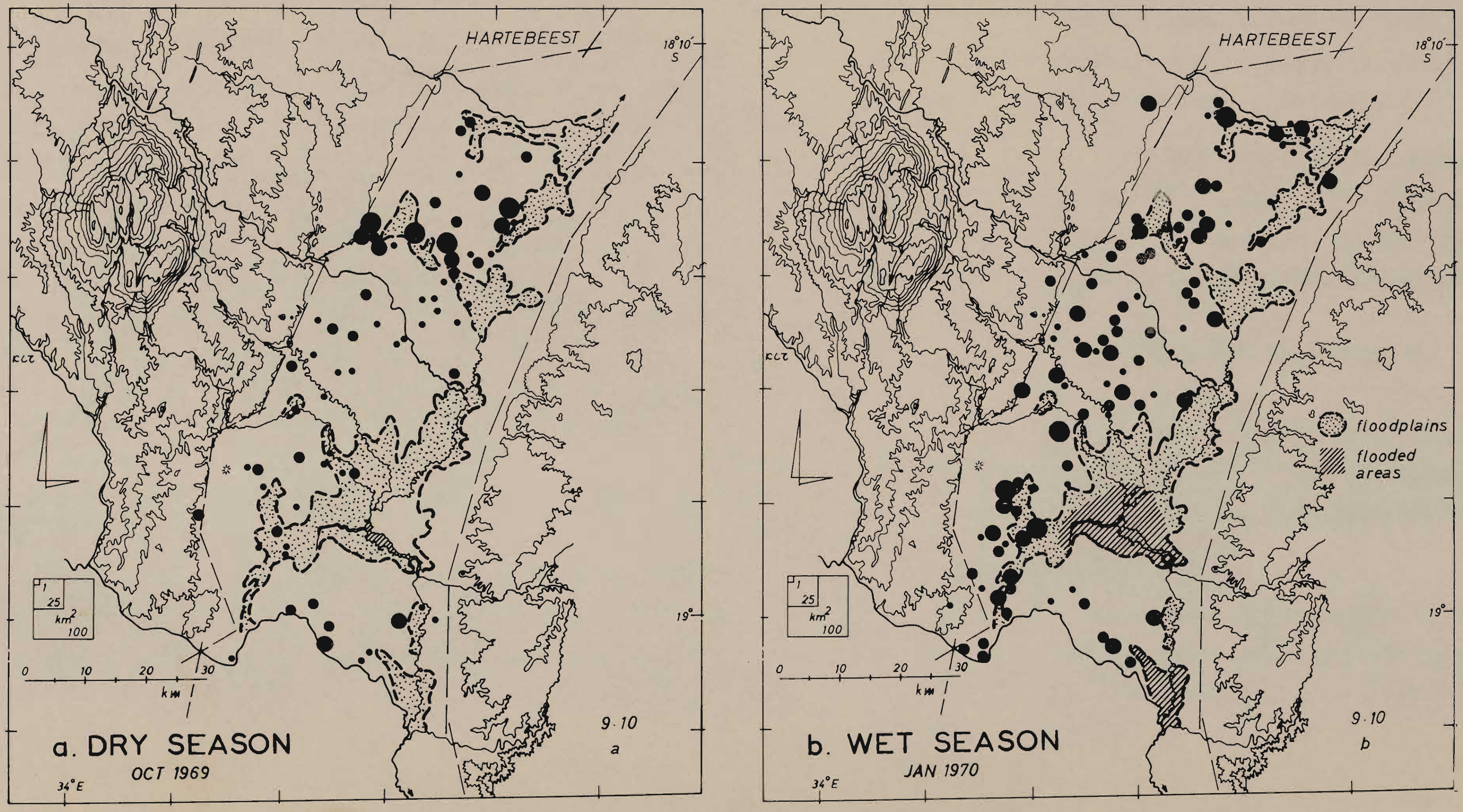
In the autumn and dry season, large aggregations of impala occur on the microperennial floodplain grasslands to the south and west of the Urema Lake. Elsewhere they are in scattered groups in the savannas between the Urema and Pungue Rivers and on floodplain ecotones in Macoreia and Lunga in the centre and north. The wet season record shows impala herds spread out and scattered over most of the Rift Valley floor.



a. DRY SEASON

b. WET SEASON

FIG 9.9 SABLE – SEASONAL DISTRIBUTION & ABUNDANCE



a. DRY SEASON
OCT 1969

b. WET SEASON
JAN 1970

FIG 9.10 LICHTENSTEIN'S HARTEBEEST – SEASONAL DISTRIBUTION & ABUNDANCE

HERD SIZE

- ● 2001 - 5000
- ● 1001 - 2000
- ● 501 - 1000
- ● 201 - 500
- ● 101 - 200
- ● 51 - 100
- ● 21 - 50
- ● 11 - 20
- ● 6 - 10
- • 1 - 5

A more detailed account of the seasonal changes in impala numbers on a floodplain-savanna junction is related in the section on floodplain rhythms. An example of impala grazing is included in Fig 9.16d.

Distribution of impala in Central Mocambique is in scattered herds up the Rift Valley to the Zambeze River and westward up the Zambeze Valley. Some are recorded slightly west of the Rift up the dry valleys which lead into the trough from the Midlands. In 1970 professional hunters reported the first sightings of some impala in the southern (Marromeu) sector of the Zambeze Delta. These animals could only have moved downriver from where the Rift Valley crosses the Zambeze area near Vila Fontes. It is not known whether these initials have become established, or what the sex and age composition was of the first colonizers. In other areas subadult males are recorded as the first colonists of new locales.

Oribi

Quantitative data for small ungulates is available only for oribi which were counted from a vehicle whilst traversing floodplains and their ecotones with the marginal savannas south and west of the Urema Lake. A total of 390 oribi were encountered in 132 km^2 giving 3 oribi / km^2, or an approximate population of 11 000 for the Rift Valley floor alone if a similar density is presumed throughout.

In the Urema sector, oribi exhibit an interesting but unexplained seasonal local movement in some years. From April until November family groups of two to three animals (65% of 145 groups) occur throughout both savannas and the floodplain grasslands. In some rainy seasons, from the end of November until March, oribi are totally absent from the floodplains irrespective of the level of flooding. At this time they are to be found in the adjacent tall grass savanna peripheral to the grassplains. It is suspected that this movement may be related to plagues of biting flies. The traverse of the floodplains and their savanna margins showed a higher density of oribi related to the ecotones between open grassland and savanna, the abrupt junctions of riverine thicket or termitaria thicket islands with the surrounding grassland, and junctions between short and long grassland.

AQUATIC COMPONENTS

Of the five ungulates in Africa which are tied strictly to water though they feed out from this base, only hippo occur in Mocambique. The others are pygmy hippo, water chevrotain, lechwe and sitatunga. The latter two occur within 200 km

and 80 km distance respectively from the northwestern corner of Mocambique (Tete' District), above the Muchinga – Gwembe escarpment of the Luangwa – Middle Zambeze Trough.

Some 3 500 hippo occur in the Gorongosa ecosystem of which 2 761 (80%) are confined to the margins of the Urema Lake. This represents the single largest hippo population remaining in Mocambique today. A first air count of hippo in the Urema Lake in November 1968 realized a minimum total of 2 250 (Fig 9.11).

A second air count five years later in October 1972 recorded a minimum total of 2 301 hippo in the Urema Lake and a probable total of 2 761, as corrected from vertical air photographs. This gives 209 tonnes/km^2 of lake or 3316 tonnes biomass in a lake area of 15 km^2. In the last count of all the waterways in Gorongosa an additional 722 (820 tonnes biomass) occurred in the Urema and Pungue Rivers and their old meanders realizing a grand total of 3 483 (Fig 9.11). The steady state of the Urema populations, in which little change had occurred after a five year interval, is significant.

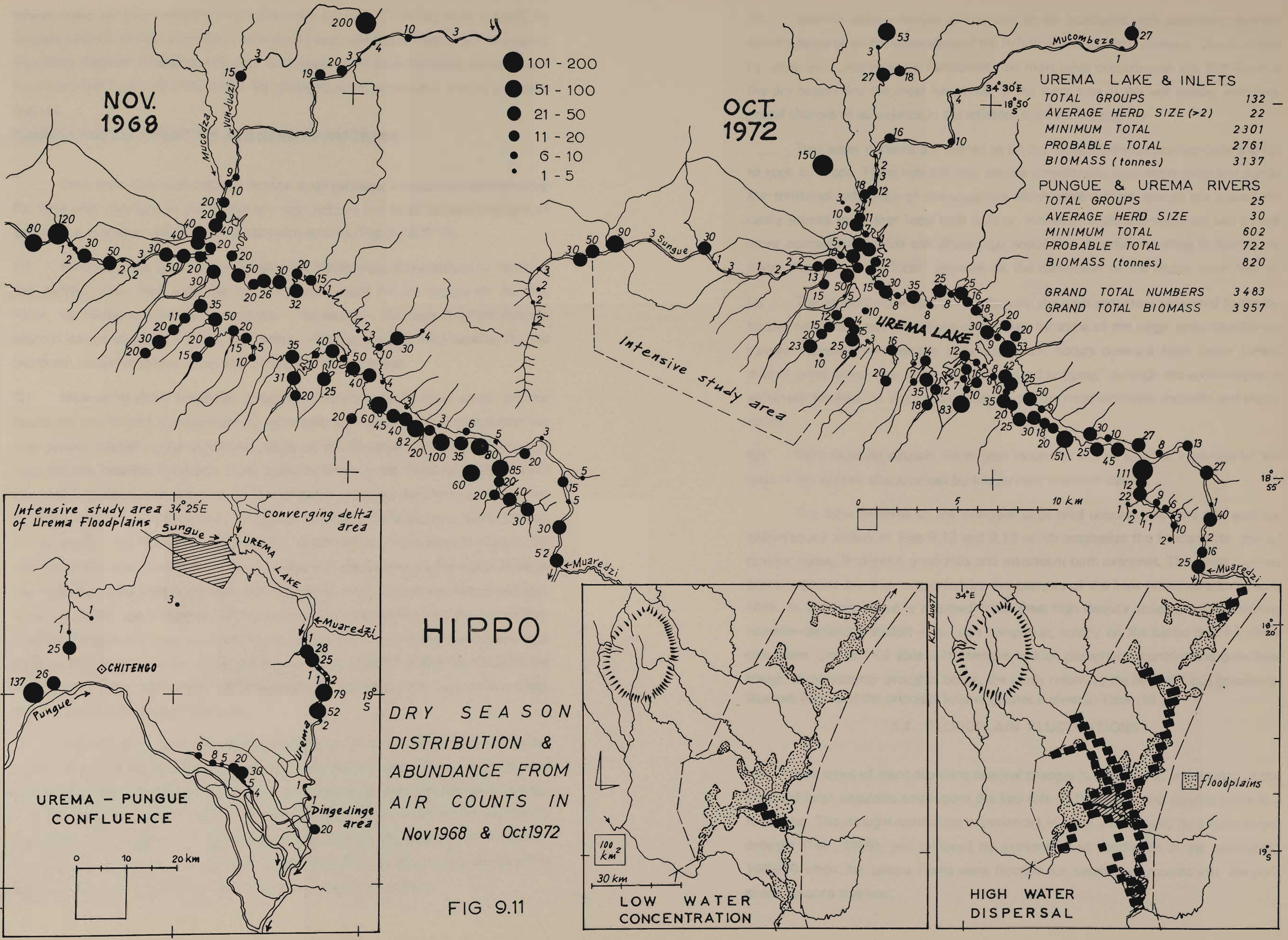
The distribution of hippo at the dry season peak in November 1968 and October 1972 contrasts with the situation in the rains and flood period (Fig 9.11). At this time an extensive spread of hippo occurs outward from the Urema Lake up the Mucodza, Vundudzi and Mucombeze Rivers as far north as Lunga pan and single animals occupy rain-filled pans in the savannas. During high floods hippo herds are distributed peripherally along the floodplain – savanna junction where they trample depressions in their favourite lying-up sites which form pans when the flood waters ebb, and are rainfilled in low flood years.

In November 1968 the average herd size in the Urema Lake was 35, and 25 in October 1972, opposed to the larger average herd size of 48 in the rivers. Hippo paths radiate 10 km out from permanent waters, which virtually includes all the country between the lake and Pungue River as grazing grounds.

ROCK OUTCROP COMPONENTS

Four wild ungulates in Africa are closely associated with rock outcrop habitats: Barbary sheep, beira, ibex and klipspringer. Of these only the last occurs in Africa south of Abyssinia, accompanied by the rock dassie and yellow-spotted dassie (Dorst & Dandelot 1970).

In Gorongosa, klipspringer occur on the mountain and its satellite inselbergs as well as on inconspicuous outcrops within the Midland miombo. There is no record of them from east of the Rift Valley in the ravines of the Cheringoma cuesta. The two



UREMA LAKE & INLETS	
TOTAL GROUPS	132
AVERAGE HERD SIZE (>2)	22
MINIMUM TOTAL	2301
PROBABLE TOTAL	2761
BIOMASS (tonnes)	3137
PUNGUE & UREMA RIVERS	
TOTAL GROUPS	25
AVERAGE HERD SIZE	30
MINIMUM TOTAL	602
PROBABLE TOTAL	722
BIOMASS (tonnes)	820
GRAND TOTAL NUMBERS	3483
GRAND TOTAL BIOMASS	3957

HIPPO

DRY SEASON DISTRIBUTION & ABUNDANCE FROM AIR COUNTS IN Nov1968 & Oct1972

FIG 9.11

dassies occur on the mountain,where they were collected from the same outcrop on Gogogo summit, as well as on the inselbergs. Klipspringer spoor were found in savanna plainsland between inselbergs and they and dassie must move between isolated rock outcrops which are within sight and are probably more explorative than is generally realized.

SUMMARY OF DISTRIBUTION AND DENSITY PATTERNS

Four main distributional and density (high biomass) patterns are exhibited by the large wild ungulates in the ecosystem, each pattern shared by at least one pair of species due to similar trophic and habitat requirements (Figs 9.12, 9.13).

(1) Riverine zones and medium to tall grass marsh areas characterised by elephant and buffalo. Four main localities for this distributional pattern occurs on the Rift Floor, (a) Nhandue River, (b) Vundudzi – Mucodza – Mupuaze Riverine area on western margin of the Rift Floor, (c) Urema – Pungue, and (d) the Mucodza, Goinha (northern margin of Urema Lake) and Dingedinge slack marshes.

(2) Medium to short floodplain grasslands (including marsh areas which dry out late in the dry season) characterised by wildebeest and zebra which form a concentration pattern related to the nutritional status of the floodplain grasslands. These animals migrate between floodplain areas higher or lower in the flood-ebb catena. Main dry season concentration areas are all the ***tandos*** surrounding the Urema Lake and the rivers entering it from the north (ie. Macoreia, converging delta, Sungue, South Urema) and especially the Dingedinge slack grasslands at the Urema – Pungue confluence. In the wet season the main congregations of wildebeest and zebra occur on the higher levels of the floodplain grasslands, again associated with the Urema Lake and the rivers entering it, as well as on the *tandos* between the Nhandue and Nhamapaza Rivers in the north (Nhamisangu, Tengane, Lunga). In the wet seson, inundation of the Dingedinge area excludes most wildlife but only in exceptional flood years (eg. 1966/67, 1969/70, 1973/74) are the herds excluded from the other floodplains during which time they form a linear concentration in the adjacent savannas.

(3) Circum-Urema Lake floodplain grasslands; an all year concentration of waterbuck and hippo which expands and contracts with the spread and ebb of flood waters. Waterbuck exhibit a periodic change of concentration around the lake and its associated ***tandos,*** rotating their grazing grounds. They also exhibit a seasonally contrasting population density pattern to zebra, due perhaps more to migratory flux of the latter. The largest number of waterbuck occur on the Rift floor during the dry season when there are the least number of zebra – in the wet season it is opposite.

(4) Savanna dambo mosaic of medium to tall grasslands with seasonally reversed density patterns on the topocatena of the Rift floor and adjacent plateaux. Characterised by sable and Lichtenstein's hartebeest, the most sable occurring on the Rift floor in the dry season and the most hartebeest in the same area in the wet season, with reciprocal changes of abundance in the adjacent miombo hill country.

Two lesser patterns are related to (a) the forest/thicket ecosystem-type and (b) to rock outcrops. These habitats may assume considerable areal importance but,due to the territorial behaviour of the ungulates which inhabit them, groups are spaced and rarely assume more than local high density. However. kudu and nyala are two closed-cover components which can attain high population densities resulting in habitat damage, thus the term "local" depends on the dimension of the closed cover habitat.

(a) The forest/thicket pattern is relatively the most sedentary compared to the extensive movement and migrations undertaken by some of the larger open country ungulates. However, considerable local movement occurs outward from larger forest/thicket areas along riverine zones with "island hopping" through the archipelagos of termitaria thickets. In this pattern kudu show the most extensive mobility and exploration.

(b) Rock Outcrop pattern. Gorongosa Mountain and its satellite inselbergs on the west of the system, characterised by klipspringer and rock dassies.

The total patterns of the principal large wild ungulates for the two seasonal extremes are shown in Figs 9.12 and 9.13 which emphasize the fundamental role of riverine zones, floodplain grasslands and marshes at both extremes. The major biomass concentrations are thus supported by the pastures of the base saturated alluvial soils (Ah). In the rains there is a spread from these high density areas to the intervening savanna–termitaria thicket – rain pan complexes, mostly on the better drained sandy clay loam Chd and Cd soils with medium to high phosphorus content and poor base status. If midsummer droughts occur, the herds return to the hygrophilous grasslands. Biomass figures of the principal large ungulates is given in Table 10.3

9.4 FLOODPLAIN FLUCTUATIONS

The series of maps depicting seasonal changes in distribution and density of the principal large ungulates emphasizes the key role of floodplain and riverine zones as a food base. The drought conditions experienced in 1968, exacerbated by a midsummer drought (Feb. 1969), was followed by extreme flood conditions in the summer of 1969/70 when the Urema Plains were flooded for nearly two months into the peripheral savanna tree-line.

After this extreme sequence a 20 km^2 section of the Urema floodplain was chosen for its year-round accessability on which to record the effects of fluctuations in the life supporting floodplain ecosystem. This intensive study area extended from the southwestern shores of the Urema Lake and its Sungue arm south to the marginal woods of fever tree and winterthorn. Total counts of all ungulates were made at two-weekly intervals for one year (3 Feb. 1969 to 11 March 1970) with December 1969 omitted. As this study area fell within the sector most frequented by tourist vehicles, the animals were conditioned to close approach and this allowed for easy counting. Counting was done from the roof of a landrover stationwagon with the aid of X10 binoculars. As various parts of the floodplain are clearly demarcated by incised hippo paths, and the mosaic of shallow slack areas supporting taller hygrophilous grasses within the larger areas of microperennial swards, no problems of double counting arose. As warthog were rare to absent they were omitted from the final analysis (Fig 9.14), as were oribi which show only local seasonal movement.

FEATURES

The floodplains dip at about 1° from the tree line to the lake margin and this is traversed by seven major hippo paths which are more deeply cut towards the lake and less so on the upper margins of the floodplain. The greater part of the plain surface is flat to faintly undulating and covered by two short perennial creeping grasses ***Cynodon dactylon*** and ***Digitaria swazilandensis*** with an average height of 5 cm over the greater part of the year, but attaining 20 cm during the rains and when flooded. Several shallow basins from a quarter to half a hectare in extent occur in the upper sector which support the aquatic hygrophilous grasses ***Echinochloa stagnina*** and ***Vossia cuspidata*** which attain more than 50 cm in height in the rains. If flooded, the two species form floating meadows over extensive areas of the floodwaters. These basins are joined to the similar lower lake shore zone by shallow drainage line depressions, mostly incised by hippo paths. The channels formed by the paths are rounded along their edges by erosion and support dense growths of the two aquatic grasses. In total the poorly drained sites with taller grass cover occupy about 8 km^2, and the well drained short grass area about 12 km^2. On the southwest margin small patches of tufted ***Eragrostis atrovirens*** occur, and in the west adjoining the Sungue is a dense sward of ***Panicum coloratum*** over 1 m high in summer and lodging to half this height in the dry season. A detailed analysis of this floodplain sector is given above (Section 8.5), and the degree of pasture utilization by ungulates in the same area is dealt with in this section and that following on food, feeding and condition (Section 9.5).

FLUCTUATIONS

Floodplain ecosystems are in a constant state of flux as seasonal changes differ every year in intensity and duration. Unlike dry land systems, which are totally dependent on direct rainfall and the moisture balance achieved with a particular substrate, floodplain dynamics are controlled by runoff from afar as well as by direct precipitation. The wetting and drying sequence on floodplains is thus a function of: (a) fluctuations in precipitation and runoff in distant catchments and (b) their own dimensions and (c) their drainage status.

In large floodplain systems such as the Okovango Delta and Kafue Flats there is a much longer time-lag between the peak in flooding at the top end of the system and that at the lower end. In the Okovango, peak flooding at the beginning of the delta occurs in Feb/March and 5 months later in July/Aug. at Maun 256 km downstream at the termination of the delta (Wellington 1955, Tinley 1966). Although the Kafue Flats are of the same order of length as the Okovango Delta, they are only 45 km at their broadest compared to 176 km in the delta, hence there is half the time-lag. There is about 2,5 months lag between peak flooding at the flats' commencement in March and at its lower end in May/June (Sheppe & Osborn 1971). The ebb is also of much longer duration in the larger systems as the drying sequence follows after the flood peaks from the upper to the lower end of the system. Because of their dimensions alone therefore, large floodplains have a built-in inertia to water loss and thus provide green pastures throughout the dry season and into the torrid pre-rains period August to October. Only exceptionally high floods exclude the majority of ungulates from these floodplain pastures in midwinter.

The effectivity of smaller floodplain systems such as the Urema in providing unseasonal green pastures for wildlife are thus most critically related to the drainage status of their depressions. If they are unbreached, shallow bodies of water of various dimensions are left behind which provide a contracting zone of green flush as the waters dry up. However, if they are breached by channels, both the amount and temporal spread of hygrophilous grassland productivity is greatly reduced to little better than that of the adjoining savannas.

The wetting and drying sequence over floodplain microrelief is the reverse of that which the system experiences as a whole, described above for the Okovango and Kafue. The lowest parts are flooded first and are exposed last on the ebb, whereas the highest parts are flooded last and exposed first. Thus a spatial sequence is superimposed on a microtopographic sequence. The intensity and duration of this superimposed sequence influences primary productivity, plant and animal phenological events, phyto-zoomass relationships, and successional dynamics of floodplain and dry land components.

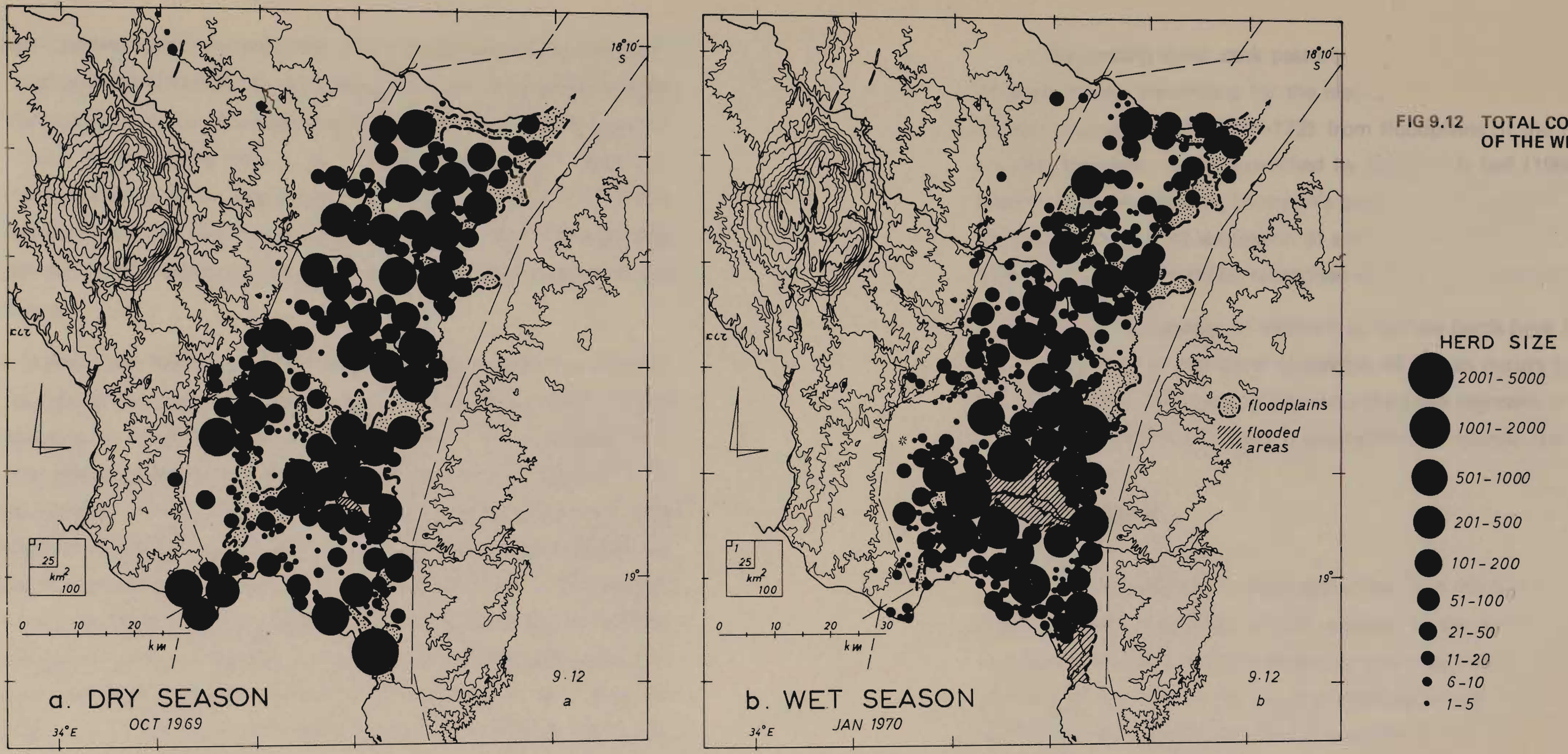


FIG 9.12 TOTAL CONCENTRATION PATTERNS OF THE WILD UNGULATES

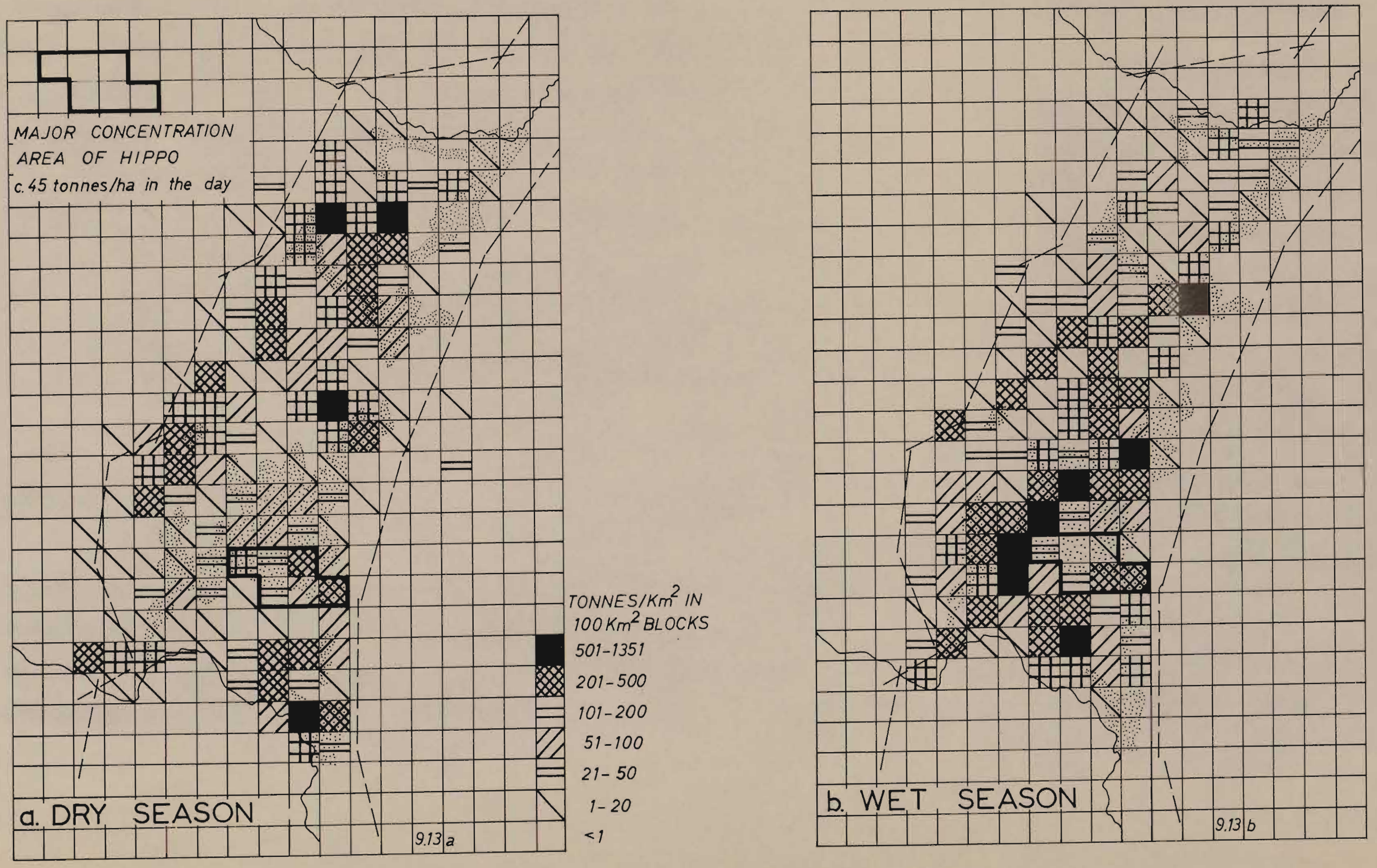


FIG 9.13 BIOMASS*
TONNES/KM² IN 100 KM² BLOCKS
*Hippo excluded

Due to their relatively small size and close proximity to the Gorongosa Mountain catchment, flood and ebb responses on the Urema Plains are sensitive to changes in precipitation and runoff from the Mountain and in the Rift Valley itself. Maximal flooding on the Urema Plains, lasting from 8 to 10 weeks in the period January to March, occurs some 2 months after the beginning of the rains. Compared to the rapid flood rise to a maximal spread, the ebb lasts for twice as long from 2 to 5 months (the latter in the lowest slack areas) depending on how slow or rapid rains tail-off on the Mountain in the autumn.

When the Urema Lake floods, water spreads outward up all the channels and basins first and inundates the upper depressions before coalescing across the short grasslands and extending up to 300 m into the marginal fever tree, winterthorn and palm savannas. The ebb sequence is in reverse; the first sites to be exposed are the upper margins and convex surfaces which flush first in response to re-exposure. The last to be exposed are the floating mats of aquatic grasses which are left stranded on top of the short grasses, but are soon eaten back to the receding water's edge. Termite hills usually remain exposed as small islands during high floods but the lower eroded hills are flooded. Depending on extent of flooding and speed of ebb, through rapid loss of water along channels, the drying sequence can be fast (2 months) or slower when the lowest slack areas dry out only at the most arid part of the year providing a last green flush before the rains. However, as pointed out in the chapter on hydrography (Ch. 5.6), most of the depressions in the Gorongosa ecosystems are breached by hippo paths if not by natural headward erosion of nickpoints. Thus the areal extent of unseasonal green pastures has been reduced to a very narrow margin or edge in most sectors, except the flattest mudflats adjoining the dry season level of the Urema Lake. On the other hand floodwaters which are too deep, or lie too long, kill off the inundated graas cover, if this is not composed of hygrophilous species, resulting in extensive bare mudflats. These bare areas are then invaded by dense swards of mudflat weed communities, (components of which are used by some of the herbivores) and later by the creeping ***Cynodon*** and ***Digitaria*** from the margins or from root bases which had survived long flooding.

GRASSLAND AND GRAZING SUCCESSION

Flood and ebb of varying intensity in every year imposes a succession of flush and availability of different grassland types to which is a closely related succession of large ungulates. The succession of grazers is a function of the feeding level preferences in each species and thus the growth form of each stage in the grasslands.

By grazing down rank pastures, the coarse grass feeders, elephant and buffalo, enhance grazing conditions for the medium to short grass feeders. First described by Vesey-Fitzgerald (1960: 161–172) from floodplains of the Rukwa Trough, this relationship has been neatly quantified by Gwynne & Bell (1968: 390–393) for the sequence zebra, wildebeest, Thomson's gazelle in the Serengeti ecosystem, Tanzania. In Gorongosa the grazing succession of species are elephant and buffalo first, on rank or coarse pastures, followed by zebra, then wildebeest, waterbuck and impala.

Where the passage of elephant or buffalo herds have flattened swaths through 3 m high grassland, the same succession of species occurs following the exposure of two subordinate softleaved grasses and the basal regrowth of the large grasses. These areas are also attractive to sable, Lichtenstein's hartebeest, reedbuck and oribi.

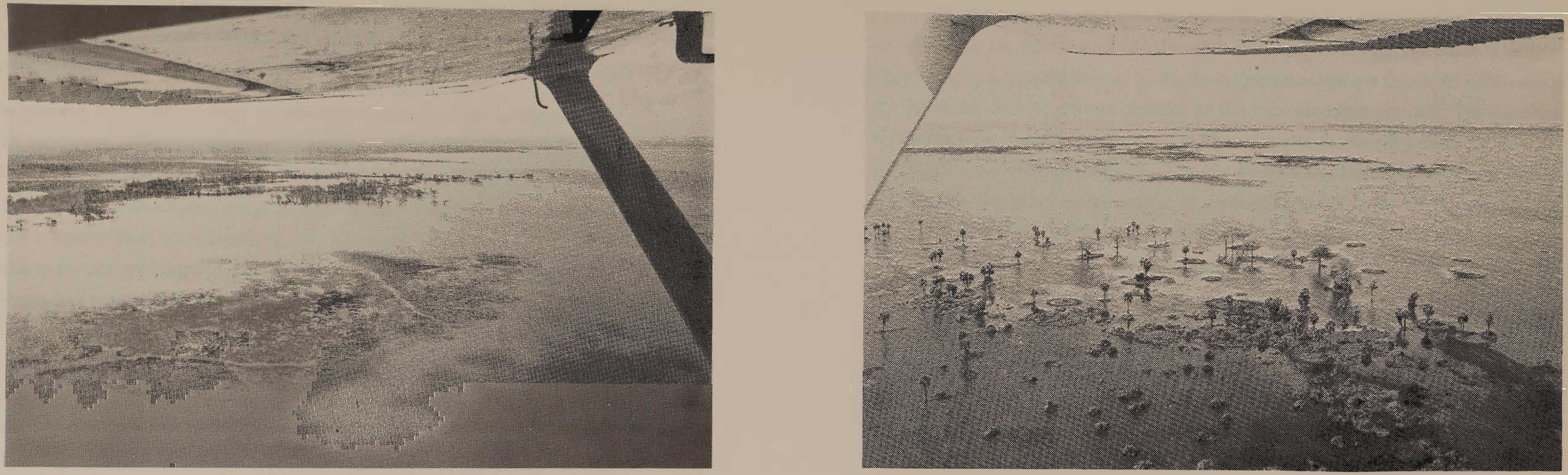
High flood patterns

All the grasslands in the system flush with the first rains in November, although extensive areas of post-fire growth withers in the torrid period. For the first two months of the rains the floodplains support high concentrations of large herbivores: elephant and buffalo on the margins of depressions and channels, zebra on the medium swards and wildebeest and waterbuck on the shorter grasslands, in a mosaic fitting that of the different pasture types.

As the floodwaters spread outwards the herds move back in linear concentration using the still exposed floodplain margins, or they are forced back into the adjoining savannas. In the adjacent savannas the pastures used most by the herds are those dominated by ***Urochloa mosambicensis, Digitaria milanjiana, Panicum coloratum*** and ***P. maximum.*** The coarse grass feeders also concentrate on the hygrophilous grasses of depressions in the savanna. Some of these grasses particularly ***Urochloa*** become dominant in basal area, if not in quantity, by heavy ungulate use. In such circumstances there is a change in growth form, the flowering culms are procumbent as opposed to the usual erect growth form when there is no grazing pressure, and vegetative growth is maximal. The short ***Cynodon dactylon*** – ***Digitaria swazilandensis*** grassland become completely inundated and the aquatic ***Vossia cuspidata*** and ***Echinochloa stagnina*** grasses rooted in depressions on the floodplains grow through, the aerial parts on buoyant stoloniferous culms forming extensive floating meadows.

As the floodwater is from several centimetres to 60 cm in depth over large areas the microperennial grasses are not killed by a two month submergence and in the shallower parts grow up towards the water surface. Deeper than 60 cm the ***Cynodon*** and ***Digitaria*** die back (or are grazed by fish?) to their largest tufts from which they grow

PLATE 22 WATER TO THE HORIZON OF THE UREMA PLAINS IN HIGH FLOOD YEARS (SUMMER 1969/70)



(A) View west of the southern margin of the Urema Plains from above the lake's eastern end. In the foreground shallowly flooded short *Cynodon – Digitaria* grasslands on a convex surface traversed by hippo paths. Leafless winterthorn woodlands in middle distance and Road 4 area in background.

(B) View north of the Urema Plains from above its southern margin (Road 4 area). Floating pastures of *Echinochloa stagnina* and *Vossia cuspidata* in the background. In the Foreground termite hill islands, winterthorn on sand, and palm on saline clay convexities of alluviocatena.

(C) View northeast of inundated marginal floodplain fever tree woodland. Southern margin of Urema Plains (Road 3–4 junction area). Dark patches in floodwaters are floating meadows of aquatic grasses.

(D) View north to Goinha sector of Urema Plains from near 'Lagoa Paraiso' (flooded slack on right). Southeast margin of lake. In the foreground *Hyphaene benguellensis* scrub-thicket and winterthorn on levees of fossil Pungue River distributary fan in middle distance.

out and recolonize the mudflats when they are exposed. Rafts of varying dimensions of the floating aquatic ***Eichhornia crassipes*** form islands which are moved by changes in wind or are carried down the Urema to the Pungue and the sea.

The extreme floods recorded in January and February 1970 inundated some 200 km^2 of the Urema Plains and the entire Urema – Pungue confluence area for two months. At the end of February and beginning of March as the waters slowly receed, stranding the floating meadows and rafts of ***Eichhornia***, the short ***Cynodon – Digitaria*** grasses flush a second time on re-exposure. The herds move back onto the still wet plains following the ebb and large herds of elephant, buffalo and zebra graze down the stranded ***Vossia*** and ***Echinochloa*** to the edge of the depressions. The channels and depressions choked with these two aquatic grasses plus ***Paspalidium obtusifolium*** are increasingly used as the autumn advances, first by the coarse grass feeders and in mid and late dry season by the short grass feeders. The first ungulates to stake their territory on the re-exposed ground are lone wildebeest bulls. They, and small wildebeest herds, often walk through extensive areas of shallows to take up a post or graze on low rounded exposed termite hills.

The high primary production and mosaic of grass types as the floods abate support the heaviest concentrations of large ungulates and also a diversity of species including eland, impala, oribi and large baboon troops in addition to the species noted above. The exclusion of the herds from the floodplains by intervention of high floods results in a bimodal maximum and minimum of ungulate density and biomass. One maximum occurs on the rain-flushed pastures until February followed by total exclusion of animals (except hippo) with a second high peak in the autumn on the ebb flush. This is followed by a second extreme low in animals (total ebb) in October (Inset in Fig 9.14).

From here on the sequence is similar to that detailed below for medium to low flood years.

Medium to Low Flood Patterns

After the maximal spread of flood waters from mid-February to mid-March in 1970, a detailed study of a 20 km^2 section of the Urema Plains was initiated in February 1971 during low flood conditions, and extended through until March, 1972 when medium floods occurred.

The composition and numbers of species at 2 week intervals expressed as a percentage of total animals and correlated with the rainfall of the ten days preceding each count clearly illustrates a number of salient features (Figs 9.14, 9.15).

On the environmental side the total reliance of floodplain and aquatic grasses (in unflooded depressions) on rain-drought sequences is marked. The rapidity of drying or wilting is a characteristic of the short ***Cynodon-Digitaria*** grasslands which occur on the better drained convex surfaces of the base saturated vertisols. The excessive soil-moisture in the depressions permits these pastures to remain greener longer, overriding the rapid aridifying effects of highly saline soils. These moisture and pasture fluctuations are depicted by means of contrasting symbols for clouds and grass in Fig 9.14. The short grasslands show a regrowth flush about 10 days after rain, if no further rain occurs the grasses wither quickly but take another 10 days to discolour.

On the animal side the grassland and grazing sequence is clearly depicted by the change in species dominance through the annual cycle (Figs 9.14, 9.15). Elephant and buffalo are rare within the intensive study area due to the predominance of short grasslands; the ***Vossia*** and ***Echinochloa*** depressions are however used mainly at the height of the rains when these areas have been partially inundated by direct rainfall and runoff. If the aquatic grasses only attain about 50 cm in height, zebra are first in the grazing sequence, as shown by their abundance in the 4th of February count. At the same time the wildebeest herds are mostly on the intervening short grasslands, but move into the grazed down depressions after the zebra, and whenever the short grasslands wither or discolour. Zebra numbers decrease, with some fluctuations by movement to and from the adjacent savannas, whenever regrowth occurs after rain. This pattern continues until mid-May when almost all zebra leave the Urema Plains for the slack pastures in the Dingedinge area at the Urema – Pungue confluence. A maximum in wildebeest numbers occurs in April and May due to influx of herds migrating from central and northern pastures to Dingedinge via the southern margins of the Urema. The arrival and length of time spent by these herds on the south Urema Plains varies with the state of the pastures in each autumn.

Following the ebb line is a zone of changing widths, dependent on microrelief at each level, of moist soil supporting a green flush (the "green zone") which moves down the alluviocatena followed by drying out (browning) on its upper margins. The herds follow the green zone and vacate all the upper margins where the grasslands have turned brown. Large concentrations of wildebeest stay on the narrowing green zone for more than a month after the zebra have left, then emigrate south to the Dingedinge area where the slacks choked by ***Vossia*** and ***Echinochloa*** growth have been grazed down first by buffalo and elephant and then zebra to a short pasture.

With the departure of the majority of wildebeest, waterbuck and impala become the dominant species on the green zone from mid-dry season (June) until the first rains in November. The small changes in wildebeest and zebra numbers during this

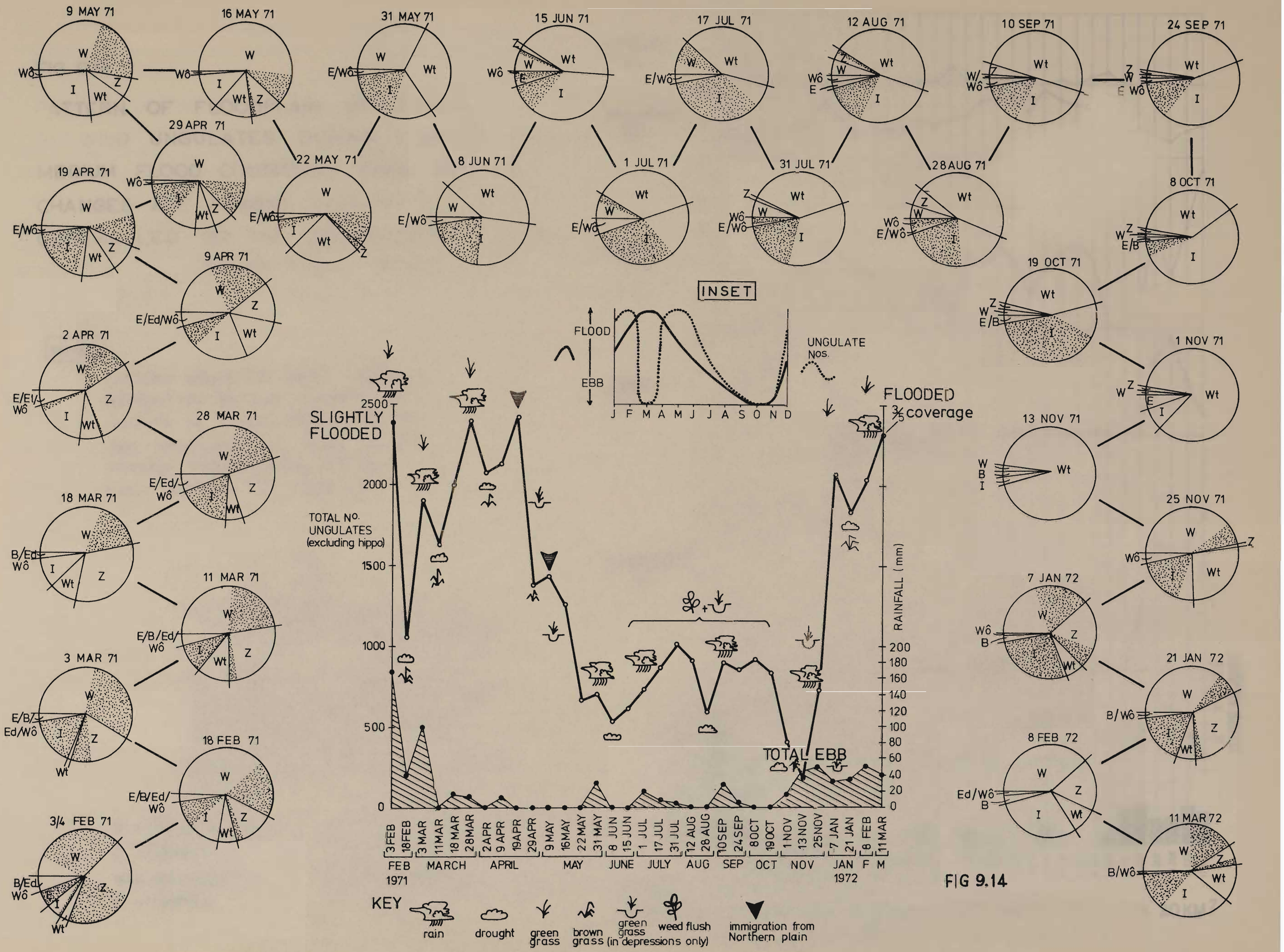

9 MAY 71
16 MAY 71
31 MAY 71
15 JUN 71
17 JUL 71
12 AUG 71
10 SEP 71
24 SEP 71
29 APR 71
22 MAY 71
8 JUN 71
1 JUL 71
31 JUL 71
28 AUG 71
8 OCT 71
19 APR 71
9 APR 71
19 OCT 71
2 APR 71
1 NOV 71
28 MAR 71
13 NOV 71
18 MAR 71
25 NOV 71
11 MAR 71
7 JAN 72
3 MAR 71
21 JAN 72
18 FEB 71
8 FEB 72
3/4 FEB 71
11 MAR 72
W
Wt
I
Z
Wô
E
B
Ed
E/Wô
E/Ed/Wô
E/EI/Wô
E/Ed/Wô
B/Ed/Wô
E/B/Ed/Wô
E/B/Ed/Wô
E/B/Ed/Wô
B/Ed/Wô
W/Wô
E/B
B/Wô
Ed/Wô B
INSET
FLOOD
EBB
J F M A M J J A S O N D
UNGULATE Nos.
SLIGHTLY FLOODED
FLOODED
3/5 coverage
TOTAL EBB
TOTAL No. UNGULATES (excluding hippo)
2500
2000
1500
1000
500
0
RAINFALL (mm)
200
180
160
140
120
100
80
60
40
20
0
3FEB
18FEB
3 MAR
11MAR
18 MAR
28MAR
2APR
9 APR
19APR
29APR
9 MAY
16MAY
22 MAY
31 MAY
8 JUN
15 JUN
1 JUL
17 JUL
31 JUL
12 AUG
28 AUG
10SEP
24SEP
8OCT
19OCT
1 NOV
13 NOV
25NOV
7 JAN
21 JAN
8 FEB
11MAR
FEB 1971
MARCH
APRIL
MAY
JUNE
JULY
AUG
SEP
OCT
NOV
JAN 1972
F
M
KEY
rain
drought
green grass
brown grass
green grass (in depressions only)
weed flush
immigration from Northern plain

FIG 9.14

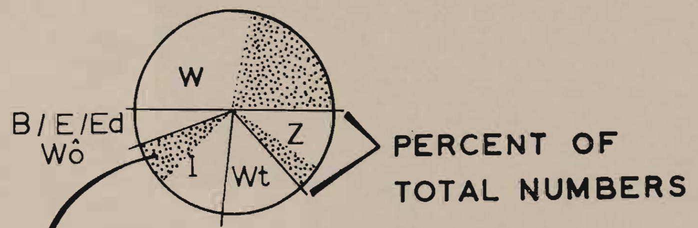
FIG 9.14

PATTERN OF FLOODPLAIN UTILIZATION BY WILD UNGULATES DURING LOW TO MEDIUM FLOOD CONDITIONS WHEN PASTURE CHANGES ARE ALMOST TOTALLY CONTROLLED BY THE OCCURRENCE OF RAIN.

STUDY AREA = 20 km^2

INSET

PATTERN EXHIBITED WHEN MAXIMUM INUNDATION OF THE FLOODPLAINS OCCURS i.e. TOTAL EXCLUSION OF THE UNGULATES AT HIGH WATER PERIOD, EXEMPLIFIED BY THE HIGH FLOODS OF 1969/70.



PERCENT OF TOTAL NUMBERS

PROPORTION OF SPECIES TOTAL INVADING THE FLOODPLAINS FROM THE SURROUNDING SAVANNAS AT DUSK (EVENING INVASION)

These animals return to the savannas at dawn.

W = WILDEBEEST

Z = ZEBRA

Wt = WATERBUCK

I = IMPALA

Wô = WILDEBEEST (territorial males)

B = BUFFALO

E = ELEPHANT

Ed = ELAND

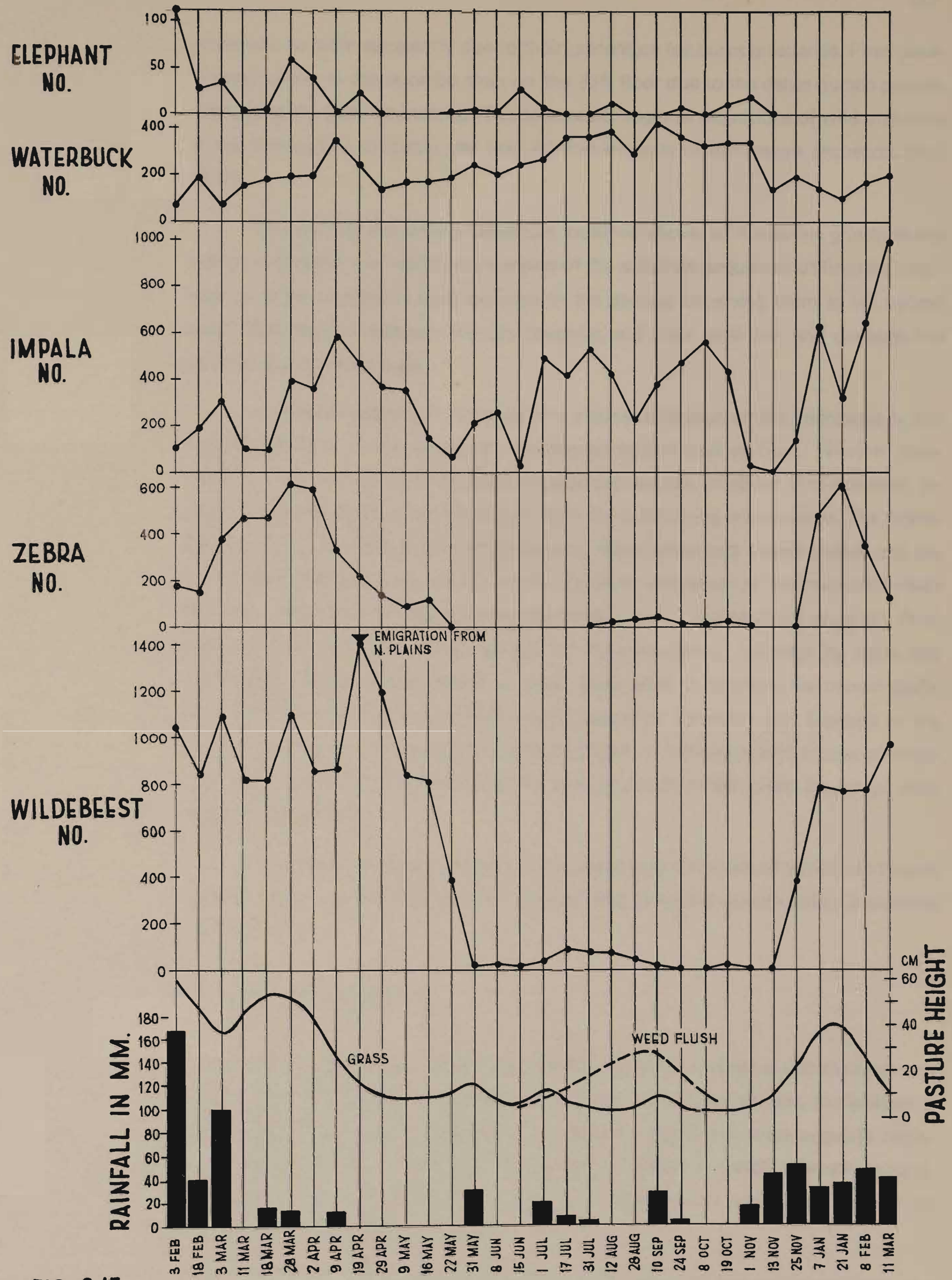


FIG 9.15

SEASONAL FLUCTUATIONS IN GRASSLAND AND GRAZING SUCCESSION ON 20 KM^2 INTENSIVE STUDY AREA OF UREMA FLOODPLAINS period is related to the effect of unseasonal showers on ***Vossia*** and ***Echinochloa*** grasses of the lower-lying sectors, attracting animals from the adjacent savannas for short periods.

The green zone at the height of the dry season is a mosaic of large mudflat areas covered in seasonal weeds, which are at the height of their development in September, green stubs of the aquatic grasses, and ***Cynodon*** and ***Digitaria*** recolonizing the drying mudflats and shooting through the mulch of stranded ***Eichhornia*** rafts. This narrow zone supports almost the entire waterbuck population, large herds of impala and 80% (2 761) of the hippo population during the torrid period (3–4 months). The hippo, however, also graze ***Cynodon*** that has turned brown if the culms are still green. Nevertheless a large number of hippo are forced to graze out to nearly 10 km at night in the adjoining savannas and the entire population are extremely emaciated for the greater part of the year (Fig 9.22).

As the waterbuck and impala are confined to the narrow green zone near the water's edge in the mid and late dry season, the view from the tree line from July on is of vast floodplains of sere grass and mirages, devoid of all herds, and which remain an empty quarter until the onset of the first rains, unless revitalised by unseasonal showers.

A marked break in impala numbers on the floodplains occurs in the first half of November, when herds return to the adjacent savannas and bush where the females drop their young. In the last part of November the impala herds and their newborn lambs return to the green zone on the floodplains (Figs 9.14, 9.15 compare counts between 19 October and 25 November).

Some ten days after the first significant spring rains (> 20 mm) have fallen, the wildebeest herds are the first to arrive on the new growth flush of ***Cynodon-Digitaria*** grassland of the Urema Plains from their dry season concentration area in Dingedinge (Figs 9.14, 9.15 compare the contrast in counts on 13 November and 25 November). Zebra arrive in large numbers later, when some grass areas have attained a medium height, having spent the interim period grazing in the intervening savanna grasslands.

DIMENSIONS OF THE SUCCESSION

On the macroscale the grassland and grazing sequence, following the catenal changes in soil moisture, and thus in green pastures, is shown by sable which move down from the adjacent miombo savanna uplands into the Rift floor where green shoots can be obtained throughout the dry season, in contrast to the coarse grass stratum on overdrained sands in the miombo. Lichtenstein's hartebeest show an opposite movement to sable apparently due to their preference for burnt grasslands. Fires usually begin earlier in the miombo than on the Rift floor due to the dense human populations along the park boundaries. The spectacular regional migrations of wild ungulates in the Serengeti is probably the best African example of macroscale sequences (Bell 1971).

The wetting and drying sequences, outlined above, of floodplain grassland and grazing succession are mesoscale examples of the substrate sequences utilized by ungulates, as is the movement from miombo to the dambos traversing them in the upland areas. The relation between the dry savannas and their local pan and drainage-line systems is on a similar scale.

A singular example of the grass and grazing succession on the microscale is that exhibited by and on the gilgai micro-basins on bottomland vertisols. Whether inundated by rain or river flooding, these circular depressions, of about 3 m diameter, remain wetter longer into the dry season than the intervening micro-ridges. The microbasins support the hygrophilous ***Echinochloa, Paspalidium*** and ***Vossia*** grasses and the microridges support either median height ***Panicum coloratum*** or the microperennials ***Cynodon dactylon*** and ***Digitaria swazilandensis***. Buffalo and elephant graze the ***Panicum*** and then the lush aquatic growth of the microbasins, followed by zebra and wildebeest. Waterbuck are present in these gilgai areas throughout the annual cycle. As the microbasins dry out, stoloniferous invasion by ***Cynodon*** and ***Digitaria*** of the basin occurs from the browned microridges. Hence in mid dry season groups of wildebeest centred on the microbasins, can be seen grazing the fresh green growth of invading microperennials.

The grasses in the microbasins, now comprising a mixture of aquatic and mesic species, are among the first sites of renewed and extended growth when unseasonal showers occur.

SAVANNA SEQUENCES

As the interplay of utilization by wild ungulates of savannas and their pan and riverine sites is similar to the succession described for the floodplains, explanation is required of changes and differences in the savanna which influence ungulate movements between the two. Essentially the floodplain system is merely a greatly expanded riverine and pan system where microrelief influences on degree and duration of wetting over-ride differences in soils.

Unlike the upland miombo savannas which occur on only a few soil types, the Rift Valley savannas occur as a mosaic on alluviocatena patterns and their ecotones which in itself is responsible for a whole chain of interactions. The soil properties in each affect the soil moisture balance and influence the occurrence of different types of grassland of varying height, density and structure. Thus in the savannas and adjoining upper margins of the floodplains, a spectrum of pastures is available to the whole range of ungulate preferences which can be obtained merely by their moving form one site to another. Each of these habitats (plant-edaphic associations) have different responses and potentials to environmental change, though all are eventually affected by continued drought conditions. Many of the savanna grasslands of the Rift floor dry out and discolour with midsummer droughts and in the early autumn (March and April) and are then shunned by the wild ungulates for the remaining green pastures, though some species retain green leaves basally.

The inherent salient feature of alluvial grasslands is that single or few species dominate over extensive areas, alternating with other single dominants on adjacent substrates (vide Section 8.5), and either provide a superfluity of preferred grazing during the rains and autumn for many ungulates at its different stages of growth, or at the other extreme are almost useless as pasture unless altered by lodging, trampling or fire well exemplified by the 3 to 4 m tall ***Vetiveria***, ***Hyparrhenia, Panicum*** or ***Setaria*** swards over large sectors of the system.

Most of the tall grasslands however have a two (or three) tiered structure, the lower storey occupied by highly favoured soft-leaved grasses. In ***Hyparrhenia*** swards the subordinate layer is formed by ***Urochloa mosambicensis*** and ***Digitaria milanjiana***, and in ***Setaria*** grassland ***Panicum coloratum*** and ***Digitaria swazilandensis*** form a lower layer with forbs. Thus the passage of buffalo and elephant through these grasslands whilst they are feeding on the second grass storey opens up the dense tall cover for a succession of other grazing species.

The extensive stands of 4 m high giant form of ***Panicum maximum*** which occur mostly in the shade of closed canopied ***Piliostigma*** tree savanna on the Rift floor remain green until June when they are in full seed. They are used mostly by buffalo and elephant in the autumn before they become rank. Early fires also destroy these swards as there is an abundance of fuel from the accumulation of lower dead leaves. If no fire occurs these shade grasslands lodge if not flattened by the large herbivores and provide green shoots for medium to short grass feeders deep into the torrid season if unseasonal showers occur.

In the autumn when the median floodplain grasslands have been grazed down the zebra move into the adjacent savannas where they concentrate in the areas of ***Urochloa mosambicensis, Digitaria milanjiana, Panicum maximum*** and ***Heteropogon contortus*** already topped by buffalo and elephant. In dry years this movement is earlier in the season and later in wet years. Either rapid drying out and fire, or both, make large areas of savanna unattractive and most of the ungulates congregate on the depressions in the savannas if the floodplain slack pasture area are still too wet. However, soon after the passage of fire large herds of zebra and wildebeest are lured away from the bottomlands and are joined by Lichtenstein's hartebeest to feed on the burnt (toasted) culms and basal leaves. The post-fire regrowth is grazed until withering occurs, when the herds move back to the bottomland or slack grazing. It is at this time that small herds of zebra and wildebeest move up into the miombo savannas following the flush of grasses there from earlier fires.

Other fluctuations in numbers and composition of ungulates on the slack green zones are caused by unseasonal showers which results in different responses in the variety of grasslands and within the same type depending on whether they were burnt or not.

In the dry season, short grasslands of all kinds, including the burnt and post-fire stages of tall and medium grasslands, whilst reacting rapidly to any unseasonal rain shower, also dry out the fastest due to lack of shade on the soil surface. In addition, leaf production in the microperennials is very small compared to the larger tufted grasses. Thus apart from slacklands, the most important pastures in the dry season are those savanna grass communities which have a mulch cover on the soil of lodged or trampled grass. The smallest unseasonal shower is then most effective, as the moisture is not lost by evaporation but penetrates the soil and is deepest beneath the mulch and in the grass root zone of each tuft from increased runoff of rain down the grass stems (Table 5.3). For example, a shower of 4 mm on 27 August 1971 penetrated from 5 to 7 cm beneath median ***Urochloa*** grassland as well as in the microperennial cover, but the unburnt median grasses continued to produce green foliage long after the shorter species or burnt areas of the same cover had dried out.

For these reasons many of the herds stay on in the savannas where unburnt areas of ***Urochloa*** occur, and only decamp to the slack areas in the final part of the torrid period. Drought years aggravated by devastating fires leave only the dry hippo lawns and narrow green zones intact. This has tremendous repercussions on migration and animal condition. Herds from long distances away appear in the park (noted by professional hunters for those areas), the riverine and slack areas are over-utilized, and most ungulates lose condition rapidly in the early autumn resulting in mortality mainly of hippo and buffalo (see Section 5.7).

DAILY MOVEMENT BETWEEN SAVANNA AND FLOODPLAIN

Within the two major rhythms of the general annual cycle exhibited by ungulates – dispersion in the rains and return to riverine zones in the dry season (with a seasonally fluctuating trophic successional pattern) – is a striking year-round daily component involving the alternate use of savanna and floodplain.

The data from a year's study of one sector of the Urema Plains shows the regularity and dimension of this phenomenon (summarized in Figs 9.14, 9.15).

The stippled areas within each pyegram represents the proportion of the total percent of each species which invaded the floodplains in the late afternoon from the adjacent savannas. Wildebeest, zebra and impala in the rains and autumn, and mostly impala at the height of the dry season, provided the most spectacular display of this evening invasion. At the break of dawn and before, lines of zebra and wildebeest trek back into the adjacent savannas. What would be the grandest spectacle of all, if it were possible to see, would be the emergence of nearly 3 000 hippo from the Urema Lake out onto the surrounding floodplains every night.

In midsummer and autumn, herds of elephant also form part of the evening invasion to feed on floating mats of ***Vossia*** grass and ***Mimosa pigra*** shrubs in the shallows. They leave the floodplains before dawn. In the mid dry season lone territorial male wildebeest also take part in the evening invasion and return to the savanna. Waterbuck is the only species which remain on the floodplains day and night.

No evening invasion of the floodplains was recorded on three of the thirty-two counts in the year, ie. on 1 November 1971, 13 November 1971, 8 February 1972 (Fig 9.14). Large baboon troops spend the nights sleeping in riverine or savanna trees marginal to the floodplains, and most of the day feeding either on the ecotone or far out on the plains returning only at dusk.

In the torrid period and hot-wet midsummer period there is some movement of individual herds to the floodplain margins for shade, elephant seeking shade as early as 09h00 in this season. The important feature is that about half of the population of wildebeest and zebra remain on the floodplains all day whilst the other half return to graze in the savanna at dawn. In impala, though the proportion varied, the majority of the local population came onto the open plains in the late afternoons of summer and in autumn when good rains had occurred. In the dry season, however, the population showed a dimorphic activity, part remaining on the floodplains all the time and the remainder moving daily back and forth. As noted previously the exodus of impala from the floodplains in the first three weeks of November relates to their calving in the bush of the savannas. Soon after giving birth the impala herds return to the ***Cynodon*** floodplain pastures.

These daily oscillatory movements were also observed between April and October on a smaller scale in most of the other floodplain or slack-savanna junctions, including the areas,Tengane, Nhamisangu, Macoreia, Goinha, Mucodza and Dingedinge. However, no wet season data is available from these areas to verify the behaviour as a general year-round phenomenon everywhere.

Adjustments in drinking behaviour to tourist activities, in Wankie National Park, Rhodesia, was noted amongst elephant, buffalo and zebra (Weir & Davidson 1965). No definite data on this subject was obtained from my intensive study area which fell within the southern sector of the park open to tourism. Elephant, however, emerged later in the evenings in the tourist season between April and November, and eland left the area altogether. In the remainder of the Rift floor, closed to tourists eland were often encountered in similar open floodplain areas during the dry season. As safari hunting areas adjoined the northern and eastern sections of the park, eland may remain shy of vehicles due to their wide ranging habit. With other species, however, the impression was gained that tourist activity formed part of a sanctuary effect furtherest from the safari hunting areas,and where least poaching occurred.

Similar daily movements though apparently on a smaller scale, were recorded by Jarman (1972) in the Mid-Zambezi Valley below Kariba, and on the Chobe River in Botswana by Sheppe & Haas (1976). As the daily movements recorded in the Mid-Zambezi Valley coincided with the preferred drinking times noted for the same species in Wankie (Weir & Davidson 1965), Jarman suggested that "at least part of the reason for the daily incursions onto the flood plain made by these species was to drink at the river" (Jarman 1972:291). In comparing the different patterns of floodplain use by the same wild ungulate species on the 20 km broad Kafue (Sheppe & Osborne 1971) with that on the narrow (1 km or less) Chobe floodplain in Botswana,Sheppe & Haas (1976) conclude that the different dimensions of the two floodplain areas was the determining factor. The size of the floodplain influences the flood regimen and thus the spatial and seasonal relations with their surroundings.

As oscillatory movements between the two major systems are exhibited throughout the annual cycle,from the time when surface water is abundant everywhere to the time when the Urema Lake is the only surface water in the area, several factors are probably at play. These factors probably act in concert or alone at different seasons, and influence each species differently.

In sum the possibilities responsible for this daily oscillatory movement between the floodplains and marginal wooded savannas include:

(1) Attraction of open places for feeding or spending the night (eg. wildebeest, zebra, impala). This is shown by the attraction of animals to open saline areas in wooded savanna or airstrip cuttings. Recorded for impala elsewhere by Jarman (1972:292).

(2) Shade seeking. Moving into marginal savannas on summer days and returning to open plains in the evening, eg. buffalo and elephant.

(3) Movement from plains to marginal wooded savanna at night (opposite to 2 above) as shown by baboon. Where floodplains are narrow, waterbuck (and lechwe in the Okavango, pers. data) also move into the marginal savanna at night.

(4) (a) Surface water availability and preferred drinking times.

(b) Availability of surface water as a result of elephant digging holes in sandy riverbeds. Local examples are the broad Nhandue and Nhamapaza 'sand rivers' which traverse the Rift floor in the north of the system.

(5) Evasion of large predators; by either the increased vigilance of several species occurring together in large numbers and/or the visual advantages of open terrain.

(6) Inadequacy of the plain's green zone in dry season. Part of the local population of the same species remain all day and night on the plains, the remainder use the adjacent savannas in the day and return to the floodplains at night. What determines which herds take part in this dimorphic behaviour is unknown.

(7) Change of feeding due to drying out (wilting) of floodplain pastures in the day when toxic amounts of hydrocyanic (prussic) acid are likely, in *Cynodon* particularly. Use of these pastures at night due to regained turgor and guttation, resulting in rapid reduction of prussic acid content after sunset. Rapid changes in prussic acid toxicity are recorded in many grasses (particularly *Cynodon dactylon*) in the torrid period after unseasonal showers or fire, in midsummer droughts and in autumn due to rapid desiccation and/or frost on the inland plateau (Henrici 1926: 494:498; Steyn 1934: 118–138). Savanna grasses in shade of trees or the green zone pastures are used at these times.

(8) Possible local movement in summer imposed by intense irritation of blood-sucking flies (*Tabanidae* and *Glossina*) mostly in the daylight and crepuscular hours and mosquitoes (*Culicidae*) at night. Mosquitoes are known to be far less numerous on the open floodplains at night, than in the adjacent wooded savannas where the effect of the nocturnal katabatic breeze from the uplands is nullified. However, on still nights there may be no difference. Certainly some animal species and individuals are more sensitive than others to 'biting flies' (eg. lechwe pers. obs.) and to the irritation of non-blood sucking muscids (locally referred to as 'wildebeest flies') which occur in swarms of almost plague proportions at the height of the wet season. These flies appear to affect oribi most who take evasive action by secluding themselves in tall dense grass patches.

Evasive action taken by animals against biting flies are recorded by a number of authors (eg. Fraser Darling 1937: 131–140; Fosbrooke 1963: 124–126; Glasgow 1963: 97–99, 105–108; Tinley 1964: 73–75; 1966: 106; 1969: 17).

(9) Adjustments of resource use patterns to human activities (including tourism, day hunting, night hunting, agriculture).

(10) Influence of the spatial dimensions of abutting systems on wetting and drying sequences, and thus the seasonal and daily sequences of utilization by herbivores through proximity or remoteness of contrasting habitat resources (their qualitative and quantitative changes).

GRAZING SUCCESSION : SUMMARY AND COMPARISONS

The migratory and local movements of wild ungulates is an opportunistic response to the availability and disposition of suitable ambient (physical and social) food resources and water. In the Gorongosa system, the coactive influences of substrate diversity, disparate wetting and drying sequences, grazing and fire, provides a year-round succession of resources in a relatively small area. However this multiformity is lost during droughts when the drying out of even the lowest slacks, and uncontrolled fires, reduce the pasture resource to a seared homogeneity for several months.

The Gorongosa example shows further that close juxtaposition of diverse systems, particularly that of savanna with slack floodplains exhibiting heterogenous wetting and drying sequences, is a fundamental feature allowing attainment of year-round life requirements through the rotation of large concentrations of ungulates on a local scale, whereas migrations of geographic dimensions (exemplified by Serengeti) are required in order to sample a parallel sequence when systems are widely separated.

The grassland and grazing succession involving wild ungulates and floodplains (slack basins) of the Urema Trough (first described in Tinley 1969c) is almost identical with that recorded by Vesey-Fitzgerald (1960, 1965) further north in the Rukwa Trough sector of the Great Rift Valley. It is also similar to that in the Ngorongora Crater, Tanzania (Estes 1968; Anderson & Herlocker 1973), and that of the Serengeti ecosystem (Bell 1971) except on a smaller scale. The pattern is, however, quite different to the typical relationship between savanna and riverine strips where there is a high concentration of ungulates along the riverine zones in the dry season only, followed by a dispersal away to the back country during the rains. This latter seasonal alternation is exemplified by the Luangua Valley (Fraser Darling 1960: 72–74; Dodds & Patton 1968) the Mid-Zambeze Valley (Attwell 1963, Jarman 1972 in Rhodesia; Tinley & Sousa Dias 1973 in Mocambique) and the Chobe River (Child 1968b; Sheppe & Haas 1976) to name a few.

Although there is a topocatenal grazing succession on the macroscale between the upland miombo savannas and the Rift Valley floor, the main difference in succession between interfan slack basins and the usual riverine situation given above, is the local rotation of high concentrations of wild ungulates at all seasons across alluviocatenas which are separated by small differences in microrelief. The microrelief differences, together with changes in soil properties and differential grazing, affect the composition, structure, productivity, and availability (phenology) of pasture food resources.

The overlay of microrelief (microcatenas) on laterally changing soils (alluviocatenas), related to differential sorting and deposition by fluvial fan processes (as opposed to lateral deposition by a river traversing the bottomland), has provided a multiplicity of substrates from which the wildlife can obtain maximal use by opportunistic migratory responses; moving laterally, and up or down. For this reason the sequences in the Urema Trough simulate, on the meso and micro scale, that exhibited by the rotatory regional migrations of the Serengeti.

Whilst the fluctuating trophic succession in the Urema Trough is generally similar to that on two other large floodplain ecosystems in southern Africa, the Kafue Flats (Sheppe & Osborne 1971) and the Okovango Delta (Tinley 1966), these two areas have different sequential patterns of utilization imposed by their large dimensions and yearly fluctuations. In the Okovango especially, the lag in floodwater spread causes an anomalous flooding regime which forces most wildlife off the floodplain in the mid to late winter dry season. Thus, in this case the ebb regrowth flush occurs in the two remaining months of the torrid period (Sept., Oct.) before the first rains dispersal to the backcountry, and the lowest slack areas of aquatic grasses are only exposed (if at all) in the autumn and early winter before the arrival of the midwinter floods. The Okovango Delta substrates have been formed in a similar manner to the fan sequences in the Rift Valley and Cheringoma Coast, whereas the deposits of the Kafue Flats appear to have been mostly laid by river meander sequences and over-levee deposits. These latter are thus soils comprised mostly of fines so that soft mud is a major feature excluding floodplain use for prolonged periods (Sheppe & Osborne 1971).

A major feature emphasized by the year-long study of a sector of the Urema floodplains, though perhaps unremarkable when pointed out, is the total reliance of the floodplain system on direct rain occurrence in low to median flood years. In these low water years, the hygrophilous grasslands are virtually reduced to the same status as savanna, causing far reaching repercussions and implications as the dry season food base and buffer action of this system is then lost. These features will be dealt with under management (Chapter 10). As low water years have been more frequent (7 out of 10 year's records) and high floodwaters are increasingly rapidly drained off, major areas of floodplain grassland must now be considered functionally as part of the savanna system. The widespread invasion of these grasslands by the scrub (sapling) phase of woody plant succession emphasises their changed status. The speed of invasion is damped by the perched position of the old floodplain substrates above incised drainage. The change to savanna status means the grassland exists as a unimodal pattern of productivity related to the incidence of rain, intensity and duration of dry periods and fire as opposed to a year-round gradient of productivity and availability typified by the floodplain system.

Another intrinsic feature of the Urema Trough is the prevalence of preferred food grasses as dominants over large areas (low diversity/maximal food base) which, under the constraints of soil moisture balance, can support massive biomass concentrations. The preferred grasses form a mosaic with grasslands dominated by species that are avoided by ungulates unless physically altered through trampling or fire. Contrasting with this feature is the medium to tall grass stratum of the adjacent miombo savannas which have a much higher diversity of grass species per unit area (up to 10X) than equal areas on the alluvia of the Rift floor. This implies a selection for low biomass and specialist grazing even before their poor attributes as pasture are considered. Their substrates are acid sand or skeletal soils of low nutritional status, except where latosols occur on basic intrusions, and vegetative regrowth must be forced by cutting, firing, or grazing. The herbivore populations which do use these grasslands are never in sufficient quantity to hold back the rank stage from being attained.

The relationships noted between ungulates and substrates on the Rift floor support Bell's (1971:92) and Jarman's (1972:298) generalization that catenal sequences underlie differential distribution of ungulates, grassland and grazing patterns over much of Africa. If the whole spectrum of wildlife is taken into consideration, however, it can be shown that various other climoedaphic gradients, or ecoclines, and spatial relations underlie the distribution, movements and patterns of utilization. Jarman's (1972) rains dispersal dry season riverine concentration is not the whole story.

Bell (1971:92) and Jarman (1972:298) list factors which may make riverine floodplain areas unfavourable habitats in the wet season, and higher catena levels more attractive, to attempt to explain why wild ungulates do disperse to the back country at this time when abundant herbage is available on the riverine areas. For the lowest part of the topocatena the factors included are: excessively muddy conditions, rank grass of poor nutritional status, easy concealment of predators and re-infestation by parasites. In comparison the higher catena levels are said to have shorter grasses, many of which are annuals considered to be of higher food value and which could more easily be kept at optimal vegetative growth by grazing pressure.

The factors listed by the above authors for the catenal migrations will probably be different in every situation and with different combinations of species and circumstances. For example, many of the mopane savanna clays are boggier in the rains than the floodplain soils, and the occurrence of annual grasses are common only where mopane savanna is adjacent to riverine floodplains. Elsewhere, dense medium to tall coarse perennial grasslands predominate on sandier soils and in miombo savannas, which have a greater diversity but dry out relatively quickly. The higher catenal levels in southern Africa whilst generally supporting shorter swards than the bottomlands are of medium to tall height, and are not depleted by grazing unless artificial water points are established.

The Gorongosa data and that from the Save (Tello & Van Gelden 1975) and Zambeze (Tinley & Sousa Dias 1973) Rivers in Mocambique suggest that perhaps two other reasons are fundamental triggers to rain season dispersion to the higher catena levels or back country.

(1) The physical removal of animals from dangerous situations, ie. from being swept away by river floodwaters. This would apply in the rushing, overwhelming flood regimes of the river floodplain systems eg. Zambeze, Luangua, Save, Limpopo, Mkuze, Umfolozi, but not in slack or basin floodplain systems exemplified by Ngorongoro Crater, Rukwa, Okovango Delta, Banhine (in Gaza region of Mocambique) and the Urema, where flooding is a gentle spreading.

(2) The partial dispersal of some plains species in Gorongosa to the higher macro-topocatenas of the upland miombo savannas on either side of the Rift floor is directly related to regrowth flush of the otherwise rank sour miombo grasses. This movement occurs prior to the rains as well as during the first rains, when the major attraction of the back country is grass flush due either to fire and/or the first rains. After this initial stage of growth, the dispersed herds cannot easily maintain the swards in a utilizable state except in local patches if surface water is available. If surface water is in unlimited supply (eg. windpumps), the herds can maintain themselves on dry or sour pastures. The perennial grasslands of the higher catena levels can never be depleted unless artificial water is provided, thus the trigger enforcing return to lower levels appears to be moisture based and to the rank status of pastures).

The work of Henrici (1928) shows that a bimodality in nutritional peaks occurs in most grasses during the growing season, one in the spring before or at the time of the first rains and the other in the autum (Mar–Apr). The midsummer low is related to relocation of nutrients from the leaves to take part in maximal growth of the stems (culms). If adequate nutrient levels in riverine pastures are depleted by excessive cropping this also would reinforce dispersal at the time of the first rains.

Another fundamental feature prompting animals to invade new areas and habitats is their innate exploratory drive. Shifts in this innate life force, enabling exploitation of available opportunities, can only be realised when the moisture constraint is broken by the incidence of rain. In moving into the backcountry the savanna-riverine relationship is, in fact, maintained by the use of rain filled pans as island riverine zones. In this way a kaleidoscopic interplay of changing populations, species associations and habitat facets are intermeshed in different combinations through the annual cycle.

In sum the differential wetting and drying (moisture status of forage and surface water) sequences underlie migrations and movements. The use and alteration of rank or dry grasslands for grazing sequences or semi-sedentary populations in non-riverine sites depends on the persistence of surface water. The riverine growth, once it has become rank, is utilizable because the confined water resource enforces concentration of ungulates large enough that they materially alter its structure, and thus maintain optimal vegetative growth on substrates that are still moist at the height of the dry season. However, even this life saving feature (and buffer to destruction of other habitats by mixed feeders) of the lowest part of a catena is lost if it is too quickly drained. The slacks or marshes are then reduced to the same status as the surrounding fast drying savannas. The incidence of rain releases the exploratory drive of animals permitting wide ranging movements to occur which may result in new centres of pupulation establishment as shown in cases where artificial water has been provided far from the riverine zones. An example of this is of wildebeest becoming established in the Kalahari National Park (Eloff 1966: 34–36). The whole significance of dispersal is aptly described by (Eloff (*op. cit.*).

Gwynne & Bell's (1968:393) contention that the grazing succession is a facultative relationship between species, rather than a competitive one fits the summer and autumn seasons in Gorongosa, but not the mid and late dry season period when there must be competition for suitable grazing.

Thus soil moisture balance, which is a function of cover and surface, porosity, drainage status of pans and lower catenal zones, and climatic fluctuations is the intrinsic factor permeating social dynamics, migration, grassland and grazing patterns, and fluctuations in density and occurrence of ungulates. As shown in the Chapter 6

(Process and Response) the moisture factor underlies all geoecological dynamics and should thus be the prime feature of any management programme.

9.5 FOOD, FEEDING, CONDITION

FOOD

The feeding sequences, described in the previous section, are corroborated by the seasonal food records for different species listed in Appendix 2, and the grass species which recur most in the diets of 13 ungulates (Table 9.3). The striking feature demonstrated by both the herbaceous and woody food records of wild ungulates, baboon and frugivores is the overlap of preferred plant foods in all trophic groups. Although these components are abundant, in different sites and different seasons they have different phenophase availabilities. Year-round utilization may be obtained from them, however, by several strategies of ecological separation or facilitation: (a) by feeding sequences (temporal and structural succession), (b) and/or a spatial separation (use of different layers or mosaic facets), (c) aggregations of different species associations at feeding stations that have an abundant product (cornucopian resources) eg. fruit trees, or merely through the differential mobility of different species and groups which permits opportunistic use of resource complexes as they are encountered.

Examples of feeding utlization by wild ungulates of the main ecosystems is summarised in diagrammatic form (Figs 9.16 to 9.20), showing level of utilization against frequency of occurrence of food species. Together these data illustrate availability and food preferences in each major system, and their various strata, indicating the kind of selection pressure various plant components are subjected to by the wild ungulate consumer level. Whereas only fresh feeding utilization was recorded for the herbaceous layers, a recency of use category for the woody strata differentiates between old use (c.> 6 months) and new (c.< 6 months). This separation indicates changes in utilization intensity related to seasonal fluctuations in ungulate density or to upward or downward trends in browsing populations.

TABLE 9.3

Grass species that recur most in wet and dry season food records of 13 wild ungulate species. Including: buffalo, eland, elephant, hippo impala, Lichtenstein's hartebeest, oribi, reedbuck, sable, warthog waterbuck, wildebeest and zebra.

GRASS	*DRY SEASON No. ungulate spp.*	*WET SEASON No. ungulate spp.*	*HABITAT*
*Urochloa mosambicensis	11	13	savanna
Vossia cuspidata	11	9	marsh
Panicum coloratum	11	9	floodplain/savanna
Echinochloa stagnina	10	9	marsh
Cynodon dactylon	8	10	floodplain/savanna
Digitaria swazilandensis	5	10	floodplain/savanna
Panicum maximum	9	6	savanna
Eriochloa stapfiana	6	7	floodplain
Setaria eylesii	10	3	floodplain
Digitaria milanjiana	5	8	savanna
Chloris gayana	6	7	floodplain/savanna
Paspalidium obtusifolium	6	7	marsh
Eriochloa fatmensis (annual)	6	6	floodplain/savanna
Heteropogon contortus	7	4	savanna
Sporobolus pyramidalis	5	5	floodplain/savanna

15 spp.

* including ***U. pullulans***

All possible selection combinations are discernable in the examples provided. Certain trees such as ***Berchemia discolor, Boscia salicifolia, Cleistochlamys kirkii, Sclerocarya caffra*** and ***Strychnos madagascariensis*** are important fruit producers but are relatively little browsed. However, under certain circumstances, for example where ***Cleistochlamys*** occurs on termitaria, the adult trees are heavily browsed by elephant. Heavy utilization of patches of miombo by elephant, interspersed with large areas of the same habitat which is hardly touched, is characteristic. These heavily used patches are returned to, often at long enough intervals to allow the torn edges of bark to heal over completely. Such selection indicates that possibly "sweet" trees relatively low in tannin (or other phenolics) content are sought after, and once used, the feeding scars remain as indicators to future elephant.

The four basic combinations of abundant/rare – preferred/avoided are thus overlain by other considerations. Many components are eaten during seasonal extremes apparently only because of their availability. An analysis comparing dispersal efficiency against level of utilization may not expose, for example, why two animal dispersed, but little browsed trees such as ***Boscia salicifolia*** and ***Euclea schimperi***, should show such different dispersal results. The former remains relatively uncommon whilst the latter can assume weed proportions.

The phenomenon, referred to earlier, of nearly pure species abundance (low diversity) of preferred high biomass supporting food plants over large areas on heavy, usually base saturated soils, is well exemplified by mopane and acacia and by the grasses ***Echinochloa stagnina, Vossia cuspidata, Cynodon dactylon, Urochloa mosambicensis*** and ***Panicum*** species on the Rift valley floor.

As their food lists show, bushbuck and impala are avid weed feeders mainly in midsummer and autumn in the Rift Valley. Impala however also utilize the grass stratum heavily at this time. Both these species eat the same fruits as other species such as elephant, bushpig and baboon and are consequently often associated with them at feeding stations (see Section 9.8).

Two important features emerge from the intensity of utilization of woody strata by elephant, and of floodplain grasslands by other ungulates. All elephant feeding samples, even those where there was excessive damage, had been more heavily utilized in the past despite the elephant increase recorded in air counts from 1 555 in 1968, to 2 542 in 1972 (Table 9.2). This could imply that prior to 1968 much higher densities of elephant occurred in the park area. If this was the case then judging by the present level of woody plant utilization, past local densities must have been between 2 and 3 elephant/km^2 or about double the present total. Several interacting features could have been responsible for changes in density, (1) influence of consecutive drought years, (2) decimation of population by ivory hunters, and (3) changes in density patterns locally or involving the whole region. In 1894 the hunter-naturalist Vaughan-Kirby (1899) recorded large elephant numbers on the Cheringoma Plateau where the best elephant hunting was to be had. But in more recent times, until about 1971, this mosaic of forest, miombo and dambos has been totally empty of elephant due to heavy hunting pressure. In fact only rare sigmoid-shaped trees, which could indicate long past elephant use, can be found. Past use of the tree layers contrasts with that of the shrub strata below 3 m which are almost without exception more heavily utilized at the time of study than previously, indicating a trend of overall increase in the low to median level browsing population (ie. impala and the tragelaphines bushbuck, kudu and nyala) as well as preferred use of this strata by elephant.

Measurement of the grazing pressure on floodplain grasslands of the Urema Plains indicates that more than 70% of the area is over-utilized primarily by the overpopulation of hippo in the lake. The selection for ***Cynodon dactylon*** grass by hippo is exemplified by the data in Table 9.4. The interaction of canalization by hippo and other factors on floodplain dynamics have been dealt with previously in Section 9.4. However, there are several aspects here which may trap the unwary observer. Floodplain grasslands are renewed twice in the annual cycle to a greater or lesser extent. First by direct rainfall, and then by a flood and ebb sequence. Thus heavy utilization is interspersed with two main regrowth periods at each end of the summer season, and two rests from grazing pressure; in midsummer if inundations are maximal, and in the dry season when pastures are brown and withered. The system is thus perennially rejuvenative with an expanding and contracting green zone under heavy utilization. Simultaneously however, the floodplains are becoming increasingly over-drained hence the overall perennial hygrophilous system is shrinking, and being replaced by the seasonal savanna system. The over-used zone is thus moving inwards over time.

TABLE 9.4

Hippo grazing on the Urema floodplains. Examples from a solitary male followed on two consecutive overcast days in adjacent parts of the plains. Only fresh bites recorded.

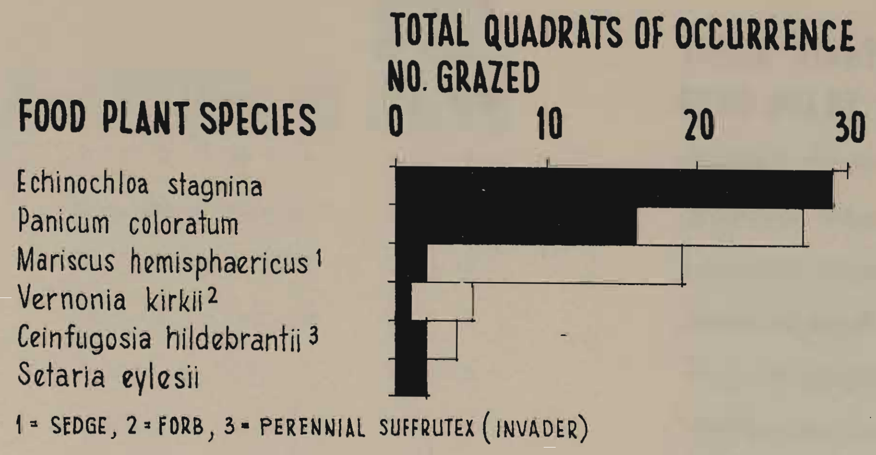
SAMPLE 1: 15 July 1970 (14h00 to 17h00)

	No. times grazed	% of total
Cynodon dactylon	344	84,4
Glinus lotoides f	56	13,0
Heliotropium indicum f	3	0,7
Vossia cuspidata	2	0,5
Alternanthera sessilis f	1	0,2
Heliotropium ovalifolium f	1	0,2
	407	100,0

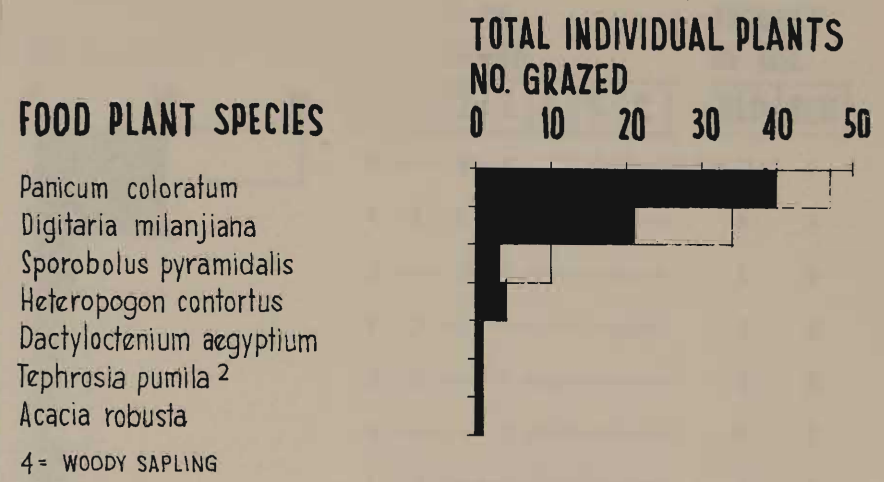
SAMPLE 2: 16 July 1970 (13h00 to 17h50)

	No. times grazed	% of total
Cynodon dactylon	333	87,3
Digitaria swazilandensis	27	7,1
Glinus lotoides f	13	4,0
Eriochloa fatmensis	3	0,8
Heliotropium ovalifolium f	2	0,5
Heliotropium indicum f	1	0,3
	379	100,0

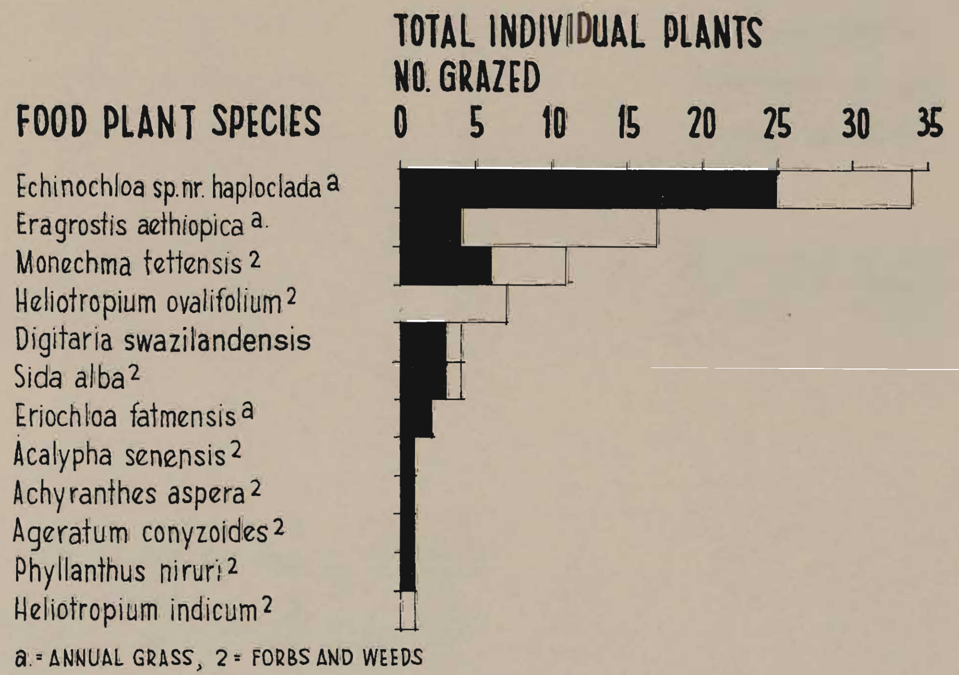
f = forbs and weeds



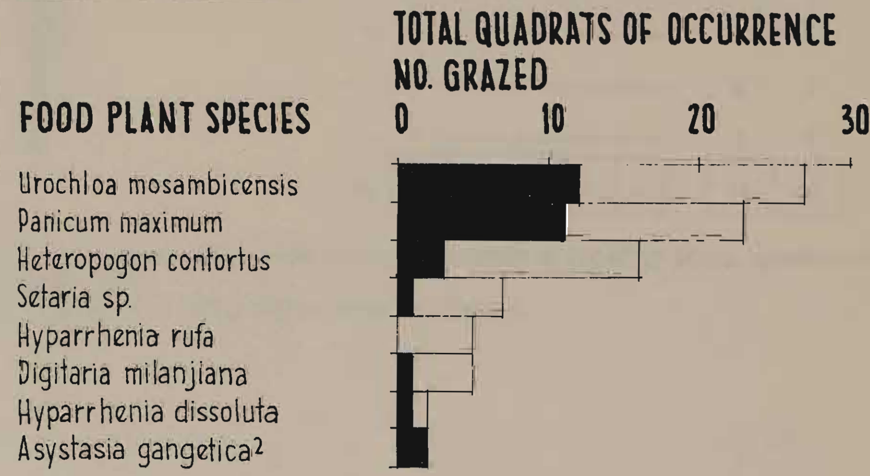
A. OCCURRENCE AND FEEDING UTILIZATION OF HYGROPHILOUS GRASSLAND PLANTS BY A BUFFALO HERD (APRIL 1973) PERCHED SLACK OF SUNGUE PLAINS WEST OF UREMA



B. OCCURRENCE AND FEEDING UTILIZATION OF SAVANNA GRASSLAND PLANTS BY A BUFFALO HERD (FEBRUARY 1971). LINE INTERCEPT METHOD (5 X 5M.).

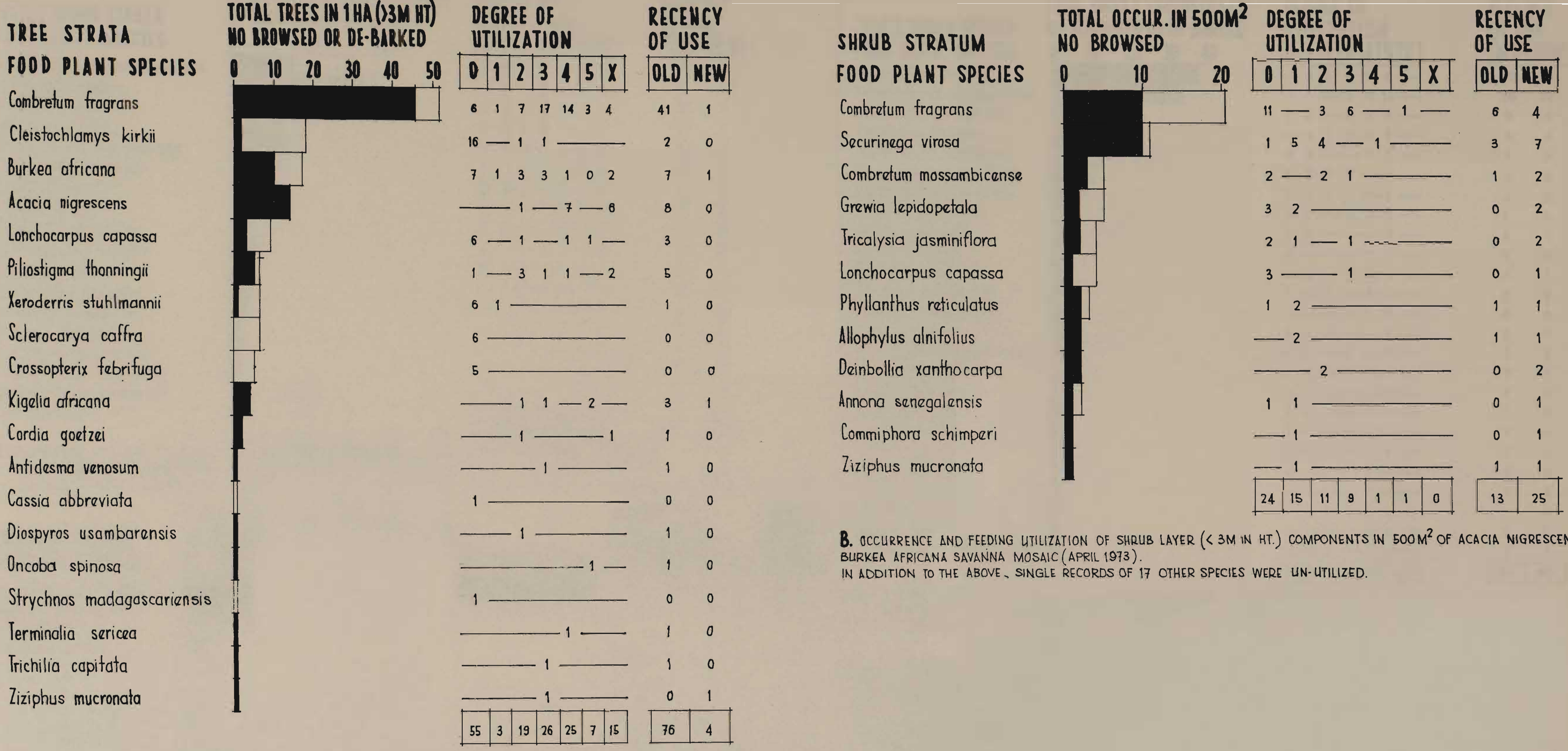


D. OCCURRENCE AND FEEDING UTILIZATION OF GRASSLAND PLANTS ON FEVERTREE - FLOODPLAIN ECOTONE BY IMPALA (FEBRUARY 1971). LINE INTERCEPT METHOD (12 X 5M.)



C. OCCURRENCE AND FEEDING UTILIZATION OF GRASS STRATUM IN ACACIA NIGRESCENS (CLAYS) - BURKEA AFRICANA (SANDS) SAVANNA MOSAIC ON RIFT FLOOR (APRIL 1973)

FIG 9.16 EXAMPLES OF GRASSLAND FEEDING UTILIZATION BY WILD UNGULATES



TREE STRATA FOOD PLANT SPECIES	DEGREE OF UTILIZATION 0	1	2	3	4	5	X	RECENCY OF USE OLD	NEW
Combretum fragrans	6	1	7	17	14	3	4	41	1
Cleistochlamys kirkii	16	—	1	1	—	—	—	2	0
Burkea africana	7	1	3	3	1	0	2	7	1
Acacia nigrescens	—	—	1	—	7	—	6	8	0
Lonchocarpus capassa	6	—	1	—	1	1	—	3	0
Piliostigma thonningii	1	—	3	1	1	—	2	5	0
Xeroderris stuhlmannii	6	1	—	—	—	—	—	1	0
Sclerocarya caffra	6	—	—	—	—	—	—	0	0
Crossopterix febrifuga	5	—	—	—	—	—	—	0	0
Kigelia africana	—	—	1	1	—	2	—	3	1
Cordia goetzei	—	—	1	—	—	—	1	1	0
Antidesma venosum	—	—	—	1	—	—	—	1	0
Cassia abbreviata	1	—	—	—	—	—	—	0	0
Diospyros usambarensis	—	—	1	—	—	—	—	1	0
Oncoba spinosa	—	—	—	—	—	1	—	1	0
Strychnos madagascariensis	1	—	—	—	—	—	—	0	0
Terminalia sericea	—	—	—	—	1	—	—	1	0
Trichilia capitata	—	—	—	1	—	—	—	1	0
Ziziphus mucronata	—	—	—	1	—	—	—	0	1
	55	3	19	26	25	7	15	76	4

A. OCCURRENCE AND FEEDING UTILIZATION OF SAVANNA TREES (> 3M IN HT) IN 1 HA OF ACACIA NIGRESCENS – BURKEA AFRICANA MOSAIC (APRIL 1973).

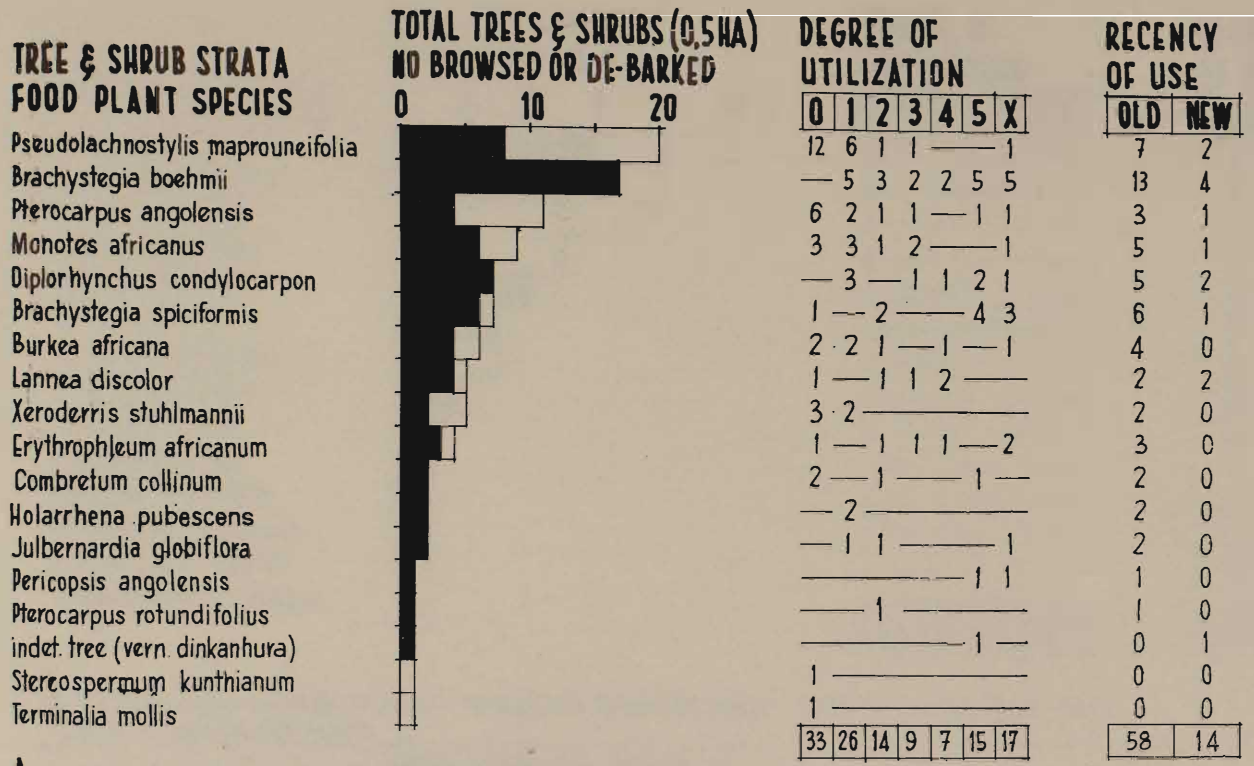
0 = UNUSED, 1 = LIGHT USE, 2 = MEDIUM USE, 3 = HEAVY USE, 4 = SEVERE USE, 5 = TOTAL USE (COMPLETELY RING-BARKED, FELLED OR DE-CANOPIED), X = DEAD.

SHRUB STRATUM FOOD PLANT SPECIES	DEGREE OF UTILIZATION 0	1	2	3	4	5	X	RECENCY OF USE OLD	NEW
Combretum fragrans	11	—	3	6	—	1	—	6	4
Securinega virosa	1	5	4	—	1	—	—	3	7
Combretum mossambicense	2	—	2	1	—	—	—	1	2
Grewia lepidopetala	3	2	—	—	—	—	—	0	2
Tricalysia jasminiflora	2	1	—	1	—	—	—	0	2
Lonchocarpus capassa	3	—	—	1	—	—	—	0	1
Phyllanthus reticulatus	1	2	—	—	—	—	—	1	1
Allophylus alnifolius	—	2	—	—	—	—	—	1	1
Deinbollia xanthocarpa	—	—	2	—	—	—	—	0	2
Annona senegalensis	1	1	—	—	—	—	—	0	1
Commiphora schimperi	—	1	—	—	—	—	—	0	1
Ziziphus mucronata	—	1	—	—	—	—	—	1	1
	24	15	11	9	1	1	0	13	25

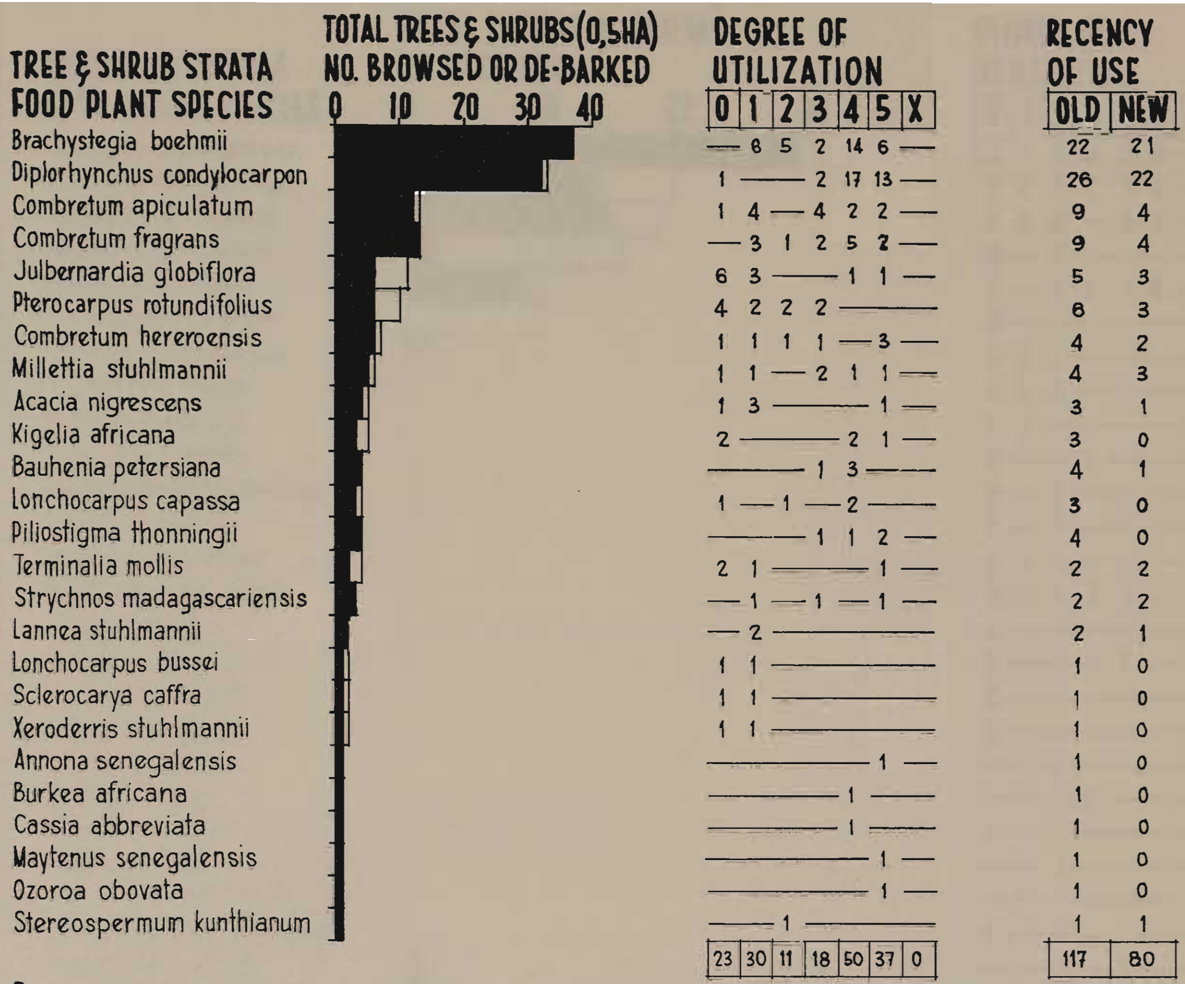
B. OCCURRENCE AND FEEDING UTILIZATION OF SHRUB LAYER (< 3M IN HT.) COMPONENTS IN 500 M² OF ACACIA NIGRESCENS – BURKEA AFRICANA SAVANNA MOSAIC (APRIL 1973).
IN ADDITION TO THE ABOVE, SINGLE RECORDS OF 17 OTHER SPECIES WERE UN-UTILIZED.

FIG 9.17

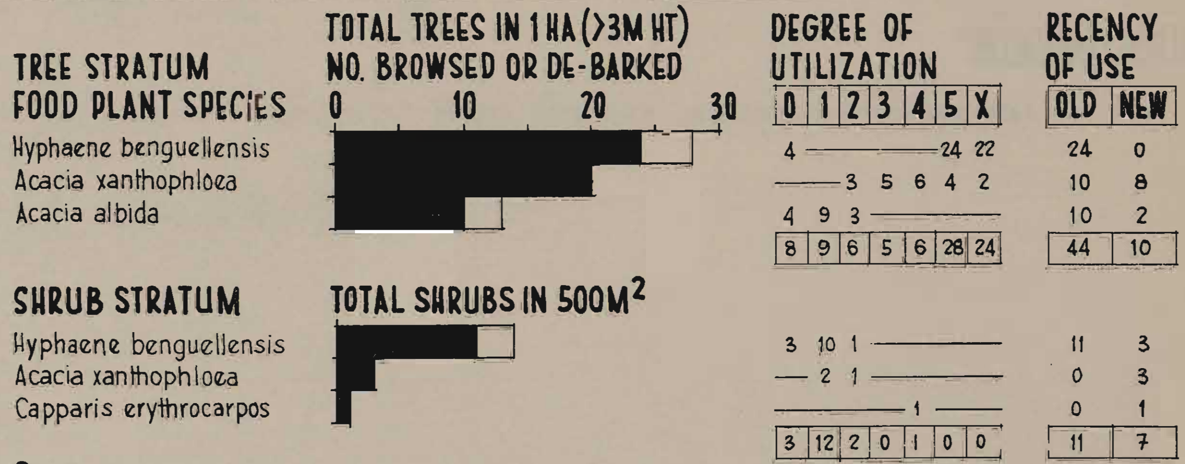
FEEDING UTILIZATION OF WOODY STRATA
IN ACACIA-BURKEA TREE SAVANNA
ON THE RIFT VALLEY FLOOR



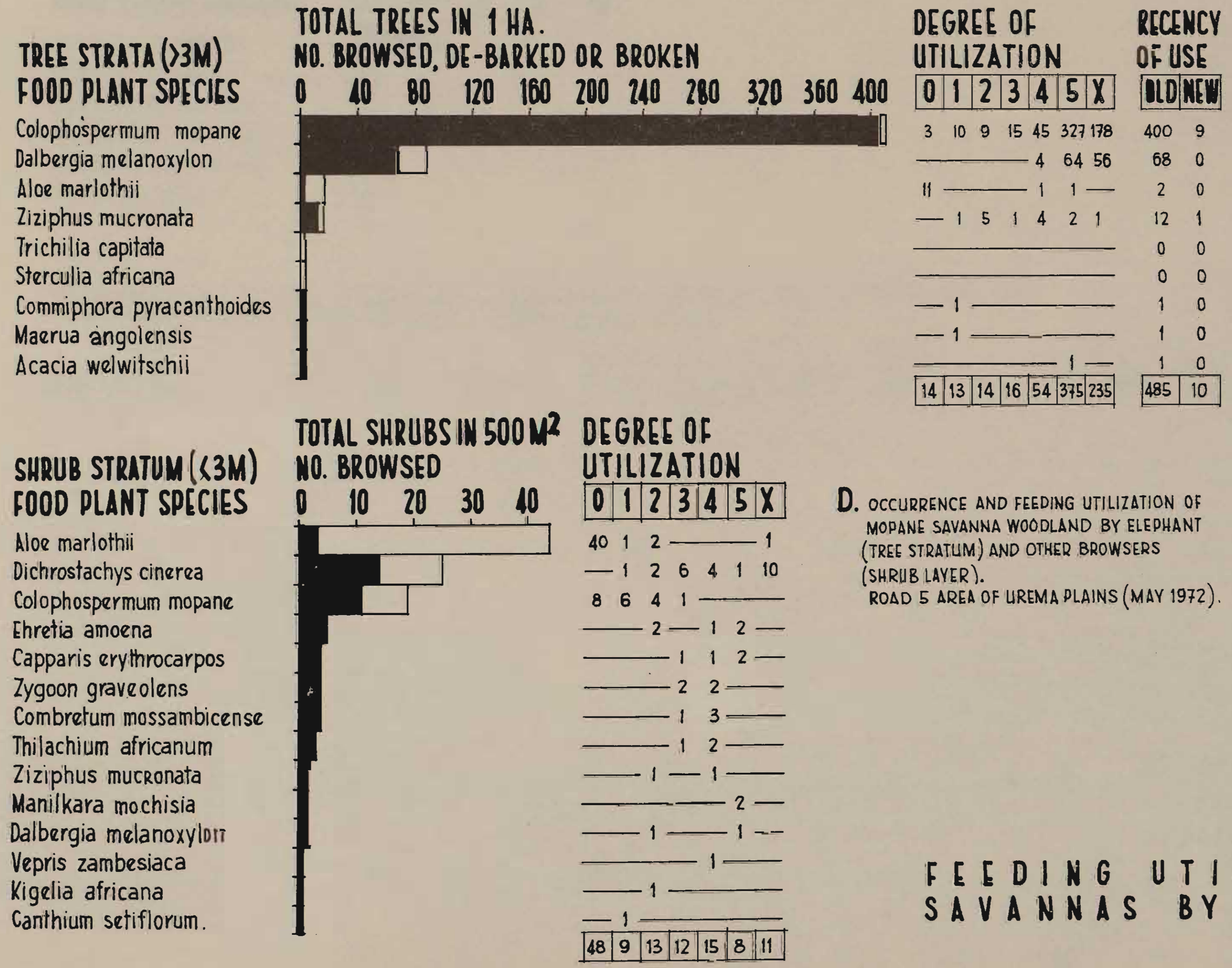
A. OCCURRENCE AND FEEDING UTILIZATION OF MIOMBO SAVANNA TREES AND SHRUBS IN 0,5 HA. BY ELEPHANT (JULY 1972) IN MIDLANDS NEAR NHAMUSENGERE FALLS, REREMBE AREA.



B. OCCURRENCE AND FEEDING UTILIZATION OF MIOMBO SAVANNA TREES AND SHRUBS IN 0,5 HA BY ELEPHANT (JULY 1972) EXAMPLE OF HEAVY UTILIZATION IN MIDLANDS SECTOR BETWEEN ENTRANCE GATE AND BUE MARIA.



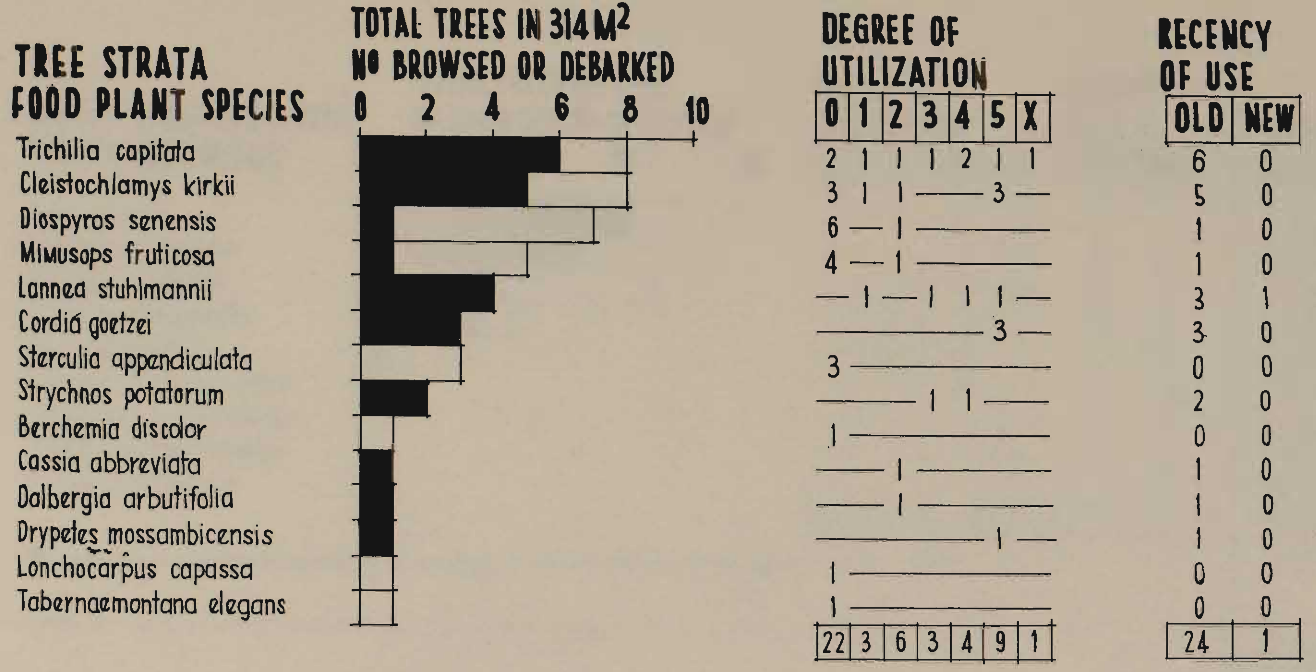
C. OCCURRENCE AND FEEDING UTILIZATION OF MARGINAL FLOODPLAIN SAVANNA WOODLAND IN 1 HA BY ELEPHANT (APRIL 1972). MIXED FEVER TREE, WINTERTHORN, PALM COMMUNITY ON A MOSAIC OF HYDROMORPHIC SALINE CLAYS, CLAY LOAM AND SAND SOILS.



D. OCCURRENCE AND FEEDING UTILIZATION OF MOPANE SAVANNA WOODLAND BY ELEPHANT (TREE STRATUM) AND OTHER BROWSERS (SHRUB LAYER).
ROAD 5 AREA OF UREMA PLAINS (MAY 1972).

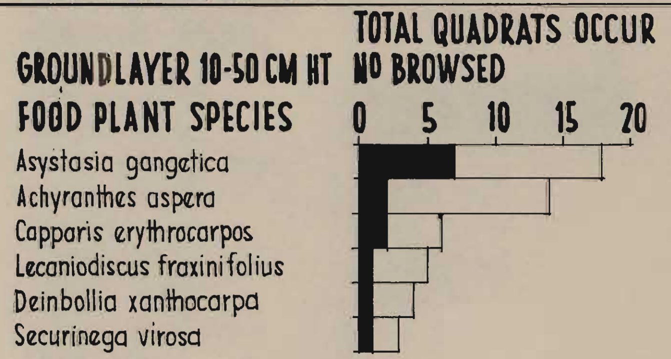
FIG 9.18

FEEDING UTILIZATION OF WOODY STRATA IN VARIOUS SAVANNAS BY ELEPHANT IN THE GORONGOSA ECOSYSTEM



TREE STRATA FOOD PLANT SPECIES	0	1	2	3	4	5	X	OLD	NEW
Trichilia capitata	2	1	1	1	2	1	1	6	0
Cleistochlamys kirkii	3	1	1	—	—	3	—	5	0
Diospyros senensis	6	—	1	—	—	—	—	1	0
Mimusops fruticosa	4	—	1	—	—	—	—	1	0
Lannea stuhlmannii	—	1	—	1	1	1	—	3	1
Cordia goetzei	—	—	—	—	—	3	—	3	0
Sterculia appendiculata	3	—	—	—	—	—	—	0	0
Strychnos potatorum	—	—	—	1	1	—	—	2	0
Berchemia discolor	1	—	—	—	—	—	—	0	0
Cassia abbreviata	—	—	1	—	—	—	—	1	0
Dalbergia arbutifolia	—	—	1	—	—	—	—	1	0
Drypetes mossambicensis	—	—	—	—	—	1	—	1	0
Lonchocarpus capassa	1	—	—	—	—	—	—	0	0
Tabernaemontana elegans	1	—	—	—	—	—	—	0	0
	22	3	6	3	4	9	1	24	1

A. OCCURRENCE AND UTILIZATION OF TREES (> 3M IN HT) IN A TERMITARIA THICKET CLUMP OF 314 M^2 (APRIL 1973).
ROAD 2 AREA ON RIFT FLOOR.

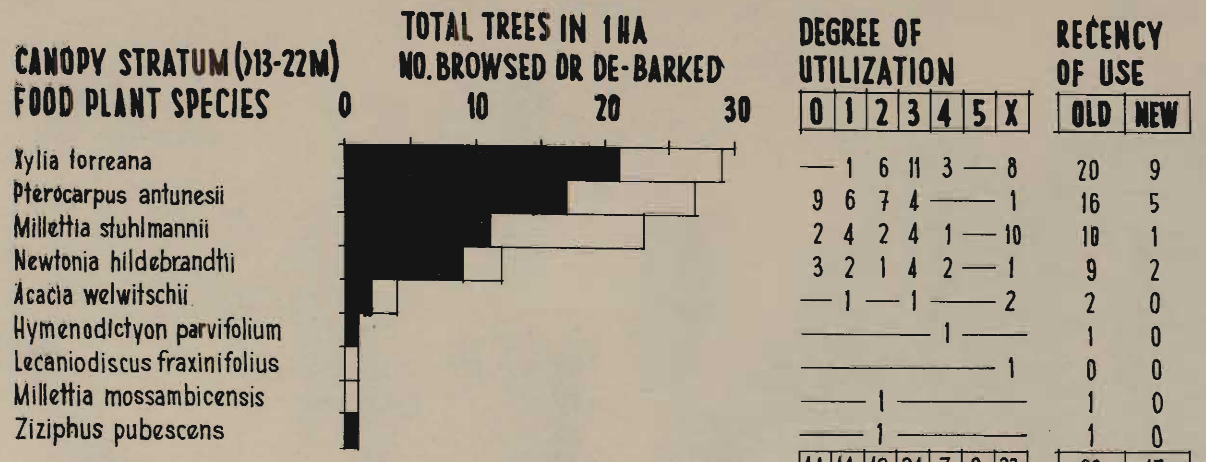


C. OCCURRENCE AND FEEDING UTILIZATION OF GROUNDLAYER FORBS AND SHRUBS IN A TERMITARIA THICKET (APRIL 1973)
IN ADDITION TO THE ABOVE 29 OTHER SPECIES RECORDED WERE UN-UTILIZED.

SHRUB STRATUM FOOD PLANT SPECIES	0	1	2	3	4	5	X
Capparis erythrocarpos	14	1	3	3	16	6	—
Diospyros mespiliformis	6	4	1	2	3	4	—
Deinbollia xanthocarpa	4	6	4	—	3	2	—
Tricalysia jasminiflora	14	—	2	—	—	—	—
Allophylus alnifolius	1	—	4	2	3	0	—
Cleistochlamys kirkii	10	—	—	—	—	—	—
Cassine schlechterana	5	2	1	—	—	—	—
Securinega virosa	2	1	3	—	1	—	—
Pavetta catophylla	5	2	—	—	—	—	—
Diospyros senensis	6	—	—	1	—	—	—
Lecaniodiscus fraxinifolius	6	—	1	—	—	—	—
Trichilia capitata	6	—	1	—	—	—	—
Dalbergia arbutifolia	4	1	1	—	—	—	—
Phyllanthus reticulatus	2	—	1	1	1	—	—
Cordia goetzei	4	—	—	—	—	—	—
Lonchocarpus capassa	2	—	—	—	1	—	—
Berchemia discolor	2	—	—	—	—	—	—
Boscia salicifolia	1	—	—	—	—	—	—
Dalbergia boehmii	—	—	1	—	—	—	—
Ehretia amoena	—	—	—	1	—	—	—
Grewia sulcata	1	—	—	—	—	—	—
Premna senensis	—	—	1	—	—	—	—
Sterculia appendiculata	—	1	—	—	—	—	—
Strychnos spinosa (warty fruit)	1	—	—	—	—	—	—
Tamarindus indica	—	—	—	—	1	—	—
Thilachium africanum	—	—	1	—	—	—	—
Trichilia emetica	1	—	—	—	—	—	—
Xylotheca tettensis	—	—	—	—	1	—	—
	87	18	25	10	30	12	0

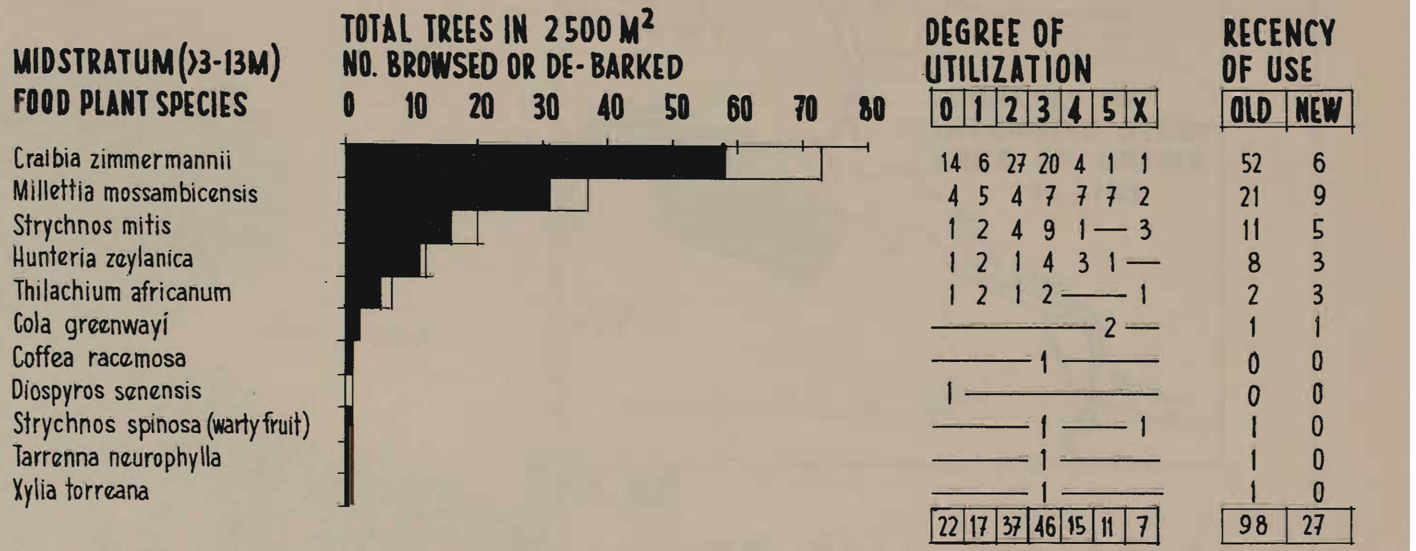
B. OCCURRENCE AND FEEDING UTILIZATION OF SHRUB LAYER IN 100 M^2 OF TERMITARIA THICKET (APRIL 1973).

FIG 9.19 FEEDING UTILIZATION OF A TERMITARIA THICKET



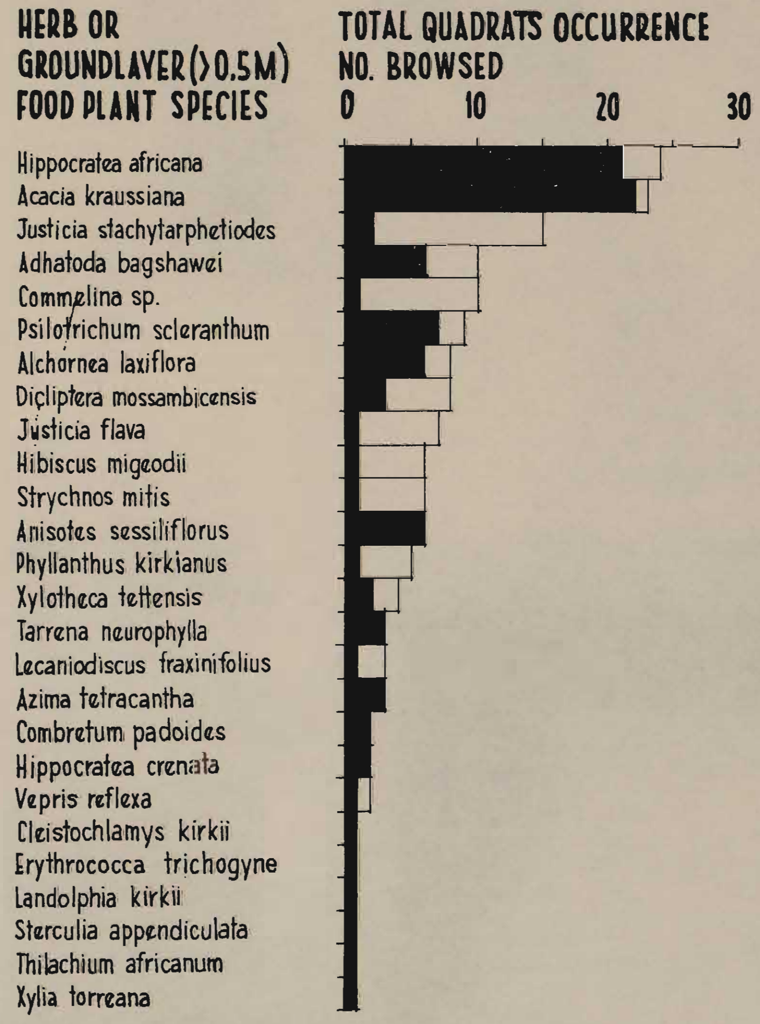
CANOPY STRATUM (>13-22M) FOOD PLANT SPECIES	DEGREE OF UTILIZATION							RECENCY OF USE	
	0	1	2	3	4	5	X	OLD	NEW
Xylia torreana	—	1	6	11	3	—	8	20	9
Pterocarpus antunesii	9	6	7	4	—	—	1	16	5
Millettia stuhlmannii	2	4	2	4	1	—	10	10	1
Newtonia hildebrandtii	3	2	1	4	2	—	1	9	2
Acacia welwitschii	—	1	—	1	—	—	2	2	0
Hymenodictyon parvifolium	—	—	—	—	1	—	—	1	0
Lecaniodiscus fraxinifolius	—	—	—	—	—	—	1	0	0
Millettia mossambicensis	—	—	1	—	—	—	—	1	0
Ziziphus pubescens	—	—	1	—	—	—	—	1	0
	14	14	18	24	7	0	23	60	17

A. OCCURRENCE AND FEEDING UTILIZATION OF DRY FOREST CANOPY TREES IN 1 HA BY ELEPHANT.



MIDSTRATUM (>3-13M) FOOD PLANT SPECIES	DEGREE OF UTILIZATION							RECENCY OF USE	
	0	1	2	3	4	5	X	OLD	NEW
Craibia zimmermannii	14	6	27	20	4	1	1	52	6
Millettia mossambicensis	4	5	4	7	7	7	2	21	9
Strychnos mitis	1	2	4	9	1	—	3	11	5
Hunteria zeylanica	1	2	1	4	3	1	—	8	3
Thilachium africanum	1	2	1	2	—	—	1	2	3
Cola greenwayi	—	—	—	—	—	2	—	1	1
Coffea racemosa	—	—	—	1	—	—	—	0	0
Diospyros senensis	1	—	—	—	—	—	—	0	0
Strychnos spinosa (warty fruit)	—	—	—	1	—	—	1	1	0
Tarrenna neurophylla	—	—	—	1	—	—	—	1	0
Xylia torreana	—	—	—	1	—	—	—	1	0
	22	17	37	46	15	11	7	98	27

B. OCCURRENCE AND FEEDING UTILIZATION OF DRY FOREST MIDSTRATUM TREES BY ELEPHANT



D. OCCURRENCE AND FEEDING UTILIZATION OF DRY FOREST GROUNDLAYER BY BROWSING UNGULATES (55 X 1M² QUADRATS)

SHRUB OR FIELDLAYER (0,5-3M) FOOD PLANT SPECIES	DEGREE OF UTILIZATION						
	0	1	2	3	4	5	X
Alchornea laxiflora	3	13	12	24	12	1	—
Craibia zimmermannii	33	16	5	5	5	—	1
Phyllanthus kirkianus	34	11	4	3	1	—	—
Millettia mossambicensis	6	4	6	5	1	—	—
Thilachium africanum	5	5	4	5	2	—	—
Pavetta catophylla	2	2	5	7	5	—	—
Xeromphis obovata	—	5	3	4	5	1	—
Acacia kraussiana	2	3	5	4	2	—	—
Xylotheca tettensis	—	1	1	4	6	—	—
Adhatoda bagshawei	3	—	5	—	1	—	—
Capparis erythrocarpos	—	—	2	1	4	—	—
Tricalysia junodii	3	1	—	—	—	—	—
Xylia torreana	1	—	—	1	1	3	—
Hunteria zeylanica	—	1	1	2	1	—	—
Strychnos mitis	1	—	—	3	1	—	—
Pavetta revoluta	—	—	—	2	2	—	—
Erythrococca trichogyne	—	—	1	3	—	—	—
Tapura fischeri	—	—	—	3	—	—	—
Vepris reflexa	—	1	1	—	1	—	—
Cola greenwayi	—	—	—	—	1	1	—
Cissus sp.	1	—	—	—	—	—	—
Cleistochlamys kirkii	—	—	—	1	—	—	—
Deinbollia xanthocarpa	—	—	—	1	—	—	—
Lecaniodiscus fraxinifolius	—	—	—	—	1	—	—
Pterocarpus antunesii	—	—	—	—	—	1	—
Strophanthus kombe	—	—	—	—	1	—	—
Vangueria esculenta	—	—	1	—	—	—	—
Ziziphus pubescens	—	—	—	—	1	—	—
Drypetes mossambicensis	—	1	—	—	—	—	—
	94	64	56	78	54	7	1

C. OCCURRENCE AND FEEDING UTILIZATION OF DRY FOREST FIELDLAYER BY BROWSING UNGULATES.

FIG 9.20 FEEDING UTILIZATION OF DRY FOREST ON RIFT VALLEY FLOOR (MAY 1972) SANGARASSA FOREST ROAD 3 AREA

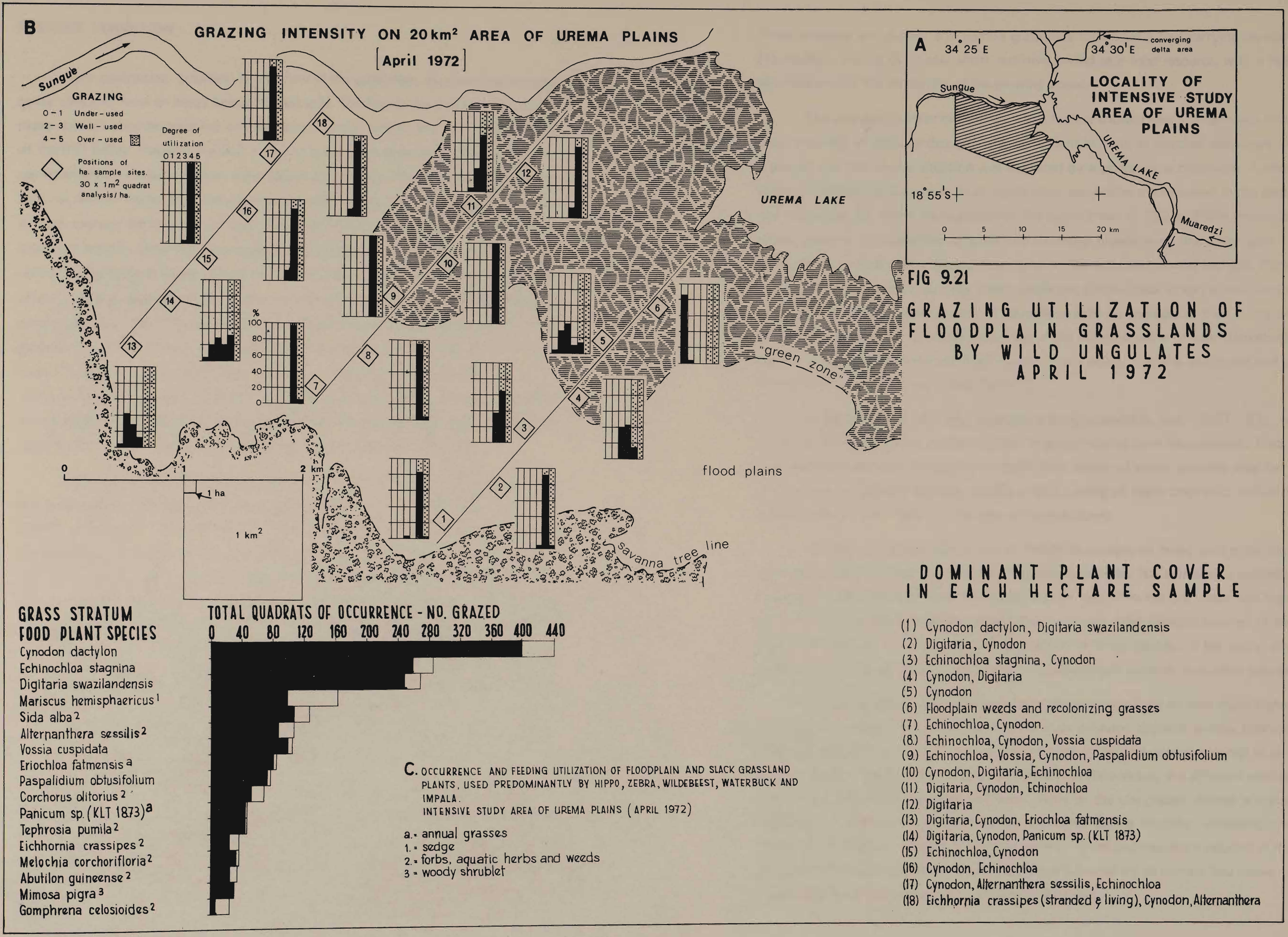


FIG 9.21

GRAZING UTILIZATION OF FLOODPLAIN GRASSLANDS BY WILD UNGULATES APRIL 1972

C. OCCURRENCE AND FEEDING UTILIZATION OF FLOODPLAIN AND SLACK GRASSLAND PLANTS, USED PREDOMINANTLY BY HIPPO, ZEBRA, WILDEBEEST, WATERBUCK AND IMPALA.
INTENSIVE STUDY AREA OF UREMA PLAINS (APRIL 1972)

a.- annual grasses
1.- sedge
2.- forbs, aquatic herbs and weeds
3.- woody shrublet

DOMINANT PLANT COVER IN EACH HECTARE SAMPLE

(1) Cynodon dactylon, Digitaria swazilandensis
(2) Digitaria, Cynodon
(3) Echinochloa stagnina, Cynodon
(4) Cynodon, Digitaria
(5) Cynodon
(6) Floodplain weeds and recolonizing grasses
(7) Echinochloa, Cynodon.
(8) Echinochloa, Cynodon, Vossia cuspidata
(9) Echinochloa, Vossia, Cynodon, Paspalidium obtusifolium
(10) Cynodon, Digitaria, Echinochloa
(11) Digitaria, Cynodon, Echinochloa
(12) Digitaria
(13) Digitaria, Cynodon, Eriochloa fatmensis
(14) Digitaria, Cynodon, Panicum sp. (KLT 1873)
(15) Echinochloa, Cynodon
(16) Cynodon, Echinochloa
(17) Cynodon, Alternanthera sessilis, Echinochloa
(18) Eichhornia crassipes (stranded & living), Cynodon, Alternanthera

PASTURE CONDITION

Two contrasting grassland types occur in the ecosystem, those on leached acid sandy soils and those on heavy base saturated soils. The former are characteristic of the higher rainfall miombo savannas and dambos on either side of the Rift, and the latter of the Rift Valley. However the Rift Valley soils were laid down by alluvial fan sequences separated by slacks or shallow water lacustrine deposits. Thus, despite a lower, more seasonal, rainfall regime than the adjacent miombo, the alluviocatenas support a mosaic of both sourveld herbage, of tall rank grasses, alternating with sweet, medium to short grasslands (chiefly ***Urochloa, Heteropogon*** and ***Cynodon***). Due to excessive hydromorphism in large areas of fertile bottomland soils in the Rift Valley, rapid growth responses are exhibited resulting in coarse rank growth similar to the miombo grasses and apparently of very low food value as they are shunned by all grazers. As a corresponding decrease in protein content of grass leaves occurs with advancing maturity, a rapidly maturing pasture is of little nutrional value for grazing ungulates soon after commencement of the growing season (Henrici 1928a, 1928b; Plowes 1957). Yet, when the same grass species are kept short by grazing or cutting, the imposed high vegetative production results in a correspondingly higher protein content (Plowes 1957: 45).

Comparative analysis of lower rainfall sweet grasslands on black clays at Matopos in Rhodesia, with sour miombo grasslands near Salisbury showed markedly contrasting differences in crude protein content. Whilst the sweet pastures contained a crude protein content of 20% in December, the sourveld values were 5,5% attaining a maximum of only 7,4% in the first week in January (Plowes 1957). A 6% crude protein intake was determined as the maintenance level for cattle in Rhodesia, however mass loss was incurred as soon as crude protein levels dropped below 12% (Plowes 1957).

In the Matopos area a drop from 20% to about 5% occurred over 6 weeks in response to drought (Plowes 1957). The detailed studies of Henrici (1928a, 1928b) in the Northern Cape – Botswana border area showed that phosphorus and starch content diminish simultaneously in grasses as soon as wilting or incipient drying occurs. Maxima of assimilation products occurred in early spring and during rains.

In southern (Myre 1971) and central (Myre & Antao 1972) Mocambique, analyses of pastures showed quite different responses of the same species in different climo-edaphic situations. ***Themeda triandra*** on heavy latosols in an arid savanna climate was biologically active from September until April, and only until February on the coast in higher rainfall on leached sands (Myre 1971). Acid miombo grasses such as ***Andropogon gayanus*** and ***A. schirensis*** were found to be of feeding value for only four to six weeks in the spring and thereafter are useless as pasture (Myre & Antao 1972). These miombo and duplex soil dambo grasslands thus have a low carrying capacity (15 ha/SU), and an extremely short nutritive period as a food resource, with a high fibre content for the remainder of the growing season.

The analyses of Henrici (1928a: 1054) further showed that a phosphorus minimum occurred in times of drought with coincident minima of starches and sugars. As a general rule the reverse situation was indicated by a phosphorus maximum. A phosphorus minimum also occurs in midsummer when assimilates are relocated to the stems and rootcrown for major development of the culms (Henrici 1928b: 1055). Hence bimodal maxima in assimilates is exhibited by many grasses with the major peak in spring (Sept – Oct) and a second lesser peak in the autumn (Henrici loc. sit). Other grasses follow a unimodal strategy with a single phosphorus peak in spring only, whilst yet others maintain a low content of assimilates with no decrease as their culms are developing year around. Monthly variations in the nutritive value of sour Bankenveld grasses in the Transvaal showed three crude protein peaks; over the equinoxes and at the summer solstice (Joubert 1954: Table 7).

In his treatment of the Serengeti grazing ecosystem Bell (1971: 91) remarks on the reduction of protein content in grasses during culm development. Thus a phenologically induced bimodality in nutritional status of many pastures may be a prime factor underlying bimodal mating and/or calving of many ungulates, including cattle (Bonsma 1939, 1940), at the time of the equinoxes.

The nutritive phenology of vlei or floodplain grasses on heavy soils is the crux to an appreciation of their high biomass supporting qualities. No local data is available, however Plowes (1957) showed that crude protein content in the dry season was highest in grasses on the bottomland black clays, and rain after drought resulted in the highest temporary rise of crude protein content in these grasses. In his study area ***Cynodon*** (kweek) was at all times higher in crude protein content than other species.

The vlei grasses in the arid savannas of the northern Cape contain much higher phosphorus in both their leaves and roots than adjacent dryland species (Henrici 1928b: 1104). The nutriment maxima and minima of the vlei grasses were not as uniform as those in the savanna, as different phases are followed by the different species. The main minima were however in March. Many of the vlei grasses showed a higher phosphorus content in the stalks than in the leaves during flooding, indicating that translocation was still in progress (Henrici ***op. cit***). A second maximum resulted in the stalks when remigration of phosphorus occurred followed by extremely low values in the culms and a higher phosphorus content in the roots.

PLATE V UREMA PLAINS IN THE RAINS SEASON

Unflooded aspect of the short *Cynodon-Digitaria* grasslands with a microcosm of the massed concentrations of ungulates.

PLATE VI UREMA PLAINS IN THE DRY SEASON – THE 'EMPTY QUARTER'.

The same area as Plate V four to five months later with golden-brown pastures typical of dried out saline grasslands.

PLATE VII SEASONAL RAIN-FILLED SAVANNA PAN AT THE HEIGHT OF THE WET SEASON (March)

PLATE VIII CONTRASTING DRY SEASON ASPECT OF THE SAME PAN SHOWN IN PLATE VII FOUR TO FIVE MONTHS LATER.

Supporting the evidence presented by Plowes (1957), the vlei grasses in the northern Cape were characterised by high phosphorus content indicating high nutrient levels (Henrici *op. cit.*). Thus similar peaks and lows occur in the nutrient content of floodplain grasses but with a greater variation amongst the different species in response to environmental changes. As with the savannas grasses, wetting and drying affects their growth and nutritive status, but the better moisture and base status of vlei soils result in rapid maturation and concomitant decrease in protein. Grazing sequences causing repeated growth flushes would maintain a high protein level.

The differential effects of dry and wet years on the nutritional status of floodplain grasslands does not seem to be recorded. It is not known for example whether high flood years in the Urema Trough would result in a predominance of pasture of low nutritional status due to the denitrifying effects of anaerobic reducing conditions of protracted inundation. It is considered that loss of nitrate in the gaseous form is enhanced by anaerobic conditions (Brady 1974: 431) which would in turn effect protein levels in the grasses. Heady (1975: 195) points out that under moist conditions in the early part of the growing season...."the water content of young forage may be so high that an animal cannot consume enough dry matter to be properly nourished". Possibly therefore, in dry years when floodplain grasslands are reliant on direct rainfall, predominantly sweet conditions result.

The detrimental effects on pasture quality of the high salt content, characteristic of floodplain and slack vertisols in the Urema Trough, is the other unknown factor. Brady (1974: 399) notes three adverse features of sodic soils on the plant cover, the most important of which in the present context is the effect of...."active sodium ions on plant metabolism and nutrition". Thus the two seasonal extremes of flooding and aridity possibly results in pasture of low nutritional value in the Urema Trough.

Judging solely from recorded observations, loss in animal condition on the Rift floor was directly related to the too rapid drying out of pastures (salinization? : see Section 9.5), which implies that any adverse effects from excessive flooding are offset by heavy grazing pressure and maintenance of high nutritional levels of the preferred floodplain pastures.

The feeding behaviour of species such as baboon, elephant, warthog,and oribi on the floodplains appear to be outward manifestations of the rise and fall in nutrient status of different parts of hygrophilous grasses such as ***Echinochloa stagnina*** and ***Vossia cuspidata.*** During the first rains leaves are grazed. In the period January to March, related either to maximal culm development or to midsummer drought, oribi feed almost exclusively on the culms of these grasses,returning to feed on the leaves in April if rains recur. In autumn and the early dry season the basal parts of these grasses are preferred by baboon, elephant,and warthog, and baboon and warthog eat the ripe seeds by stripping the inflorescences through their mouths.

In the Save Valley in central Mocambique,seasonally flooded alluvial grasslands, similar to those of the Urema are estimated to have a carrying capacity of 3 – 4 ha/SU (Myre & Antao 1972). In addition to the high protein content reported for ***Cynodon dactylon*** (eg. Plowes 1957; Dougall & Glover 1964) which together with ***Digitaria swazilandensis*** is the major short grass pasture in Gorongosa, Myre and Antao (1972) record highest percentages of protein, calcium and phosphorus in the savanna grass ***Urochloa mosambicensis,*** followed by ***Panicum maximum*** and ***Heteropogon contortus.*** In Table 9.3 ***Urochloa*** leads in the dietary preferences of 13 wild ungulates in Gorongosa, and ***Urochloa*** savanna grasslands occur on soils of high phosphorus content. Grassland dominated by ***Urochloa*** is classed at 6–8 ha/SU pasture (Myre & Antao 1972).

Relatively little is reported in the literature regarding the nutritive status of browse foods through the annual cycle. Analyses of Karoo bushes in South Africa indicated a tendency for bimodal equinoctial peaks in protein content (Du Toit ***et al.*** 1940) which may be related to the bimodal rainfall regime experienced in the Bushmanland region.

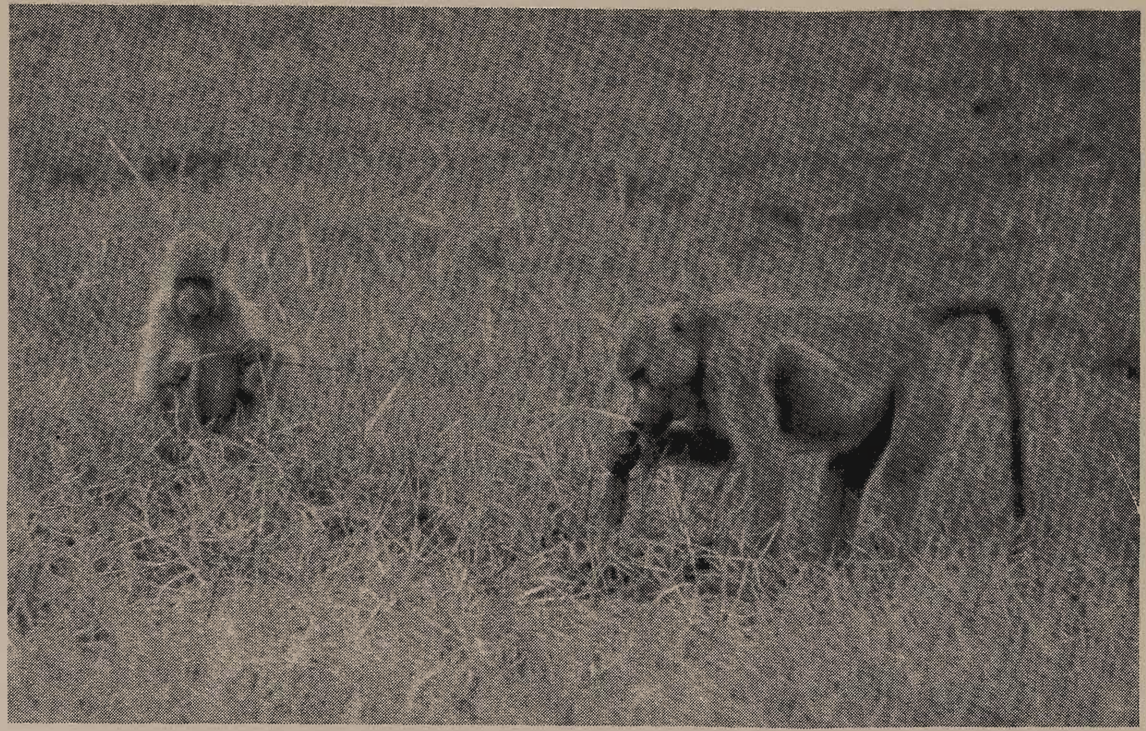
Five preferred browse foods in the Transvaal bushveld, analysed on a monthly basis, showed crude protein peaks in spring or early summer and again in late summer or autumn (Tables in Bonsma 1942). Of the five, mopane showed August, November and January/February peaks; ***Combretum apiculatum*** October and January peaks; ***Boscia albitrunca*** October, December and April peaks; and two ***Grewia*** species October – November and January/February peaks. These species exhibited several phosphorus and calcium peaks through the year related to the solstices and equinoxes (Tables in Bonsma 1942).

In Mocambique two browse foods, mopane and ***Combretum apiculatum*** were analysed during different phenophases (Myre & Antao 1972). Both trees showed highest crude protein content in the spring (vegetative phase), and then again in the fruiting phase. Calcium content in both species was lowest in spring and highest in the fruiting phase, while phosphorus content remained the same through the growing season.

The tendency of two nutritive peaks in spring and autumn interspersed with two lows, appears to be related to the spring flush of new growth followed by a second high with the reproductive phases and the major low during the dormant period. The incidence of rain, droughts, soil moisture balance, and thermal changes must all affect fluctuations in the nutrition levels indicated by the woody species noted above.

PLATE 23 ECOTONES, SLACKS & MIGRATION

(A) Ecotones, a preferred feeding station of Lichtenstein's hartebeest. In the above example, grazing the sweet grasses on the termite hill pediment.



(B) Baboon *Papio ursinus* in shallow waters of slack in autumn feeding exclusively on basal parts of the aquatic grass *Vossia cuspidata*.

(C) Part of a series of long lines of wildebeest and zebra migrating from the northern *tandos* (Nhamisangu, Macoreia) to the southern 'green zone' margins of the Urema Lake.

(D) Wildebeest and zebra grazing the last 'green zone' pastures of slack floors in the dry season when the surrounding savanna grasslands are dry and/or burnt out.

The widespread occurrence of double flowering and fruiting in some trees at the time of the equinoxes, give support to the possibility of bimodal nutritive peaks in many other woody plants. Bimodality in mating and/or calving in mixed feeders and browsing wild ungulates is reported by several authors eg. Bigalke (1970) for springbok, Simpson (1973) for Zambeze bushbuck, and Anderson (1975) for impala. Whether fluctuations in nutritive levels of browse foods show parallel patterns to the grasses related to both phenophase activity and seasonal changes in the African savannas still apparently awaits analysis.

PHYSICAL CONDITION OF THE WILD UNGULATES

During the 1971/1972 intensive study of a sector of the Urema Plains a monthly record was kept of physical condition of the wild ungulates (Fig 9.22). Animal condition was determined by the visual assessment method of Riney (1960). Individuals and the proportions of herds were assigned to one of three condition classes: (a) ***good*** – characterised by rounded contours of the posterior, (b) ***poor*** – characterised by extreme angularity of the posterior due to protruding skeletal processes, including the rib cage, (c) ***fair*** – intermediate between (a) and (b).

With the exception of zebra, those ungulate species most frequently encountered were recorded. Zebra proved to be difficult probably due to the disruptive effect of their stripe patterns (Child 1968a) and recording on this species was discontinued.

The condition of grasslands was visually assessed by three features: (a) wilting, (b) discolouration (browning), (c) avoidance by grazers or a change in use of aerial portions to basal parts. These features together indicated the nutritional status of perennial grasses linked to the phases of their seasonal life processes of growth, reproduction and decline (translocation to roots), and interrupted by environmental factors which reset the phenophases.

The physical condition of seven ungulate species is correlated with the environmental conditions that pertained between February 1971 and March 1972 on the Rift Valley floor (Fig 9.22). This period covered the second, and beginning of the third, in three consecutive years of low flooding and less than mean annual rainfall (averaging 150 mm below the mean). The most prominent feature recorded is the grave physical condition of the three largest high biomass herbivores. Hippo are in chronically poor condition for the greater part of the year followed by elephant and buffalo. The third biomass group containing wildebeest, hartebeest, waterbuck and impala show a normal sigmoidal curve related to the seasons, with a rise in condition in the first rains, good condition over the summer to autumn, and decline in mid-winter and torrid period.

As the major portion of the hippo population is confined to the environs of the Urema Lake, which shrinks to an area of about 15 km^2, it is not surprising that they are in poor condition for the greater part of the year. This is particularly so as the hippo biomass is dependent on over-grazed lawns of ***Cynodon dactylon*** and ***Digitaria swazilandensis*** which undergo rapid episodic changes related to fluctuations in wetting and drying sequences and the aridifying affect of sodic alluvial clays. Unless a high soil moisture level is maintained these pastures also undergo daily wilting and nocturnal recovery of turgor until they are dried out completely. As the foodplains are increasingly over-drained, their primary productivity is in rapid decline, and the adjacent savanna grasslands are burnt out every year which affects elephant and buffalo particularly.

However, another aspect of the hippo situation is illustrated by an isolated herd of about 140 hippo on a cut-off meander of the Pungue River. They are within 10 km distance of two other isolated herds of some 25 animals each, but no others occur for another 30 km (Fig 9.11). Their site is in the southwest corner of the park and is surrounded by extensive swards of 3–4 m high, coarse ***Hyparrhenia, Panicum*** and ***Pennisetum*** grasslands in which islands of over-grazed and sheet eroded hippo-lawns have been formed by these short grass feeders. Vertical aerial photographs of the large herd showed that every animal in the herd was in poor condition. Thus hippo are dying amidst plenty as the tall pasture around them, unstimulated by burning or cutting is structurally unavailable, rank, and thus nutritionally poor.

Rapid maturation and decline in food value of the grasslands appear to be the main factor triggering excessive utilization of trees by elephant, rather than the occurrence of fire which only occurs two to three months later in the annual cycle (Fig 9.22). It is not understood why most of the elephant herds are in poor condition when there is super-abundant browse on the Rift floor, especially of termitaria thickets which are unaffected by fire. The small male groups and lone tuskers are exceptions, all being in fair to good health throughout the year. By choice, the elephant in Gorongosa are reliant in the dry season on the remaining slack hygrophilous pastures, as shown by their distribution in the air counts and ground records of feeding. These sites are being increasingly over-drained and provide in the dry months only a narrow margin of green contested for by buffalo and most other ungulates especially zebra, wildebeest, and waterbuck.

In sum the availability and suitability of grasslands and woody strata as food through the annual cycle is governed by the interplay of the following features:

(1) rain occurrence and amount, and extent of rainless periods between each fall;

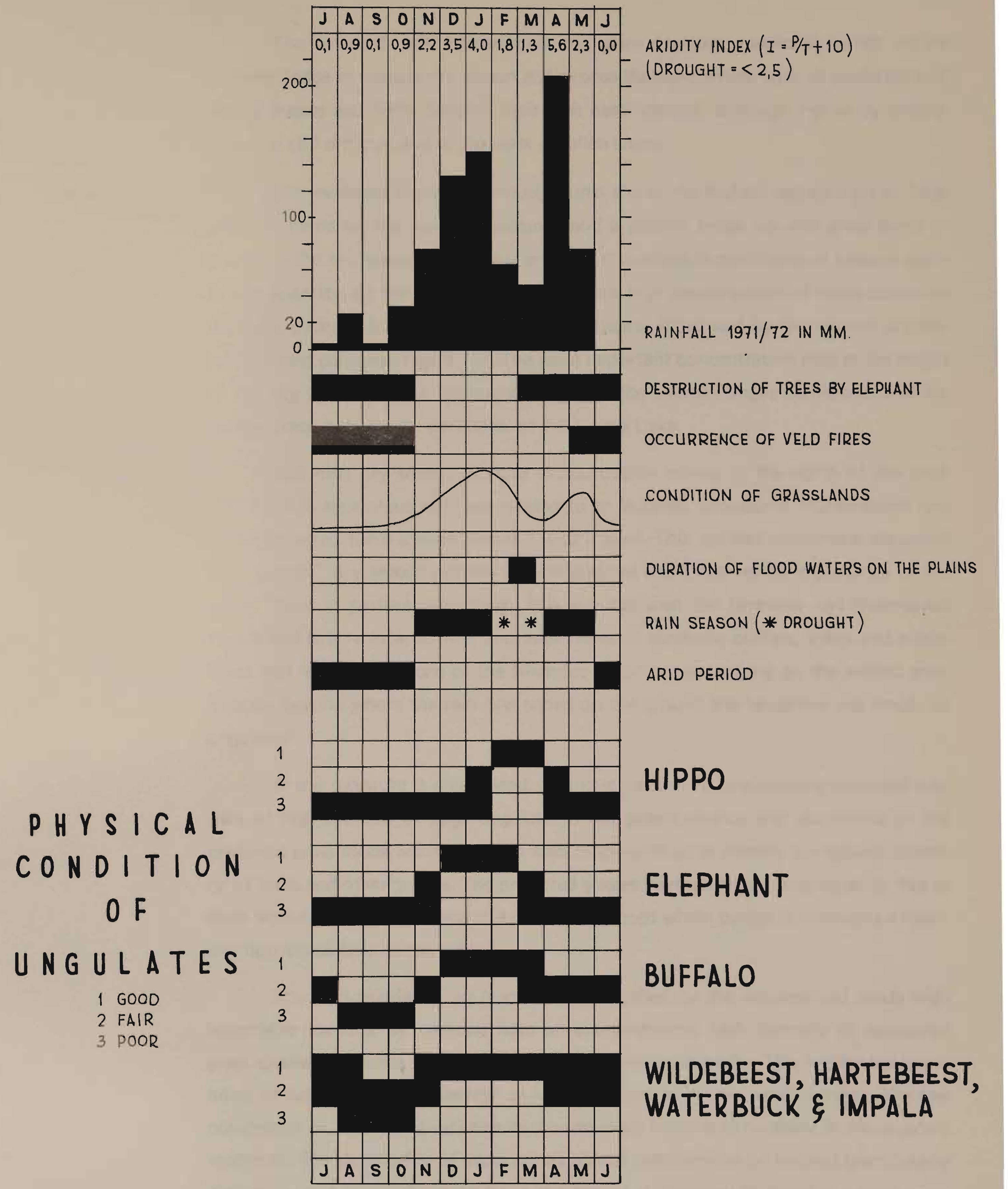


FIG 9.22

DIAGRAMMATIC SUMMARY OF THE RELATIONSHIP BETWEEN PHYSICAL CONDITION OF WILD UNGULATES AND ENVIRONMENTAL FACTORS COVERING THE PERIOD 1971/72

(2) heavy rains and flooding on base saturated soils in a hot climate, resulting in rapid maturation of grasses with concomittant drop in protein content and excess of rank fibrous foliage;

(3) the rank grasslands are only utilized if they are physically altered (ie. re-structured, with forced vegetative regrowth of high nutritional value) by trampling, grazing (or cutting) or fire;

(4) the preferred sweet grasslands, which cover smaller areas than the sour grasslands, become over-utilized during the summer and autumn grazing sequence and at the height of the dry season when they are fulfilling a life supporting role;

(5) the inadequate narrow dimension of the green zone in the dry season; most of the hygrophilous grasslands are now functionally equivalent to the seasonal savannas due to excessively fast run-off of rain and river floodwaters from floodplains and slacks, causing a too rapid drying out and thus loss of primary production;

(6) influence of the distance of surface water from pastures on whether they can be utilized sufficiently by coarse grass feeders to maintain their productivity;

(7) matching or dissimilar phenophases in the various ecosystems, in the different strata in each system, and of similar species in different situations (ie. the influence of mass and staggered food availability).

Animals, therefore, have a wide choice of foods through the annual cycle resulting from a multiplicity of dissimilar climo-edaphic influences, gradients, and responses of superimposed phenophases. However, choice for the grazing ungulates, in particular, is suddenly reduced by drought and/or the incidence of fire.

The over-riding factor aggravating the rapid decline of the preferred pasture resource is the increasingly rapid drainage of the floodplains and slacks, which enables the base saturated soils to exert a maximal aridifying and saline influence which must adversely effect the nutritional status of the pastures. The dense swards of grass extending to beyond the horizon in the miombo and in the Rift Valley gives an illusion of a super-abundant food resource, the falseness of this is however indicated by the chronically poor condition of the three largest ungulates. But this illusion could be made a reality by damping runoff and physically altering the rank grasslands (see Section 10.3). Low numbers of elephant and buffalo in the herbivore spectrum would result in even larger areas of useless coarse pasture than occurs at present. But it is these rank grasslands which are particularly used by specialist tall grass grazers such as sable and Lichtenstein's hartebeest, which select the nodal shoots and leaf fascides for example.

The areas of rank ***Hyparrhenia*** and giant ***Panicum maximum,*** which escape burning, lodge in the late dry season and expose the subordinate layer of preferred soft leaved grasses and forbs (and/or their own basal shoots), although ingress by smaller grazers is still difficult due to the mass of fallen stems.

The evidence from two annual counts shows the highest aggregations of large ungulate herds on the summar pastures, and a general break up into small herds or groups in the dry season empathetic with the disruption in continuity of pasture quality and quantity. At the same time a second local high concentration of herds occurs on the slack pastures as they become available, clearly illustrated by the wet and dry season biomass patterns (Figs 9.13). The most important concentration sites at the height of the dry season are the Dingedinge slacks at the Urema-Pungue confluence and the narrow green zone on the perimeter of the Urema Lake.

The high dry season biomass concentration shown in the north of the park (Fig 9.13) is anomalous as it was related to an isolated, unseasonal thunderstorm rain which occurred there a week before the air count. This isolated occurrence disrupted the "typical" dry season pattern but emphasized the fundamental importance of the water factor in pasture utilization. This area between the Nhandue and Nhamapaza Rivers had largely escaped fire, and large herds of elephant, buffalo, zebra and wildebeest had left the environs of the Nhandue River to concentrate on the wetted area. Exactly beyond where the rain line ended on the ground the landscape was empty of ungulates.

If soil moisture is maintained, a unique pasture feature allowing extended support of high biomass of large ungulates is the predominance and abundance of the preferred grass foods, which occur in association with an extremely low species diversity of forbs and other grasses. The preferred grasses have a high carrying capacity due to their abundant vegetative reproduction when grazed which probably maintains a maximal nutritional level in the leaves.

The acid grasslands on leached soils, typified by the miombo and sandy high watertable dambos, by contrast have an extraordinarily high diversity of associated grass species and forbs and an extremely low carrying capacity. This implies the possibility of sustaining a large variety of herbivore species in very small number. The low occurrence of soft leaved varieties may however be limiting to diversity in the ungulate spectrum. The significance of depauperate animal communities on leached (particularly the white sand podzols) substrates in the tropics is discussed in detail in a notable paper by Janzen (1974).

PLATE 24 ELEPHANT FEEDING ON *CYNODON* LAWN GRASS

A large bull and teenage male ('tsotsi'), in marginal floodplain fever tree, winterthorn and palm savanna woodland.

Amongst many others, he makes an important point, in comparing equatorial and temperate forests, which is clearly applicable to the sour and sweet grassland types in Mocambique. The sea of acid grasslands, as opposed to the more circumscribed and disjunct areas of sweet grassland on fertile soils, may have a far greater primary production or standing crop than the latter, but only a fraction of it is suitable or utilizable from the herbivore's point of view.

High herbivore diversity and biomass on the more homogenous grasslands of fertile soils is enhanced by the grazing succession, which results in the multiplication of primary productivity and diversification of feeding levels where the same predominant grasses are favoured by most species.

9.6 MOVEMENT AND MIGRATION

The preceding sections show that both local movement and the seasonal emigration and return of many wild ungulates is goverened chiefly by seasonal and episodic changes in the food resources of different ecosystems. Whether the large aggregations of common ungulate species displace or affect the movements and habitat use of shy species such as sable and Lichtenstein's hartebeest is unknown. Nor is it known whether there are adverse effects of crowding at the height of the dry season which influence emigration or dispersal when the rains arrive.

Four main kinds of movement occur in Gorongosa of which the first, and to a lesser degree the second, categories can be termed migrations. The four categories are expressed by the ungulates in various combinations or singly.

(1) Longitudinal within the Rift Valley (migratory responses to phenology of alluviocatenal systems).

(2) Transverse altitudinal movement between Rift Valley and miombo uplands (migratory responses to phenology of topocatenal gradients).

(3) Local day and night alternation between open plains and savannas (related to predator avoidance, drinking, feeding and resting behaviour).

(4) Periodic and episodic movements following the change in availability of foods related to the incidence of unseasonal rain, drought and fire; also to staggered fruiting times of the same plant species in different sites (e.g. ***Sclerocarya caffra, Diospyros mespiliformis***), or gathering of animals to mass fruiting in one sector (e.g. ***Acacia albida*** pods abundantly available in the dry season chiefly along the southern margin of the Urema Plains).

The lines of the main seasonal migrations and movements are summarised in Fig 9.23. The large ungulates which obtain most of their life requirements by moving mainly along the Rift Valley floor are buffalo, wildebeest, waterbuck, zebra, impala, and hippo. The ungulates which require both the Rift floor and hill country on either side are elephant, sable, Lichtenstein's hartebeest, and eland. Of the species which move primarily along the Rift Valley plains, zebra and waterbuck (which share the same habitat, except the shallow water zone) show contrasting population density patterns. The largest number of waterbuck within the park occur during the dry season when there are the least number of zebra; in the wet season it is the opposite. In the rains small groups of waterbuck have been seen from the air, moving in lines north towards Dimba Marsh.

Of those that use the Rift floor and adjacent hill country, sable and Lichtenstein's hartebeest, which use the same habitat, show an opposing density pattern. The most sable occur on the Rift floor in the dry season, and the most hartebeest in the same area in the wet season. Small groups of zebra, wildebeest and buffalo also move up into the ***Brachystegia*** savannas periodically following the new growth after unseasonal rain or post-fire flush of grass. It is suspected that some interchange of zebra groups occurs across the Cheringoma Plateau between the Rift Valley and the southern Zambeze Delta population at Marromeu.

Movement and migration therefore, largely explores the availability of suitable food resources of uneven distribution and the seasonal changes in habitat structure and physiognomy. As the wild ungulates in Gorongosa are mostly water dependent species, in the dry season exploration is controlled mostly by the occurrence of surface water, and with the advent of the rains the widespread supply of water allows full expression of opportunistic exploration particularly in the Rift Valley where there is generally a minimum of the one rain-filled pan per hectare.

In 1969 with the experienced assistance of José Tello (chief warden at the time), experimental marking of certain ungulates for migratory studies was carried out. A number of buffalo, elephant, wildebeest, and zebra were captured by immobilization with the tranquillizing drug ***etorphine*** (M99) using the Palmer Cap-Chur gun, and marked using a variety of methods including ear-notching, collars, tags, cold branding, and paints. With the exception of the ear notches the results were disappointing and further attempts were discontinued as the use of a light aircraft proved quicker and more efficaceous for monitoring migratory movements. In addition field staff were relatively few and widely spaced thus any sitings would have been minimal in the 10 000 km^2 area.

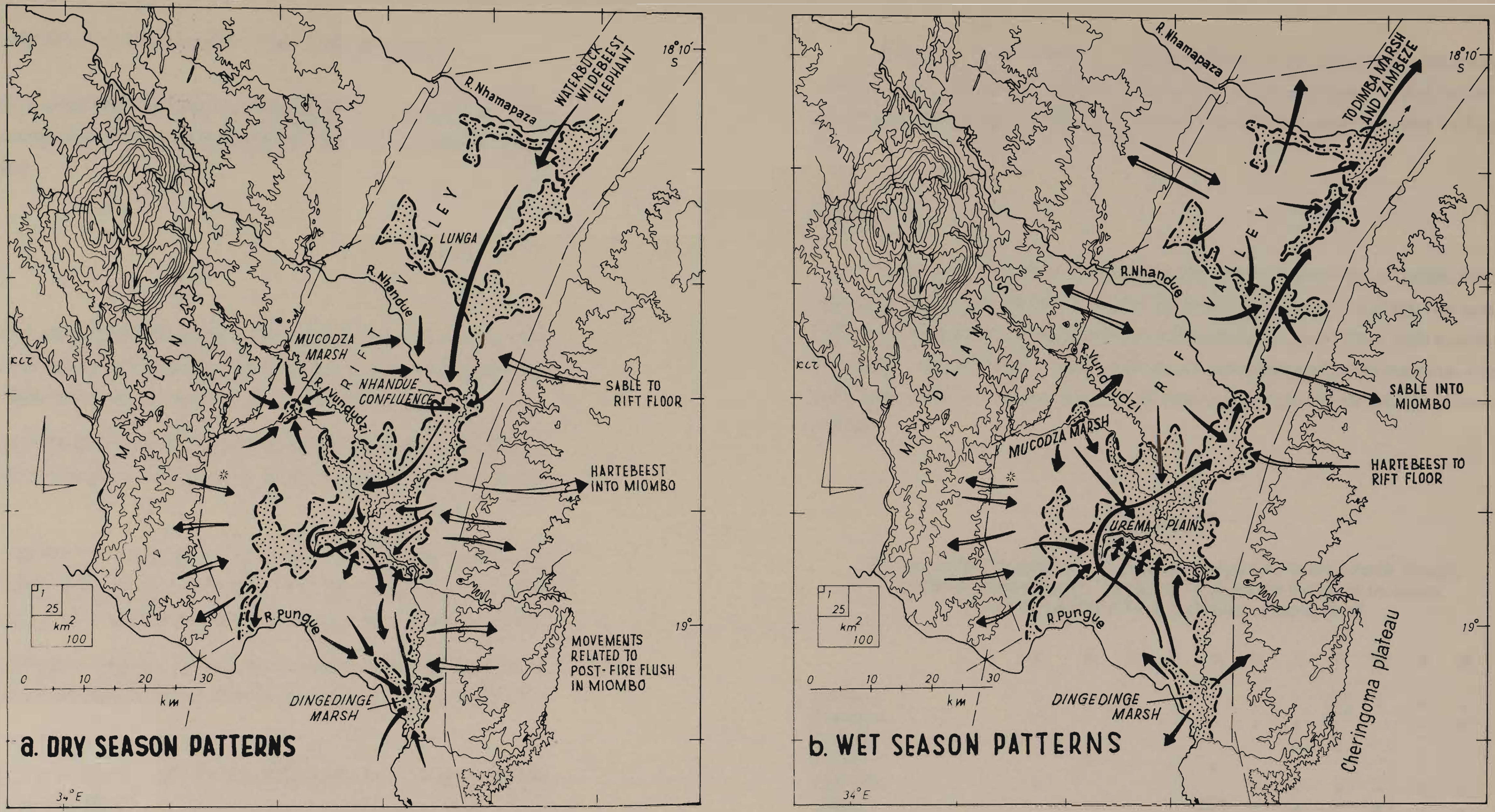


FIG 9.23 MOVEMENT AND MIGRATION OF WILD UNGULATES IN THE GORONGOSA ECOSYSTEM

ALLUVIOCATENAL
TOPOCATENAL

9.7 NATALITY, MORTALITY AND THE SEASONS

Minimal data is presented in this section as natality and predation was planned to be part of the second stage research programme for Gorongosa on population ecology and management.

NATALITY

The months in which newborn young were recorded in the park are noted in Table 9.5. Inadequate quantative data allows for only the conspicuous peaks to be marked. The ***prima facie*** data indicate four kinds of reproductive strategies.

(1) Torrid period birth peak exemplified by Lichtenstein's hartebeest. Most calves are born in pre-rain scorched period when post-fire grass flush occurs, indicating mating in the first rains.

(2) Births with the first rains, exemplified by impala and wildebeest. Mating in the wildebeest occurs mainly over the autumnal equinox and the month following. Impala were recorded mating over the same time until May and again over the spring equinox.

(3) Bimodal equinoctial peaks, e.g. impala (two breeding peaks are recorded for impala in Zululand by Anderson 1975), and other species, e.g. bushbuck (Simpson 1973).

(4) Almost year-round calving with peaks unidentified, e.g. buffalo, elephant, hippo, nyala, waterbuck and zebra.

Hippo calving peaks 6° N of Gorongosa in the Luangwa Valley occur from January to March (Marshall & Sayer 1976) and 6° S in the Kruger National Park peaks are later, in April and May (Pienaar ***et. al.*** 1966).

MORTALITY

Predation

Routine collection of skulls and lower jaws of all definitely identified lion kills was made by ranger and research staff and housed at the Chitengo field laboratory. This, of course, biased the evidence in favour of adult ungulates as predation on young leaves little to no skeletal remains. A preliminary work on the lions of Gorongosa including predation is being prepared by J.L.P.L. Tello.

The lion kills recorded from the Urema Plains sector of the park were predominantly old male buffalo, wildebeest, zebra, and waterbuck to a lesser extent. In the dry season adult hippo were killed in abundance around the Urema Lake and its Sungue arm.

Disease

Apart from high parasite infestation rates in some ungulates collected, the resident and visiting veterinarians from the Veterinary Institute in Lourenco Marques reported no evidence of diseases which can attain epizootic proportions, such as anthrax, heartwater, and rinderpest. The serious impact that strongylid gastro-intestinal infestations have on the beef economy in Mocambique is reported by Silva & Goncalves (1972).

TABLE 9.5

Months in which newborn ungulates were recorded in the Urema Trough, Gorongosa National Park. Conspicuous peaks are indicated by boxes. (Data recorded by J.L.P.L. Tello and the author)

	J	A	S	O	N	D	J	F	M	A	M	J
Buffalo	+					+	+	$\boxed{+}$	+	+	+	
Bushbuck					+	+	+			+	+	
Bushpig							+	+				
Eland		+	+	+	+							
Elephant	+					+	+	+	+	+	+	
Impala					$\boxed{+}$	+	+	+	+	+	+	
Kudu	+		+		+		+	+	+			
Lichtenstein's Hartebeest		+	$\boxed{+}$	+	+	+						
Nyala	+		+	+	+			+	+	+	+	+
Oribi					+		+	+		+		
Red Duiker					+		+					
Reedbuck	+		+	+					+			
Sabie		+	+	+	+	+	+	+	+			
Suni					+	+						
Waterbuck	+	+	+	+	+	+	+	$\boxed{+}$	+			
Warthog			+	+	+	+	+	+				
Wildebeest					+	$\boxed{+}$	+					
Zebra	+	+	+	+	+	+	+	+	+			

Plant poisoning

Accounts of losses in wild ungulates from plant poisoning is rarely reported. Many of the symptoms are easily confused with anthrax (Steyn 1934; Mönnig & Veldman 1961). Anthrax outbreaks occur during seasonal extremes, mainly in October in the Kruger National Park (Pienaar 1961),and over the equinoxes in Etosha National Park with a maximum peak in March and April (Ebedes 1974). These outbreak periods are therefore coincident with the most rapid fluctuations in climatic factors, and with growth and wilting of grasslands, plus the pre-rains spring flush of geophytes and suffrutices which are often the only green plants available at the time.

In the torrid period in Gorongosa, buffalo in extreme debilitated conditions with swaying hindquarters and blood tinged diarrhoea, were encountered where large areas had been burnt out. No reports of anthrax or other disease were made by the resident veterinarian. In October 1972 large numbers of buffalo died with the above symptoms and professional hunters in the north of the ecosystem on the Rift floor reported deaths of eland, nyala (mainly males), reedbuck, warthog, waterbuck and zebra. October 1972 was the second year of less than mean annual rainfall and the greater part of the country had been burnt out. Some of the buffalo deaths were close to watering points.

Two eland encountered by the hunters ran and fell repeatedly, lying on the ground and pawing the air (cycling movements). A similar behaviour was reported for bushpig in the south of the park at the same time. These latter symptoms are typical of plant poisoning by liliaceous genera (***Ornithogalum, Urginea, Gloriosa***) known collectively as ***slangkop*** in South Africa, or of tulp poisoning by ***Moraea (Iridaceae)*** all of which occur in the area (Steyn 1934 & ***pers. com.***). Another likely culprit which is abundant on certain floodplain sectors (e.g. Macoreia) is the horse-tail ***Equisetum ramosissimum.*** This plant remains green when all grasses are completely dried out, or it reshoots in October before the grasses. The symptoms caused by its consumption are similar to those noted above, including staggering, falling down, and shivering of the body, but the poisoning is apparently not fatal (Steyn 1934: 201).

Apart from the possible sources of poisoning mentioned above, a likely widespread source that I became aware of in Gorongosa, is the natural development of lethal amounts of prussic (hydrocyanic) acid in certain grasses under wilting conditions. There is apparently no published reference to the effect of prussic acid of wilted pastures on wild ungulates hence this subject is explored briefly here.

In South Africa, where it is known as ***'geilsiekte'***, "prussic acid poisoning is one of the most fatal and common forms of plant poisoning that occurs in animals, especially sheep, goats and cattle. It is responsible for annual losses of thousands of animals . . . . aggravated by . . . . rapid climatic changes as rain followed by drought, heat, frost. . . ." (Mönnig & Veldman 1961: 223).

In summarizing the conditions responsible for producing fatal amounts of prussic acid, Steyn (1934 & ***pers. com.***) lists the following: wilting in hot dry weather (especially in pre-rain spring), post-fire flush in dry weather, bruising, trampling, early frosts in the autumn, the rapid flush and wilting of grasses in over-grazed sheet eroded areas. This author also makes the important point that high protein grasses and those occurring on fertile base saturated soils are most liable to produce toxic amounts of prussic acid when wilted. The addition of nitrogen fertilizer for example, stimulates the production of prussic acid when wilting conditions occur.

Of the grasses which produce high concentrations of prussic acid in the Cape-Botswana border area (Henrici 1926), and near Pretoria (Steyn 1929, 1934), the following occur in Gorongosa: ***Aristida congesta, Cynodon dactylon, Eustachys paspaloides, Pogonarthria squarrosa, Sorghum verticilliflorum*** and ***Themeda triandra.*** Other grasses in Gorongosa with high protein content which may be suspected are ***Digitaria swazilandensis, Urochloa mosambicensis*** and possibly hygrophilous grasses such as ***Echinochloa*** and ***Vossia.***

In ***Cynodon, Eustachys,*** and ***Sorghum***, prussic acid content increased from early morning until about 14h00 followed by a slight decline until 18h00 and a rapid decline to zero at sunset (Steyn 1934). Wilted grasses tested several hours after turgidity was regained from rain, showed negative results (Henrici 1926). This author noted that in her study area the development of a purplish-red colour on drying out was a field diagnostic feature of grasses with little to no cyanogenetic compounds, and those containing these compounds never showed this discolouration.

Mönnig & Veldman (1961) note that the symptoms for anthrax, heartwater (rickettsioses) and prussic acid poisoning are similar. Prussic acid is a rapid and fatal poison. . ."large amounts causing death almost instantaneously with spasms and respiratory paralysis" (Steyn 1934). Pienaar (1961: 8) describes the symptoms for anthrax in wild ungulates during an outbreak in the Kruger National Park ". . . .in the majority of cases it appeared that death occurred suddenly and there were few or no signs of kicking or struggle. A zebra was found dead with a mouthful of green grass on which it has been feeding. . ." which fits closely the symptoms described for lethal prussic acid poisoning (Steyn 1934 & ***pers. com***; Mönnig & Veldman 1961).

Experiments by Steyn (1933, 1934) showed that sulphur administered to stock during circumstances leading to wilting of pastures was an efficient poisoning preventative treatment. In Etosha National Park a longterm detailed study by Ebedes (1974) showed highest occurrence of anthrax deaths in wild ungulates over the spring and autumn periods. He suggests that animals which recover, may build up an immunity in adults which is then broken by an unknown stress factor.

The summer and autumn grazing in Etosha is concentrated on ***Enneapogon desvauxii*** grassland, a high protein species which shows rapid flush and wilting responses to environmental changes. This grass can thus be highly suspected of being a major producer of prussic acid in wilting conditions.

Most of the natural springs and borehole waters used by wildlife in Etosha have a high sulphur content. In the same area many gravel pits were made for the removal of road construction material, and these bare depressions are filled by the rains in summer and are important nuclei for anthrax (Ebedes 1974). Ebedes has for many years held that the gravel pits were a prime culprit in the explosive increase of anthrax in the summer grazing area of Etosha (***op. cit***). It is possible that these gravel pit waters are deficient in sulphur and thus provide no natural preventative to any prussic acid effects, which if it does not kill them, could lower the resistance of wild ungulates to anthrax or any other disease. If prussic acid poisoning turned out to be the unknown stress factor, the use of sulphur in drinking water will have far reaching application in wildlife areas with endemic anthrax. Henrici (1926) and Steyn (1931, 1933) describe a simple chemical field test for determining cyanogenesis (prussic acid formation).

DROUGHT

Some examples of environmental extremes on wildlife in the Urema Trough were related by hunters from the region. A hunter of the early days in Gorongosa reports that an extreme drought occurred in 1934. This was aggravated by burnt out grasslands and large numbers of buffalo, hippo, waterbuck, and wildebeest died. At that period zebra are said to have been numerically dominant and only few died in the drought. The Urema Lake dwindled to a narrow water and the Vundudzi River from Gorongosa Mountain only just flowed (Mr. J. Gamble, Muda Sugar Estates, Beira District, ***pers. com.*** 1969).

Another extreme drought period was experienced over the consecutive years 1953 to 1954 when high numbers of hippo, waterbuck, and wildebeest died. A slight flow continued in the Vundudzi River but the lake was again reduced to a narrow strip of water. Coincident with their poor condition, some of the waterbuck and wildebeest may have been infected by disease as many tribespeople died after eating the meat of these two species (data from old game guards born and bred in the Chitengo area, ***pers. com.*** 1969).

FLOODING AND WET YEARS

Flooding of the Urema slack-basin is gentle, but along the Pungue, Nhandue and Nhamapaza Rivers it is sudden and strong. Mass deaths from flooding is however not reported from these rivers. In the Marromeu sector of the Zambeze Delta large numbers of buffalo were killed by Zambeze floods prior to the construction of Kariba (Tinley & Sousa Dias 1973: 111). The last major flood occurred in December 1958 when many buffalo and waterbuck were said to have been washed out to sea.

In the Kruger National Park (Dr. G.L. Smuts ***pers. com.***) a general relationship has been noted between the increase of buffalo and decrease of wildebeest in high rainfall years, and the reverse in low rainfall years. Evidence from a Zululand game ranch showed that wildebeest calves were most affected by tall grass conditions in wet years and highest losses occurred under these circumstances amongst the yearlings (C.L. Tinley ***pers. com.***).

No conclusive data is available from Gorongosa on the differential influence of cold snaps associated with frontal polar air incursions, or of dry and wet years on the various ungulate species. Wildebeest alone showed a marked coincident rise in population during the three consecutive dry years 1970–1972 (Table 9.2).

9.8 ANIMAL FEEDING ASSOCIATIONS

In the geoecological evolution of a landscape and its biotic associations the preferential seed dispersal of plant foods favoured by animals, forms a major selective pressure or bias. In the Gorongosa ecosystem the predominantly bird and mammal dispersed plant components of all thicket types and forest, which are actively invading savanna and grassland, emphasizes the dimension of this bias.

The enormous, complex, and fascinating field of animal associations in the sea and on land are dealt with in part by Allee ***et. al.*** (1949: Ch. 23, 35), Limbaugh (1961), Moynihan (1968, 1973), Cott (1975), and Wilson (1975) amongst others. A classic symbiotic relationship in the African savannas, involving widely divergent animals with a common interest, is that of the greater honeyguide ***Indicator indicator*** with the ratel and man in search of the products of the African honeybee ***Apis mellifera*** – analysed in detail by Friedman (1955: 25–71).

In the present study, the interspecies associations of birds and/or primates with ungulates in fruit-eating relationships are reckoned to be one of the most important multiplier effects in system dynamics, due to the synchronous combination of seed dispersal activities at both the arboreal and terrestrial levels. What is dropped or dislodged by the arboreal species is used directly by the attendant terrestrial species below.

An important component of ecosystem evolution and replacement is therefore any reinforcement of the selective bias, a multiplier effect, by interspecies feeding associations. The multiplier effect is compounded by the centripetal influence of the fruit tree as a perch, resulting in the devlopment of tree-base thickets of animal-preferred fruit species.

Some species which do not, as far as I know, take part in interspecies associations, such as the frugivorous civet cat, can have an inordinate influence on succession by their habitual use of the same dung middens. The implications of these preferential selection pressures will be dealt with in the following section on animal succession.

The vertebrate feeding relationships in Gorongosa can be grouped around 3 main categories of animal or other central factor:
(a) 'beaters', (b) 'caterers', and (c) 'socializers'. Most of the associations are opportunistic responses to food availability and the faunal make up of a particular circumstance. The above categories can act singly, or in concert, change kaleidoscopically with circumstances, and include a fourth category 'protectors' not dealt with specifically here. The 'protective' role afforded by one or all of several species occurring together relates to the positive advantages of their different levels of danger perception or awareness in different situations (refer to Moynihan's work quoted below). Another kind of protective role is the nesting association of passerine birds with the nests of 'protectors', eg. weaver birds nesting in the same tree as a bird of prey, or waxbills nesting next to hornets. In most of the interspecies associations noted in Gorongosa a symbiotic relationship exists between the animals, which exhibit by their reactions complete understanding to each others alarm calls, feeding calls, and behavioural postures or signals associated with threat, food finding, and danger.

From 250 sight records of higher vertebrate associations on the Rift floor, some examples from each category are given below with emphasis on baboon – ungulate associations in the savanna – thicket mosaic of the Rift floor, and hornbill – samango monkey – ungulate associations in forest.

'BEATERS'

Embraced by this category is any abiotic or biotic factor which makes a food resource more freely available through physical disturbance. At the simplest level are veld fires, attended by many birds such as kites, marabou stork, black-necked heron, bee-eaters, drongo, flycatchers, bulbuls, and shrikes during the day, and replaced at sunset by myriads of bats, feeding on the disturbed insects. In the forests of the mountain and Cheringoma coast, the rain of insects disturbed by columns of driver ants (***Dorylus*** sp.) is attended by alethes, robins and sheppardias.

Birds and dragon-flies follow the passage of large mammals, or even a vehicle, to feed on disturbed insects. In wooded terrain drongos hawk insects disturbed by feeding elephant and in aquatic sites jacanas crowd around elephant or hippo feeding amongst water grasses and lilies. A more conspicuous and common example of the same relationship is that of cattle egrets with buffalo and elephant, or with domestic stock. A game ranger in Gorongosa once recorded a ground hornbill used simultaneously as a perch and as a 'beater' by carmine bee-eaters. In East Africa this has been recorded for kori bustard as well as for ground hornbill (Cott 1975).

'CATERERS'

'Caterers' are animals which by their method of feeding make food resources easily available for other animals. Lion kills provide food for vulture attendants, and tree felling by elephant makes browse available to smaller browsers. These are two examples amongst many. In this category the arboreal frugivores play an important role by dropping or knocking fruit onto the ground where it is then available to many other species of animal. Both the 'caterers' and the 'beaters' are nuclear species in Wilson's (1975: 358) terminology, which other species seek out and follow. Those that seek them out are referred to as attendant species (***op. cit.***). The nuclear position of baboon in feeding associations in the Rift Valley habitats is illustrated by the preliminary data depicted in Fig 9.24. This figure only shows "the tip of the iceberg" in fact, as records are totally biased to those that were easily observed. The association of bushbuck, warthog, dwarf and banded mongoose with baboon is probably very much higher, and there are probably seasonal changes in the predominant attendants.

When the associated sounds of baboon and/or falling fruit are heard from a tree, species such as elephant, bushbuck, impala and red duiker often stop what they are doing and move towards this particular feeding station. Here they feed on the shower of partially bitten, rejected and disturbed fruits which land beneath the tree. An example of this behaviour was provided by a herd of 20 impala grazing on the floodplain-savanna ecotone. One hundred metres away, without attendants, was a large troop of baboon feeding on the ground. A little later at the sound of an ***Acacia albida*** pod dropping with a rattle onto the ground, the oldest (apparently) female impala

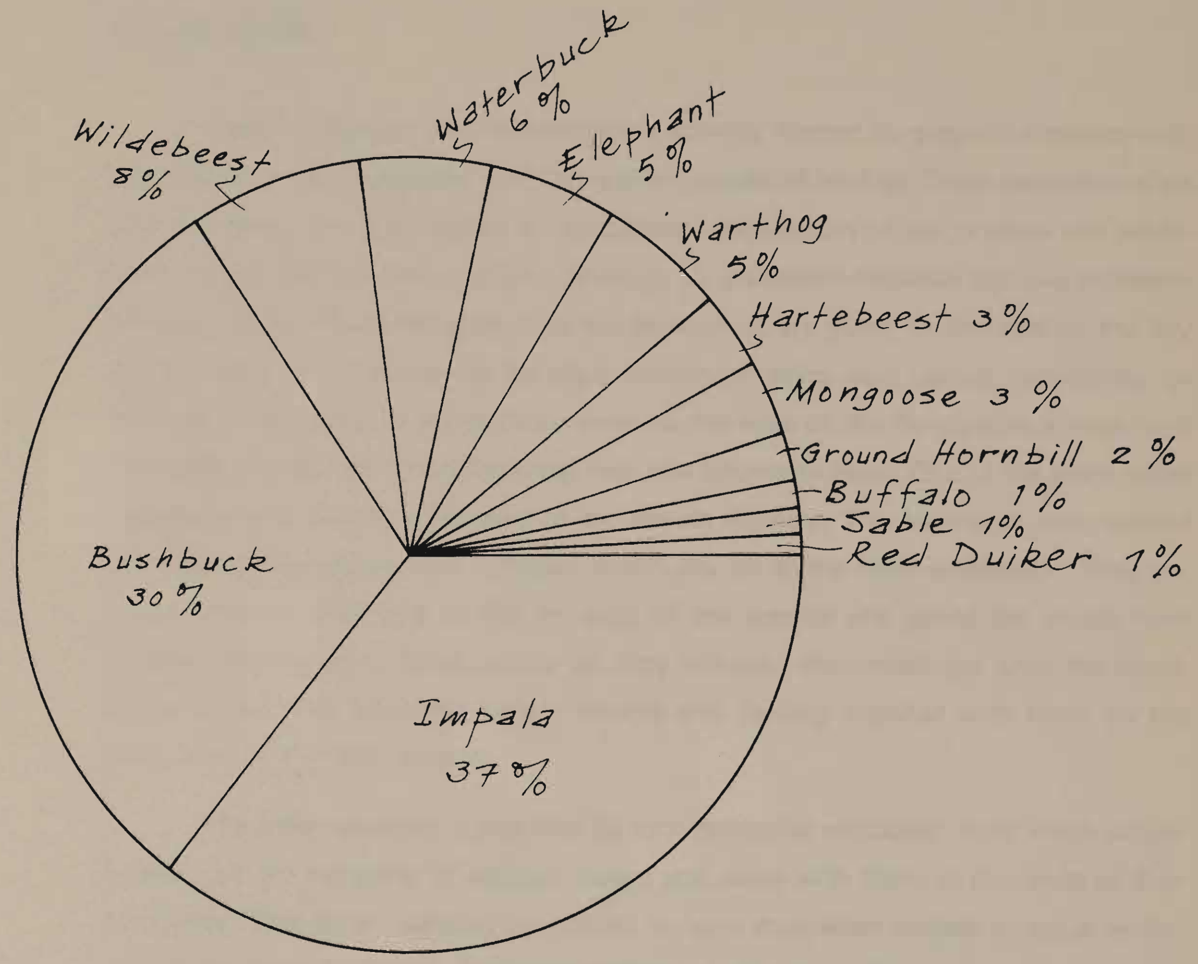


Fig 9.24 ANIMALS THAT ASSOCIATE WITH BABOON ON THE RIFT FLOOR IN THE GORONGOSA ECOSYSTEM.

looked up immediately to the canopy of the tree, where the baboon were now feeding, turned and walked over, followed by the other impala, to feed on the falling pods. None of the other impala had looked up but they followed close behind the old female. When the baboon moved through the canopy to an adjacent tree the impala followed beneath, and stayed with the primates for more than five hours. My observations support De Vore & Hall (1964: 58–59) who state that impala and bushbuck "seem to actively seek out baboon groups and stay with them for most or all of the day". The period that they remain in association appears to be related to habitat make-up and to baboon feeding strategies. The association of impala and/or bushbuck with baboon is recorded from most areas where they occur together, but there are apparently regional differences in the tendencies of any other species to associate with baboon (Elder & Elder 1970).

In the forests of the Gorongosa transect, silvery-cheeked ***Bycanistes brevis*** and trumpeter ***B. buccinator*** hornbills and samango monkey feeding on fruit in the canopy act as nuclear species to ungulate attendants including blue duiker, red duiker, suni and bushbuck. Associated at one ***Ficus polita***, for example, in the forests of the Cheringoma coast, were both species of hornbill with suni and red duiker below them feeding on fallen fruit. In the Rift Valley a pair of red duiker were observed to follow a troop of samango from the security of a forest into the adjacent savanna-termitaria thicket mosaic. On the way to a termitarium thicket the samango stopped to feed on ***Acacia nigrescens*** flowers, and those dropped were eaten by the duiker. Inside the island-thicket the duiker were feeding on fruit of ***Cassine schlechterana*** and ***Berchemia discolor*** dropped from the canopy.

In thicket on the Rift floor a bush squirrel ***Paraxerus cepapi*** was noted in attendance to a red duiker which had pawed up potato-like tubers; the squirrel darted down and collected pieces of the tuber chopped up by the duiker's hooves. In the Cheringoma forests tribal hunters report suni feeding on the fruit flesh being dropped by a red squirrel ***Paraxerus palliatus*** that was more intent on getting at the kernel.

In the Congo equatorial rain forest, long-tailed hornbill ***Tropicranus albocristatus***, monkeys and a large squirrel form feeding associations (Chapin 1939: 352). The monkeys, feeding on fruits, act as 'beaters' by putting up insects which are taken by the hornbill, and as 'caterers' by biting off some of the fleshy parts of the fruits exposing the kernel which the squirrel is after.

A coarse feeder such as elephant provides masses of partially digested and broken fruit in its dung. The dung is invaded by insects such as scarabid beetles and termites. Baboon feed on the outer parts of broken up marulla ***Sclerocarya caffra*** fruits, and bush squirrel eat the seed kernels of marulla and the termites found in the dung (one stomach sample contained 50% of each). Many other animals such as francolin, guineafowl and mongoose search elephant dung for food. The large communal dung heaps formed by white rhino are also centres of food searching activity for many kinds of animals (Player & Feely 1960).

'SOCIALIZERS'

Under this group are the associations actively formed by gregarious species with other species, not necessarily with the primary intent of feeding. These associations are over and above the more casual or coincidental associations of, say, a zebra and wildebeest mosaic on the same pasture, although all gradations between the two extremes probably occur. Two examples of active association are given. In the heat of the day whilst a herd of 16 adults and subadult waterbuck males were resting, ruminating, or sparring in the shade of winterthorn trees on the edge of the floodplains, a large herd of impala entered the floodplains just over one kilometre away. One of the older males looked up and watched the dots of the impala intently. This individual then walked off towards the impala herd followed eventually by all the other waterbuck. They traversed the one kilometre to the far edge of the treeline and joined the impala herd without feeding once. After joining up they followed the impala out onto the floodplains for another kilometer before settling and feeding together with them on the green zone of the lake margins.

The other example is provided by lone territorial wildebeest bulls which actively seek out the company of baboon troops and move with them to the limits of their territories. This latter association appears to be a mutualism related to sociality and mutual alertness to danger. Although feeding is not necessarily involved, the lone bull will have more opportunity to feed because of the baboons alertness. Low attentiveness on the part of ungulates in the company of primates seems to be a common feature of these associations (Struhsaker 1967, Washburn & De Vore 1969). In the Rift savannas, vervet monkey troops have been noted in association with one or other of the following ungulates: bushbuck, impala, oribi, and lone wildebeest bulls. It was not ascertained whether these were feeding associations, or which were the nuclear and attendant species.

No data was obtained in Gorongosa on whether fruit eating associations of canopy and ground level feeders (or other symboises) were confined solely to daylight hours and whether other associations were formed at night, eg. between animals such as bushy-tailed galago, fruitbats, civet, side-striped jackal, bushpig and other ungulates.

The occurrence of interspecies gregariousness is a conspicuous feature in the savanna-thicket mosaic of the Rift Valley where high densities of primates and ungulates occur. It also appears to be a common feature in the forest area, but was not recorded from miombo, probably due to the general scarcity of larger mammels in that system. Mixed bird parties are however encountered in miombo as in the other wooded systems.

In analysing the occurrence of mixed bird flocks in the Andes Moynihan (1973: 17–18) points out some salient features. The members of these mixed bird parties showed ". . . pronounced intraspecific geographic variation in their interspecific behaviour". In one sector the mixed bird flocks were small with few species which remained as coherent parties for brief periods. In other sectors mixed parties were "larger, more stable, cohesive, and complex". In yet other areas mixed flocks were quite absent.

To account for these pecularities in mixed bird flocks and the mixed primate associations which occur in Central and South America Moynihan (1973) provides perceptive insight into the factors at play, which seem so be closely applicable to the associations observed in Gorongosa and elsewhere in Africa. "It is obvious that the development of flocking depends on several factors. There are positive correlations among densities of populations, thickness of vegetation, and frequency and elaboration of interspecific gregariousness within regions. But these cannot account for the whole of the major geographic trends. They do not explain the exceptions. There must be something else involved. This would appear to be an "invasion" or "frontier" effect. Interspecific gregariousness seems to go up with exposure to, or anticipated number of, invasions from or into other regions of the same life zone or an adjacent zone . . ."

. . . .'What is the functional significance of this apparent connection of interspecific gregariousness with frontiers, strays, and invasions? The advantages of mixed flocking from the point of view of a straying bird in the unfamiliar area are obvious and much the same as in the monkeys cited above. By associating with experienced local individuals, a stray may be able to discover and identify food and/or danger relatively rapidly. . . . .It may be difficult for an animal to join and follow strangers without also developing some tendency to allow itself to be joined and followed by strangers. It seems to be characteristic of most animals that they cannot, at least do not, support very great qualitative difference in kind of social responses. . . a species that is gregarious in some circumstances usually tends to be gregarious in other circumstances." In reference to the mixed monkey associations Moynihan (1973) also lists feeding habits, territorial behaviour and distribution and abundance of foods as underlying factors.

This subject is also explored in detail by Wilson (1975: eg. pp 49–59, 353, 358), who includes examples from insect societies as well. He suggests that insects surpass the vertebrates in the development of social symbiosis due to a far greater dependence on altruism, and that this "indiscriminate generosity opens up multiple lines of entry into the energy flow of the colony". It would not be surprising if in-depth studies of vertebrate associations, in Africa at least, showed far greater symbiotic, if not altruistic, relationships than may generally be believed. A literature survey alone would probably prove suprising.

In the examples of feeding symbiosis related from Gorongosa an outstanding feature appears to be the opportunistic use by individuals, or groups, of the changing scene in abundance, and the diversity of circumstances which they can exploit. These conditions comprise an interplay of the feeding, social, and security behaviour of other species – their unconscious role as 'beaters', 'caterers', and 'warners' or 'protectors'. Exploitation of these features appears to be derived from learned correlations resulting from high frequency of interspecies encounters. From this exploitation of advantageous and usable features in the behaviour of other species facilitative, if not altruistic, symbiotic relations are developed.

Whether some of the vertebrate feeding associations may be a means of obtaining access to resources falling within the bounds of agressively territorial species does not seem to have been,noted. This feature is shown to be a fundamental adaptive feature of interspecies fish associations on reefs, where schooling is a ". . . .mechanism for circumventing the territoriality of competitors" (Robertson ***et. al.*** 1976).

Moynihan (1973: 18) suggests that the frequency of interspecific gregariousness appears to go up with the diversity of juxtaposed communities and ecotones. The conspicuous difference in occurrence of interspecies associations between the Rift Valley and miombo savannas is probably directly related to the influence of the extraordinary heterogeneity in the Rift as opposed to the homogeneity of unbroken miombo over large areas. These influences are in turn underlain by a heterogeneity of fertile substrates in the Rift, each with different constraints and potentials, as opposed to relatively homogeneous leached soils in the miombo (cf. Janzen 1974).

In the Rift the matrix of contrasting (in physiognomy, structure or biotic content) communities in close juxtaposition provides a multiplicity of interfaces which intermesh in mosaic patterns. The plant food resources such as preferred grasses, browse and fruits have a clumped dispersion within each community and many of these and their individual plant components, such as fruit trees, exhibit a staggered series of phenophases or, at the other extreme, mass fruiting over one period.

Thus herbivores of all kinds are induced to move and explore an uneven food resource which brings species into contact with changing plant and animal matrixes in space and time. Where uneveness in the food resource is aggravated by rarity, or widely separated occurrence, contacts are likely to be infrequent, as in the miombo for example. Conversely an uneven but closely packed food resource would promote high frequency of contacts, as in the Rift Valley.

As evinced by the differences in degree and kind of biotic succession between and within systems, uneven herbivore selection pressures have far reaching influences in the kinetics of geoecological succession and thus landscape evolution. These aspects are explored in the following section.

9.9 ROLE IN GEOECOLOGICAL SUCCESSION

Ecosystems and their biotic communities are in a kinetic state of multi-directional change as a result of climatic fluctuations, geomorphic processes and the responses and interactions of the living constituents. The life processes of plants and animals in themselves bring about changes in the system due to their individual (eg. dominants), and compounded (coevolutionary) effects such as fruit feeding associations. The changes can be advantageous, or inimicable, to the plant and animal constituents. In the latter case the constituents will be replaced by others, better adapted or more tolerant of the altered conditions.

The various ways by which communities and the environment are altered by animals include: seed dispersal and thicket encroachment; pan making; hill building by termites; draining of marshland by path making; physiognomic, structural and floristic change to habitats by large herbivores. In this regard Fraser Darling (1960: 91–93) provided a first analysis of the stratification and niche structure of African ungulates as noted in Zambia. The widespread invasion of grasslands by scrub due to excessive populations of grazing ungulates is well documented from all parts of the Continent (eg. Mostert ***et. al.*** 1971, Acocks 1975, for South Africa). In parts of East Africa the opposite situation results from excessive population densities of elephant which destroy forest or wooded savanna and inhibit their expansion, so that with the aid of fire these communities are being reduced and replaced by grasslands (Laws 1970, Laws ***et. al.*** 1975). Concomitant with increase of grassland is the build up in grazing populations such as buffalo and hippo (eg. as reported in the Luangwa Valley by Marshall & Sayer 1976: 394), and the contraction of tsetse fly, for example, in other areas (Ford 1966). Such changes thus have reciprocal effects throughout all component parts of ecosystems and communities.

In examples of the role of animals in affecting ecosystem change in Gorongosa, emphasis will be on the following aspects:

(1) geoecological effects, (2) utilization modification of plant communities, and (3) woody plant seed disersal.

GEOECOLOGICAL EFFECTS

The most important agent of change in the Urema Trough is the hippo. Their habitually used footpaths radiate out to grazing areas from riverine day-retreats. These paths also link all marsh and pan areas. Whilst footpaths aid the spread of floodwaters in flat areas, once incised their canalizing effects have far reaching repercussions in floodplain ecosystems.

Slacks, marshes, and pans are inundated by direct rainfall and the spread of floodwaters across the convexities separating one depression from another. In the ebb these basins again become isolated and the waters gradually contract and dry up through the dry season. The tempo of drying up is different in each basin due to their disparate dimensions. As the water dries up a margin of green pasture is provided, which contracts with the water to the lowest part of the depression toward the end of the dry season.

In the wet season and flood period, the hippo paths are canalized by the animals' movement to and from the depressions over the soft ground. The canalizing effect changes the entire dynamics of the depressions due to over-drainage and the hygrophilous grasses dry out nearly as rapidly as the adjacent savannas. Not only is a valuable pasture resource lost, but the excessive waterlogging which kept scrub encroachment at bay is no longer operative. Thus savanna invasion of the depressions occurs causing extinction of hippo habitat. An aquatic marsh grass system characterised by hippo and wildfowl is then replaced by acacia and impala and all other savanna features and components. By this process path making by hippo is a cause of their own local extinction.

The geoecological effects of hill building termites has been noted in Section 6.3. Ungulate activity around or on top of the hills wears them down reversing the microrelief to provide a minimum of one, and maximum of about three, pans per hectare, in the Rift Valley. Each of these become seasonal aquatic systems with annual fish and perennial hygrophilous grasses.

Each island pan provides green pasture through until the mid dry season and is intimately related with the adjacent termitaria thickets composed of preferred browse and fruit plants.

PLATE 25 PHYSICAL CONDITION & GEOECOLOGICAL ROLE OF HIPPO

(A) Vertical photo of a hippo herd showing typical poor condition of Gorongosa hippo in the dry season (note conspicuous spinal ridge in most animals).

(B) Hippo path used in the wet season across soft floodplain clay. Subsequent erosion shows all land facets in miniature of valley cut and fill processes (eg. valley widening by multiple-lateral nickpoints, aggraded (fill) donga bed fixed by grass, bare pseudo-levee (waxing slope) and gullies invaded by woody plants).

(C) Borassus palm savanna with 3 m high *Hyparrhenia rufa* grass stratum trampled out and overgrazed by hippo and sheet eroded. The subordinate lawn grass pastures preferred by hippo have extended and even-aged *Acacia sieberana* invades the new erosion surface at left and right.

(D) Headward eroding nickpoint incising floodplain grassland at head of hippo path. New phase of savanna invasion above the nickpoint and in the incision. Note three age groups of fever tree invasion.

UTILIZATION MODIFICATION OF PLANT COMMUNITIES

The dry forest patches on the Rift floor are generally small and linear as they are confined to the duplex sands of distributory channels and splays of fossil alluvial fans. Hence many ungulates, such as wildebeest and zebra, which do not normally enter forest, pass through them to the open terrain on the opposite side. Elephant and buffalo utilize the forest for shade and food, the former browsing the field layer and mid-stratum and the buffalo the herbaceous layer. Once opened up by these activities they are then used for shade purposes by other species as well which bares the understorey further.

Fire impinges little on dry forest as the abrupt soil change at the ecotone results in a relatively short grass cover. In dry forest the upper canopy trees are clumped and a more continuous cover is formed by the mid-stratum trees, and to a lesser extent the shrub layer. In those forest patches where the lower two layers have been opened up no suni were encountered, only red duiker. Wherever undamaged patches occurred the suni was present. This relationship probably involves a food factor, and cover from one of the suni's main predators, the crowned eagle.

The structural alteration of grasslands by the grazing succession and movement of large herds of buffalo through 4 m high grassland is noted above. Selective grazing by some species results in floristic changes in grasslands and maintenance of short grass conditions exemplified by the hippo lawns adjacent to the Urema Lake. It is probable that these conditions are exploited by the wildebeest population which on its own could only maintain suitable pasture in patches. An excessive reduction of hippo would result in a rapid change of floodplain grassland structure with opposing effects on many animal constituents particularly species such as wildebeest and buffalo.

The over-utilization of many termitaria thickets, resulting in retrogressive succession and microrelief reversal, causes local extinction or occlusion of the island thicket biota (see Section 6.3). Conversely these and other clump thickets are protected from fire by ungulate utilization as this results in a trampled out perimeter which acts as an effective firebreak.

DISPERSAL OF WOODY PLANT SEEDS BY ANIMALS

In the Gorongosa system animal dispersed seeds from forest, thicket and savanna are distributed in suitable sites as a result of the behavioural patterns of the various dispersants. These patterns are in response to nuclear sites in the various habitats which have a centripetal attraction to high frequency of use. They include: (1) perch sites, (2) watering sites, (3) bare or sparsely grassed sites. The more important animal dispersants of woody plant seeds, from mainly drupaceous or baccate fruits, are listed in Table 9.6.

As revealed by detailed metre quadrat analyses of the groundlayer in various systems, seedlings and saplings of bird and mammal preferred species were related mainly to the above sites and were absent or extremely rare in the intervening grass ground cover between tree crowns.

Perch sites

In the first category of nuclear sites of attraction are biotic and inanimate prominences of all kinds, including: trees, termite hills, stumps, rock outcrops, fence posts, and buildings. The most efficaceous means of invasion and replacement of savanna by thicket is through development of tree-base thickets composed of bird and mammal dispersed fruit species. The hard, shot-like seeds of euphorbiaceous trees, such as ***Androstachys johnsonii*** and the succulent tree euphorbias, which are thrown by explosively dehiscing capsules are picked up off the ground by turtle doves and wood doves. The faeces, dropped from the trees that these birds use for resting or roosting contain some undamaged seeds, hence the frequency of these plant species in thicket clumps of all types. Classic descriptions of the sequential invasion of thornveld by animal dispersed thicket species whose seeds were dropped beneath individual trees is given by Bews (1917) for Natal, and in other parts of the world by Ridley (1896, 1930: 385–386).

In addition to the activities of birds and primates, the habit of caching seeds by both the bush and red squirrels (San Viljoen ***pers. com.***) against objects, such as logs or tree trunks, must play a vital multiplier role in thicket extension. A vivid description of the seed storing habit of the British grey squirrel is given by Ridley (1930: 379–382). In the same account evidence is quoted from an American study which showed that after forest is destroyed by fire or felling, the seeds stored and forgotten by squirrels germinate and the new forest which develops is composed of 75% of the favoured squirrel foods.

TABLE 9.6

Important animal dispersants of woody plant seeds in the Gorongosa ecosystem. (R = confined mostly to the riverine strips)

	MOUN-TAIN	MID-LANDS	RIFT VALLEY	COAST
BIRDS				
Guineafowls				
Crested Guineafowl	+	R	+	+
Doves and Pigeons				
Rameron Pigeon	+			
Delagorgues Pigeon	+			
Red-eyed Turtle Dove		+	+	+
Cape Turtle Dove	+	+	+	+
Laughing Dove	+	+	+	+
? Tambourine Dove		+	+	+
? Blue-spotted Wood Dove		+		+
? Emerald-spotted Wood Dove			+	
Cinnamon Dove	+			
Green Pigeon	+	R	+	+
Turacos				
Green-crested Turaco	+			+
Purple-crested Turaco		R	+	+
Grey Loerie			+	
Mousebirds				
Speckled Mousebird	+	R	+	
Red-faced Mousebird			+	
Hornbills				
Trumpeter Hornbill	+	+	+	+
Crested Hornbill	+	+		+
Grey Hornbill			+	
Red-billed Hornbill			+	
Yellow-bill Hornbill			+	
Crowned Hornbill	+	+	+	+
Barbets				
Black-collared Barbet		+	+	+
White-eared Barbet	+	R	+	+
Yellow-fronted Tinker Barbet		+		
Golden-rumped Tinker Barbet		R	+	
Green Tinker Barbet	+			
Crested Barbet		+	+	
Orioles				
European Golden Oriole		+	+	+
African Golden Oriole		+	+	+
Black-headed Oriole		+	+	+
Green-headed Oriole	+			
Bulbuls				
Black-eyed Bulbul		+	+	+
Terrestrial Bulbul	+	+	+	+
Yellow-streaked Bulbul	+	+		
Stripe-cheeked Bulbul	+			
Yellow-breasted Bulbul			+	+
Sombre Bulbul	+	+	+	+

Table 9 (continued)

	MOUN-TAIN	MID-LANDS	RIFT VALLEY	COAST
Thrushes, Chats, Robins				
Olive Thrush	+			
Gurney's Thrush	+			
Mocking Chat	+			
Natal Robin	+	R	+	+
Heuglin's Robin	+	R	+	+
Cape Robin	+			
Bearded Robin		R	+	+
White- browed Scrub Robin			+	
Starred Robin	+			
Swynnerton's Robin	+			
Palm Thrush			+	+
White-breasted Alethe	+			+
Starlings				
Wattled Starling			+	
Plum-coloured Starling		+	+	+
Blue-eared Glossy Starling		+	+	
Lesser Blue-eared Glossy Starling		+	+	
Black-bellied Glossy Starling	+	R	+	+
Red-wing Starling	+	+		
White-eyes				
Yellow White-eye	+	+	+	+
MAMMALS				
Fruit-bats				
Wahlberg's Epauletted Fruit Bat	+	+	+	+
Peter's Epauletted Fruit Bat	?	?	+	+
Giant Fruit Bat			?	+
Egyptian Fruit Bat		?	?	+
Bocage's Fruit Bat		+	?	?
Primates				
Bushy-tailed Galago	+	R	+	+
Samango monkey	+	R	+	+
Vervet monkey		+	+	+
Baboon	+	+	+	+
Carnivores				
Side-striped Jackal		+	+	+
Civet		+	+	+
Tree Civet	?	+	?	+
Ungulates				
Elephant	+	+	+	+
Blue Duiker	+			+
Red Duiker	+		+	+
Suni			+	+
Nyala			+	
Bushbuck	+	R	+	+
Impala			+	
Kudu		+	+	
Bushpig	+	R	+	+
Rodents				
Bush Squirrel			+	
Sun Squirrel	+	+		
Red Squirrel	+		+	+

In Gorongosa, beneath the canopy of each baboon sleeping tree are dense patches of the termitarium and tree-base thicket tree and shrub components (see Appendix 2 for a list of baboon foods). These are heavily browsed by impala and bushbuck. Melton (in press) in his study of animal associations with termitaria in Uganda found that baboon, during the day, preferentially defaecate on termite hills. This implies that preferential use is probably made of other perches as well, such as rock outcrops or trees.

In mango trees around our house at Chitengo Camp on the Rift floor, fruit bats ate figs taken from a neighbouring ***Ficus sycamorus*** 20 m away, and seedlings germinated from the rejected seeds dropped under the trees and in the tree crotches. The importance of seed dispersal by fruit bats in the floristic composition, and growth of thickets and forest, is emphasized by Ridley (1930), Van der Pijl (1957, 1972) and Vazques-Yanes ***et. al.*** (1975).

Watering sites

The second category includes all sites where fresh or brak surface water is used by birds and mammals, that is,streambanks, dongas, ravines, kloofs, fountains, springs, pan and lake margins. On floodplains, and in areas where sheet and rillwash occur, many woody plant seeds are also dispersed by waterflow and are left in recognizable swashline patterns. Examples of these are common in mopane and acacia savannas, and the fever tree woods marginal to floodplains. The superimposed influence of zoochory to perch sites here reinforces the importance of emminences and obstructions as sites of seed deposition.

Bare or sparsely grassed sites

The third category is of bare or sparsely vegetated patches which are attractive to many animals, particularly cats and ungulates, including elephant, eland, impala, black rhino amongst fruit and pod eating ungulates and wildebeest and zebra amongst grazing species. Elephant are responsible for large scale dispersal of seeds everywhere, and especially along their paths. This is evinced by the clumped and linear occurrence of many favoured species such as borassus palm ***Borassus aethiopum*** and marulla ***Sclerocarya caffra*** along paths as well as in riverine and other sites.

On the Rift Valley floor and in the coastward forest-dambo mosaic of the Cheringoma cuesta the civet is a prime mover in the development and extension of thicket and forest. A list of the fruits eaten, as determined by the seeds from their middens, is given in Appendix 2 for the two areas. Civet are omnivorous with a frugivore bias as shown by quantitative analysis made from miombo of the Salisbury district in Rhodesia (Smithers ***pers. com.***). His results showed 57% fruit, followed by 43% Murids and insects taken in the dry season; in the wet season 65% insects and 35% fruit.

Civet habitually use dung middens, which are related to openings in the herbaceous cover away from perch sites such as termite hills. The middens however occasionally occur within the crown area of trees, particularly on forest margins. As shown by the profile transect of ***Androstachys*** thicket abutted against coast fynbos ***Philippia simii*** (Fig 8.19), seed germination from the middens has resulted in small scrub-thicket islands of forest trees. Where these occur on suitable substrates they develop into larger thickets, and coalesce laterally into extensive patches mostly from later seeding by birds. In other areas of the Cheringoma, civet middens beneath miombo savanna canopy trees are composed almost entirely of dense scrub-thicket islands formed by several ***Rubiaceae.*** However, fruits of certain species characteristic of termitaria and riverine sites,such as ***Cleistochlamys kirkii,*** eaten by civet fail to grow beyond the seedling stage in midden sites as conditions for them are unsuitable. Their dispersal to termitaria and tree-base sites is thus probably chiefly by birds.

If conditions are favourable, mass seed germination of single or mixed woody species occurs on the dung middens, and these develop to form dense thicket patches. The midden is continued to the side of the old one, now grown over with young trees, and so on, resulting in the formation of different aged thickets. In the Rift Valley, clumps of a favoured fruit tree ***Diospyros usambarensis*** of various ages occurring adjacent to current middens best illustrate his phenomena. The fruits eaten by civet are from the same species which are eaten by birds (eg. green pigeon), primates, elephant and others. These fruit species are typical of tree-base thickets, termitaria and streambanks on the Rift floor, and from termitaria, riverine sites and evergreen forest on the Cheringoma Plateau.

From his studies of bird formed thickets in Malaya, Ridley (1930: 385–386) describes the sequence of habitat changes which occur: "It is in this way that from isolated trees or bushes a thicket may spring up in a very short time around the tree or through the bush, and as the thickets increase in size and become the roosting place of more birds, copses may be formed, then more extensive woods, and finally forests". By this process woody plant invasion is accelerated in a saltatory manner.

IMPLICATIONS AND AN APPRECIATION

Floodplain grasslands are maintained by seasonally excessive flooding and waterlogging. As indicated in previous sections (5.8, 6, and 8) this factor alone is responsible for the treeless grasslands on the Rift floor, and in dambos of the miombo system. As a natural process these grasslands will be incised by headward erosion of nickpoints resulting in increasingly rapid runoff. As soon as the soil moisture balance is tipped towards the mesic or xeric, savanna and/or thicket components invade the grasslands on any slight emminence.

As the flora contains herbaceous and woody plants which have wind and water dispersed seeds as well, the entire successional replacement of ecosystems and communities by these species could take place in the absence of animals. Hippo paths however can both accelerate the natural processes or initiate a new sequence of erosion in floodplain and slack-basin areas on the Rift floor. The activity of a single animal species, in this case the hippo, has therefore considerably altered the tempo of geoecological change on the Rift floor, which has simultaneously accelerated the reduction of their own habitat, jeopardising the survival of the species in the Urema Trough area. In accelerating or setting in motion the replacement of grassland by savanna and thicket components through the canalizing action of their paths, hippo are responsible for not only precluding their own existence but also that of all biotic constituents dependent on the open grassland ecosystem. Canalization also sets in train developmental changes in soil properties.

The obverse side of the hippos' predominantly geohydrological role in landscape change is that exemplified by selection biases of frugivores within the biotic community, due to their multiplier effect. Dispersal and successful development of favoured fruit trees reinforces their predominance and further use by increasing their density and thus the frequency of centripetally attractive feeding stations. In this manner the number of vertebrate interspecies associations is multiplied by frequency of contact, which allows a flow of kaleidoscopically changing associations as the aggregations move from one feeding station to another. On the one hand mutualistic interrelations between species is reinforced, and on the other the trend or swing in habitat change is exponentially enhanced for frugivores, but physically (physiognomic and structural) it is increasingly altered by the maturation and coalescence of thicket clumps. These changes preclude many of the frugivores originally responsible for the replacement sequences, but others from closed habitats become intermeshed in the changing aggregations of plant and animal constituents.

The separate or combined influences of geomorphic action of hippo, and the community selection pressure of frugivores results in the same sequence, that of grassland replacement by wooded savanna and thicket/forest. These progressive ecosystem sequences continue until a new homeostatis is attained at which time geomorphic surface replacement can result in a retrogressive sequence. In Gorongosa all sequences are occurring and are active under present-day conditions. In East Africa the action of elephant combined with fire is opening up wooded country to grassland dominated systems.

Ross (1962: 231–342) points out that plant and animal components of systems become separated into dominants and subdominants thus ". . . .in biotic communities some species or groups of species produce special ecological conditions which, superimposed over the general climatic and edaphic conditions of the area, have a profound limiting effect on the occurrence of other species in the community. These influencial species are known as dominants. . . ." Hippo and frugivores are reckoned to be first level dominants in the Rift Valley sector of the Gorongosa ecosystem at present, buffalo and elephant forming a second level of dominants. Tomorrow the scene may change, particularly if there is a crash in hippo numbers and a continued increase in elephant. In the precincts of Gorongosa Mountain, and especially on the Cheringoma Plateau, frugivores are a dominant influence in ecosystem dynamics. Their impact is less conspicuous in the closed Midland miombo and in the summit grasslands on the mountain where fire and climo-edaphic constraints may cancel their influence.

In sum, the factors responsible for natural afforestation processes are: aerobic drainage, effective woody seed dispersal, overgrazing, early dry season (autumn) incidence of fire, or protection from fire. Conversely maintenance or expansion of grasslands are influenced by waterlogging or flooding, rotting of woody plant seeds in the growing season, late dry season fires, overbrowsing (eg. by elephant), and clearing by man for cultivation, timber and firewood. As demonstrated by comparative examples from the Rift Valley and Cheringoma Coast, the absence or removal of one animal from a system, for example hippo, would greatly alter the tempo of change allowing natural dampers such as soil cohesive properties and dense grass cover to preserve slack and marsh systems for much longer periods.

Other facets of community evolution are the reciprocal selective influences between plants and animals. For example there is a growing body of evidence that the stimulus for non-overlapping flowering times in many plants is due to competition for pollinators (eg. Robertson 1924, Mosquin 1971, Pojar 1974, Reader 1975, Heinrich 1975). A parallel but converse selective bias is suggested for the staggered fruiting phases of many rain forest animal-fruit plants, due to interspecific competition for dispersants (eg. Snow 1966, 1971; Smythe 1970; McKey 1975; Howe & Primack 1975).

In this regard it is interesting to speculate whether the abundance of pods produced by the riverine winterthorn tree ***Acacia albida*** and its flowering and leaf flush at the "worst" time of the year is more than an evasion of flooded summer conditions. As the pods are avidly consumed by all wild ungulates and primates, the seeds are probably dispersed mainly by zoochorous means as well as water; the typical dry season concentration of ungulates in riverine zones may have reinforced the climo-edaphic influence or imposed its own selective influence. The fever tree ***Acacia xanthophloea,*** which occurs on different soils in the same sites as the winterthorn, shows a wet season phenophase activity and the distribution of seedlings and saplings indicate their seeds are more conspicuously dispersed in swashlines by the flood and ebb of inundations, or by rains.

By reciprocating opportunism of the circumstances presented to them by a kaleidoscopically changing matrix of plant and animal species, the living constituents selectively multiply, and thus bias, physical (geohydrologica) and biotic (preferred fruits, over-grazing etc.) processes in various directions. These coactions affect the tempo and content of geoecological succession, directed by the deeper climo-edaphic constraints or opportunities presented by the different substrates of various geomorphic surfaces. These physical changes in a plant's and animal's habitat themselves produce a re-orientation of dominant and subdominant or prime mover species relationships, which affects the kinds of community selective pressures operative in space and time.

REFERENCES / WILDLIFE

ACOCKS, J.P.H.
1975 Veld types of South Africa (2nd edt.) ***Bot. Surv. S. Afr. Mem.*** No 40.

ALLEE, W.C., EMERSON, A.E., PARK, O., PARK, T. & SCHMIDT, K.P.
1949 ***Principles of animal ecology.*** W.B. Saunders Co. Philadelphia & London.

ANDERSON, G.D. & HERLOCKER, D.J.
1973 Soil factors affecting the distribution of the vegetation types and their utilization by wild animals in Ngorongoro Crater, Tanzania. ***J. Ecology*** 6(3): 627–652.

ANDERSON, J.L.
1975 The occurrence of a secondary breeding peak in the southern impala. ***E. Afr. Wildl. J.*** 13: 149–151.

ANSELL, W.F.H.
1960 ***Mammals of Northern Rhodesia.*** Govt. Printer, Lusaka.

ATTWELL, R.I.G.
1970 Some effects of Lake Kariba on the ecology of a floodplain of the Mid-Zambezi Valley of Rhodesia. ***Biol. Cons.*** 2(3): 189–196.

BELL, R.H.V.
1971 A grazing ecosystem in the Serengeti. ***Scientific American*** 225(1): 86–93.

BEWS, J.W.
1917 The plant succession in the thorn veld. ***S. Afr. J. Sci.*** 14: 153–172.

BIGALKE, R.C.
1970 Observations on springbok populations. ***Zoologica Africana*** 5(1) : 59–70.

BONSMA, J.C.
1939 Breeding seasons on cattle ranches. ***Farming in S. Afr.*** Vol. 14, p. 230.
1940 The influence of climatological factors on cattle. ***Farming in S. Afr.*** Vol. 15: 373–385.
1942 Useful bushveld trees and shrubs. ***Farming in S. Afr.*** Vol. 17: 226–239.

BRADY, N.C.
1974 ***The nature and properties of soils*** (8th edt.) MacMillan, NY, London.

CHAPIN, J.P.
1939 The birds of the Belgian Congo. Part 2. ***Bull. Amer. Mus. Nat. Hist.*** Vol. 75.

CHILD, G.
1968a ***Behaviour of large mammals during the formation of Lake Kariba.*** National Museum of Rhodesia.
1968b ***An ecological survey of northeastern Botswana.*** United Nations Development Programme, FAO No. TA 2563, 155 pp.

CLANCEY, P.A.
1971 ***A handlist of the birds of southern Mocambique.*** Mems. Inst. Invest. cient. Mocamb. 10, 11 Series A.

COTT, H.B.
1975 ***Looking at animals.*** Collins, London.

DARLING, F. FRASER

1937 *A herd of red deer.* Oxford University Press, London.

1960 *Wild Life in an African Territory.* Oxford University Press, London.

DE VORE, I. & HALL, K.R.L.

1975 Baboon ecology. In: *Primate behaviour: Field studies of monkeys and apes,* edited by I. De Vore. Holt, Rinehart & Winston. NY pp. 20–52.

DODDS, D.G. & PATTON, D.R.

1968 *Wildlife and landuse survey of the Luangwa Valley.* FAO/UN., Rome.

DORST, J. & DANDELOT, P.

1970 *A field guide to the larger mammals of Africa.* Collins, London.

DOUGALL, H.W. & GLOVER, P.E.

1964 On the chemical composition of *Themeda triandra* and *Cynodon dactylon. E. Afr. Wildl. J.* 2: 67–70.

DU PLESSIS, S.F.

1969 *The past and present geographical distribution of the Perissodactyla and Artiodactyla in Southern Africa.* MSc. Thesis, University of Pretoria. 333 pp.

DU TOIT, P.J., LOUW, J.G. & MALAN, A.I.

1940 A study of the mineral content and feeding value of natural pastures in the Union of South Africa. *Onderstepoort J. Vet. Sci. Anim. Ind.* 14(182): 123–327.

EBEDES, H.

1974 Anthrax epizoötics in Etosha National Park and an historical note on anthrax in northern South West Africa. *SWA Nature Conservation Division, cyclostyled* MS. 86 pp + 9 figs, 25 tables.

ELDER, W.H. & ELDER, Nina L.

1970 Social groupings and primate associations of the bushbuck *Tragelaphus scriptus). Mammalia* 34(33): 356–362.

ELOFF, F.C.

1966 Range extension of the blue wildebeest. *Koedoe* 9: 34–36.

ESTES, R.D.

1968 *Territorial behaviour of the wildebeest (Connochaetes taurinus Burchell, 1823).* Phd Thesis, Cornell University, USA.

FORD, J.

1966 The role of elephants in controlling the distribution of tsetse. *IUCN Bulletin New Series* No. 19: p. 6.

FOSBROOKE, H.A.

1963 The stomoxys plague in Ngorongoro, 1962. *E. Afr. Wildl. J.* 1:124–126.

FRIEDMANN, H.

1955 *The honey-guides.* Smithsonian Inst. *U.S. Nat. Mus. Bull.* No 208: pp. 25–71.

GALPIN, E.E.

1926 Botanical survey of the Springbok Flats. *Bot. Surv. S. Afr. Mem.* No. 12.

GLASGOW, J.P.

1963 *The distribution and abundance of tsetse.* Pergamon Press, London, NY.

GWYNNE, M.D. & BELL, R.H.V.

1968 Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* 220: 290–393.

HEADY, H.F.

1975 *Rangeland Management.* McGraw-Hill, NY.

HEINRICH, B.

1975 Bee flowers: A hypothesis on flower variety and blooming times. *Evolution* 29: 325–334.

HENRICI, Marguerite.

1926 Preliminary report upon the occurrence of hydrocyanic acid in the grasses of Bechuanaland. *11th and 12th Reports Dir. Vet. Educ. & Res.* Part 1: 494–498.

1928a The relations between the amount of carbohydrates in the leaves of Armoedsvlakte grasses and the meteorological factors. *13th and 14th Reports Dir. Vet. Educ. & Res.* Part 1: 1041–1074.

1928b The phosphorus content of the grasses of Bechuanaland in the course of their development. *13th and 14th Reports Dir. Vet. Educ. & Res.* Part 2: 1077–1208.

HOWE, H.F. & PRIMACK, R.B.

1975 Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica* 7(4): 278–283.

JANZEN, D.H.

1974 Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6(2): 69–103.

JARMAN, P.J.

1972 Seasonal distribution of large mammal populations in the unflooded Middle Zambezi Valley. *J. Applied Ecol.* 9(1): 283–299.

JOUBERT, D.M.

1954 The influence of winter nutritional depressions on the growth, reproduction and production of cattle. *J. Agric. Sci.* 44(1): 5–65.

LAWS, R.M.

1970 Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1–15.

LAWS, R.M., PARKER, I.S.C. & JOHNSTONE, R.C.B.

1975 *Elephants and their habitats.* Clarendon Press, Oxford.

LIMBAUGH, C.

1961 Cleaning symbiosis. *Scient. Amer.* 205(2): 42–49.

MARSHALL, P.J. & SAYER, J.A.

1976 Population ecology and response to cropping of a hippopotamus population in eastern Zambia. *J. Ecology* 13(2): 391–403.

McKEY, D.

1975 The ecology of coevolved seed dispersal systems. In: *Coevolution of animals and plants* edited by L.E. Gilbert and P.H. Raven, University of Texas Press, Austin.

MELTON, D.A.
1972 *Environmental heterogeneity produced by termitaria in western Uganda with special reference to mound usage by vertebrates.* MSc Thesis, University of British Columbia, 345 pp.

MÖNNIG, H.O. & VELDMAN, F.J.
1961 *Handbook of stock diseases.* Nasionale Boekhandel Bpk. C.T. JHB. (Revised edt.)

MOYNIHAN, M.
1968 The "Coerebini": A group of marginal areas, habitats and habits. *Amer. Natur.* 102: 573–581.
1973 The evolution of behaviour and the role of behaviour in evolution. *Breviora* No. 415: 29 pp.

MOSQUIN, T.
1971 Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22: 398–402.

MOSTERT, J.W.C., ROBERTS, B.R., HESLINGA, C.F. & COETZEE, P.G.F.
1971 Veld management in the O.F.S. Region. *Dept. Agric. Techn. Serv.* Bulletin No. 391.

MYRE, M.
1971 *As pastagens da região do Maputo.* I.I.A.M. Memórias No. 3.

MYRE, M. & ANTÃO, L.R.
1972 Reconhecimento pascícola ac Vale do Save. *I.I.A.M. Comunicações* No. 75, 180 pp.

PETRIDES, G.A.
1975 Principal foods versus preferred foods and their relation to stocking rate and range condition. *Biol. Cons.* 7: 161–169.

PIENAAR, U. de V.
1961 A second outbreak of anthrax amongst game animals in the Kruger National Park. *Koedoe* 4: 4–17.

PIENAAR, U. de V., VAN WYK, P. & FAIRALL, N.
1966 An experimental cropping scheme of hippopotami in the Letaba River of the Kruger National Park. *Koedoe* 9: 1–33.

PINTO, A.A. da Rosa
1959 Um esboço da avifauna sedentária da Região da Gorongosa, Mocambique. Proc. First Pan-Afr. Congr. *Ostrich* Suppl. No. 3: 98–125.
1968 Lista sistematica das aves do Parque Nacional da Gorongosa.

PLAYER, I.C. & FEELY, J.M.
1960 A preliminary report on the square-lipped rhinoceros *Ceratotherium simum simum* (Burchell) *Lammergeyer* 1(1): 3–24.

PLOWES, D.C.H.
1957 The seasonal variation of crude protein in twenty common veld grasses at Matopos, Southern Rhodesia, and related observations. *Rhod. Agric. J.*, 54(1): 33–55.

POJAR, J.
1974 Reproductive dynamics of four plant communities of southwestern British Colombia. *Can. J. Bot.* 52: 1819–1834.

READER, R.J.
1975 Competitive relationships of some bog ericads for major insect pollinators. *Can. J. Bot.* 53: 1300–1305.

RIDLEY, H.N.
1896 Dispersal of seeds by birds. *Natural Science* 8: 180.
1930 *The dispersal of plants throughout the world.* Reeve and Co. Ashford, England.

RINEY, T.
1960 A field technique for assessing physical condition of some ungulates. *J. Wildl. Mgmnt.* 24(1): 92–94.

ROBERTSON, C.
1924 Phenology of entomophilous flowers. *J. Ecology* 5: 393–402.

ROBERTSON, D.R., SWEATMAN, H.P.A., FLETCHER, E.A. & CLELAND, M.G.
1976 Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* 57: 1208–1220.

ROSS, H.H.
1962 *A synthesis of evolutionary theory.* Prentice-Hall Inc. New Jersey.

SHEPPE, W. & OSBORNE, T.
1971 Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs* 41(3): 179–205.

SHEPPE, W. & HAAS, P.
1976 Large mammal populations of the lower Chobe River, Botswana. *Mammalia* 40(2): 223–243.

SHORTRIDGE, G.C.
1934 *The Mammals of South West Africa.* Vol. II. Heinemann, London.

SILVA, J.A., CRUZ, E. & GONÇALVES, A. CASTELO BRANCO
1972 A estrongilidose gastrintestinal dos ruminants em Moçambique – resultados de um ensaio para combate à helmintose no núcleo bovino do posto zootéctnico de Angónia. *Veterin. Moçamb.* 5(2): 69–75.

SIMON, N.
1962 *Between the sunlight and the thunder.* Collins, London.

SIMPSON, C.D.
1973 Tooth replacement, growth and ageing criteria for the Zambezi bushbuck – *Tragelaphus s. ornatus* Pocock. *Arnoldia* (Rhod.) 6(6): 1–25.

SMITHERS, R.H.N. & TELLO, J.L.P.L.
1976 *Check list and atlas of the mammals of Mocambique.* Museum Memoir No. 8, Trustees of the National Museums, Salisbury, Rhodesia.

SMYTHE, N.
1970 Relationships between fruiting seasons and seed dispersal methods in a tropical forest. *Amer. Nat.* 104: 25–35.

SNOW, D.W.
1966 A possible selective factor in the evolution of fruiting seasons in tropical forest. ***Oikos*** 15: 274–281.
1971 Evolutionary aspects of fruit-eating by birds. ***Ibis*** 113: 194–202.

SPINAGE, C.A.
1962 Rinderpest and faunal distribution patterns. ***Afr. Wildl.*** 16(1): 55–60.

STEYN, D.G.
1929 Recent investigations into the toxicity of known and unknown poisonous plants in the Union of South Africa. ***15th Rept. Dir. Vet. Serv.*** pp 777–803.
1931 Geilsiekte and its detection in the field. ***Jour. S. Afr. Vet. Med. Assoc.*** Vol. 2: 23–26.
1933 The diagnosis, treatment and prevention of vegetable poisoning. ***J. S. Afr. V.M.A.*** 4(2): 193–201.
1934 ***The toxicology of plants in South Africa.*** C.N.A. pp 118–138.

STRUHSAKER, T.T.
1967 Ecology of vervet monkeys ***(Cercopithecus aethiops)*** in the Masai-Amboseli Game Reserve, Kenya. ***Ecology*** 48(6): 891–904.

SYDNEY, Jasmine
1965 The past and present distribution of some African ungulates. ***Trans. Zoo. Soc. Lond.*** Vol. 30, 397 pp.

TELLO, J.L.P.L. & VAN GELDER, R.G.
1975 The Natural history of nyala ***Tragelaphus angasi*** (Mammalia, Bovidae) in Mozambique. ***Bull. Amer. Mus. Nat. Hist.*** 155(4): 321–386.

TINLEY, K.L.
1964 Some observations on certain tabanid flies in north-eastern Zululand (Diptera: Tabanidae). ***Proc. R. ent. Soc. Lon.*** (A), 39(4–6): 73–75.
1966 ***An ecological reconnaissance of the Moremi Wildlife Reserve, Botswana.*** Okovango Wildlife Society, Johannesburg, Gothic, C.T.
1969a Dikdik ***Madoqua kirki*** in South West Africa: Notes on distribution, ecology and behaviour. ***Madoqua*** 1: 7–33.
1969b First air count of the buffalo of Marromeu. ***Veterin. Mocamb.*** 1(2): 155–170.
1969c The ecological limits of Gorongosa National park, Moçambique: And the maintenance of wilderness. ***Report to the Mocambique Govt.*** Fauna Branch of the Veterinary Services of Moçambique. Mim. 93 pp. + 45 figs.
1975 Habitat physiognomy, structure and relationships. In: ***Die Soogdiernavorsingsinstituut 1966–1975.*** Symposium proceedings. Publication of the University of Pretoria, New Series. No. 97: 69–77.

TINLEY, K.L. & SOUSA DIAS, A.H.G. DE
1973 Wildlife reconnaissance of the Mid-Zambezi Valley in Mocambique before formation of the Caborabassa Dam. ***Veterin. Moçamb.*** 6(2): 103–131.

VAN DER PIJL,
1975 The dispersal of plants by bats (Chiropterochory). ***Acta bot. neerl.*** 6: 291–315.
1972 ***Principles of dispersal in higher plants.*** Springer-Verlag. 2nd edt.

VASSE, W.
1909 ***Three years' sport in Mocambique.*** Pitman & Sons, London (translated from the French by R. & H.M. Lydekker).

VAUGHAN–KIRBY, F.V.
1899 ***Sport in East Central Africa.*** Rowland Ward, London.

VAZQUEZ–YANES, C., OROZCO, A., FRANCOIS, G. & TREJO, L.
1975 Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. ***Biotropica*** 7(2): 73–76.

VEDDER, H.
1966 ***South West Africa in early times.*** Cass, London.

VESEY–FITZGERALD, D.F.
1960 Grazing succession among East African game animals. ***J. Mammalogy*** 41(2): 161–172.
1965 The utilization of natural pastures by wild animals in the Rukwa Valley, Tanganyika. ***E. Afr. Wildl. J.*** 3: 38–48.

WEIR, J.S. & DAVISON, E.
1965 Daily occurrence of African game animals at water holes during dry weather. ***Zoologica Africana*** 1(1): 267–273.

WELLINGTON, J.H.
1955 ***Southern Africa: A geographical study.*** Vol. 1. Cambridge University Press, London.

WILSON, E.O.
1975 ***Sociobiology: The new synthesis.*** Harvard University Press.

WILSON, V.J.
1966 Observations on Lichtenstein's hartebeest ***Alcelaphus lichtensteini*** over a three-year period, and their response to various tsetse control measures in eastern Zambia. ***Arnoldia (Rhod.)*** 2(15): 14 pp.

CHAPTER 10 – CONSERVATION

Contents

10.1 INTRODUCTION / 175
10.2 PROTECTION & UTILIZATION / 176
10.3 MANAGEMENT / 179
  Habitats / 179
  Ungulates & Prime Movers / 180
  Carrying Capacities / 181

CHAPTER 10 – CONSERVATION

10.1 INTRODUCTION

The present and future survival of wildlife and natural areas in Africa depends almost exclusively on the favour of the rural human populations in everyday contact with them. All conservation measures will be fruitless until these populations are made to realize the value of these areas by obtaining immediate tangible benefit from them, and until they are involved in their protection and utilization as part of the regional economy in the widest sense. Simultaneously, there must be modification of traditional land-use to intensive practices, and of practical education for promoting sound husbandary of their habitats. These three facets are the crux to changing the deteriorating conservation trend on the continent.

In large parts of Africa, national parks, forest reserves, and other specially protected sites were given total preservation status without thought of further consequences. Such status was necessary in the initial stage to ensure that they were not encroached on by human activities. But after this critical point had been overcome, there has not been reassessment of the protected resources in the light of the natural processes of the landscape. Many of these resources, specially protected for their unique features, are now threatened internally by natural processes of succession.

In the larger national parks, protection has resulted in population explosions of the large herbivores with attendant damage to the habitats. Culling programmes have been initiated in some to balance the herbivore populations with the pasture resource. The products of these culling programmes, typically, are never tasted by the surrounding human populations. Either private enterprise, or the central goverment, are the sole receivers of any financial advantage from such programmes. The same consequences result from tourism in national parks – the surrounding human populations, apart from those who are employed in the park itself, obtain no material advantages from it. In this way natural reserves of all kinds have existed as islands and have not contributed directly to the regional economy.

In Africa there is a total of 91 species of wild ungulates, as compared to only 20 in South America, for example, (determined from Dorst & Dandelot 1970, and Keast 1972, Ch. 8 respectively). This unique assemblage of herbivores was, and still is in parts, the protein basis of the peoples of Africa, with the exception of certain groups such as the Maasai pastoralists. But decimation over vast areas in the name of development, tsetse control and unbridled hunting has reduced this resource, the remnants of which are protected today in national parks. But in many parks these wildlife populations are now threatened by their own overpopulation due to sanctuary effect, and the damage of this on their habitats.

Fraser Darling (1960) has given the most lucid exposition of the potential of the indigenous African ungulates as a bountiful resource. He makes the point (p. 133) that the necessity of cropping overpopulations of ungulates in most national parks, and the example of efficient utilization of the meat, in some "exposes the inadequacy of the notion that national parks should be absolute sanctuaries". Ledger (1964), Talbot ***et. al.*** (1965), and Laws ***et. al*** (1975), amongst others, corroborate this thesis.

National parks and nature reserves protect in available form many types of information and resources (for example, plant and animal protein) for direct or future use, either to increase the productivity of the adjacent human habitats, or, as living laboratories for research on the dynamics of natural systems. These dynamics include geomorphic and biotic succession, interrelationships, and interdependence. This information is fundamental for distinguishing natural changes in the environment from those induced by man. In sum, they are sites protecting the diversity and dynamism of man's environment for his continuing survival and stability, socially and biologically.

10.2 PROTECTION AND UTILIZATION

The natural areas of the African continent must be seen in their geographical, ecological and cultural context. Their diversity in each region or locality should be used in accordance with their intrinsic properties for a variety of criteria – from near total protection (eg. for endemics) to rural hunting areas. In this way natural areas and wildlife will be integrated as part of the whole man-land relationship, well-expressed by Dasmann's (1975) ***Conservation Alternative*** . In 1968 a plan was put forward for involvement of rural people with the management and protection of Gorongosa National Park. Surrounding Gorongosa are more than 30 000 peasant cultivators, part of whom are fully occupied with beekeeping, which depends on undamaged ***Brachystegia*** (miombo) woodlands. As the area is occupied by tsetse fly, nagana precludes the use of domestic stock, hence the people are mostly dependent for their protein on the wildlife resource. On the one hand, the plan included total utilization of a sustained yield culling programme for reducing the hippo and buffalo populations, and on the other, encouragement of the use of the miombo system within the park by the beekeepers. In this way a mutualism would be drawn from the people's dependence on protein supply and undamaged miombo, and the dependence of all on rural vigilance against commercial poachers, unrestrained fireing and hunting, and damage to forests and catchments by shifting and cash crop cultivation. In short, creative co-operation with the rural inhabitants was planned to the benefit of all aspects. Unfortunately political changes have left this plan (Tinley 1969) in limbo. However present interest and enthusiasm in the cultural and resource values of natural areas in Mocambique engenders optimism for rational land use and the maintenance of wilderness areas there (Paul Dutton pers. com.).

The dimension of any economic advantage to the surrounding human populations depends on the size of the natural area and its turn-over of products. A large national park with alluvial grasslands capable of producing more than 500 tonnes of meat a year from wildlife will have a far greater sphere of influence than a small natural area, especially if the latter is only capable of providing forest products. But the two resources are incomparable, because they are quite different. The sphere of influence of small natural areas would be far greater if there were many of them. The crux of any possible future increase in wildland rests on the success of the present natural areas in taking part in the regional economy.

Over the last 5 years an extremely successful red-meat production scheme, coupled with hunting, was initiated and built up by my brother, Charles Tinley, on Bester's Game Ranch of 6000 ha in the Zululand thornveld. In the first year (1972), 100 animals were culled for hunting only, fetching R7 500. In the second year, 350 animals for hunting only, fetched R25 000. In the third year 1 800 were culled for red-meat production plus hunting, providing R90 000 (of which 20% was from hunting).

In the fourth year (projected) 2 800 would be cropped, fetching R140 000 (Arnott 1974). A small, meat processing factory was built locally at a cost of R90 000 which was repaid in less than a year by the game resource. Hunting was not confined to trophy animals, thus a much larger clientele could be supported by the local ranch populations.

This unique venture has proved the value of game as a capital–less resource which can grow on its own turn-over. In Arnott's (1974) words "there's meat for Africa, if you're game". Vital now is for this expertise and experience to be spread across the continent.

In addition to the wild ungulate resource many other natural veld products from the savannas and forests are heavily relied on by rural people. An idea of the importance and multiplicity of veld products is shown by the following list: Animal foods (including fish), drought foods, honey, wax, bark tubes for hives, timber, thatch, firewood, twine, fruit, seeds, medicines, oils, dyes, gums and resins, spices, spinages, tuber foods, tannins, weaving materials, scents, hunting materials including poisons used in fishing.

It is clear that under high population demands only some of these products, for example thatch, can be reaped on a rational basis without harm to natural communities in parks. Whilst others, for example, timber for construction purposes, should be stopped as soon as possible and be replaced by timber from plantations. It is vital however, that each reserve is seen as a natural resource belonging to the regional community. In this way the people will get out as much as they put into the resources in the way of rational use and protection.

Rational use implies two fundamental requirements. Practical knowledge of the productivity and availability of the product and an authority which ensures that management methods are in accordance with these determinants. Thus practical studies are required to determine allowable take-off of certain products in addition to the maintainence of the various systems in each reserve.

A tree producing a special medicine, or high protein seed, requires study to ascertain what its life requirements and conservation status are; its method of dispersal, whether its productivity is associated with certain soils, slope aspects, other plant species, fire or climatic factors, etc. Can it be propagated most easily by cuttings or from

seed. Without this data it is possible to starve amidst plenty, or to eliminate the resources that are rare or localised. The strategy used for assessing the conservation status of communities or their components in Mocambique is summarised in Table 10.1.

As the destiny of natural areas and rural development, based on human and environmental values, are bound inextricably together, it is unacceptable to have wild ungulate populations confined to parks where their future is in jeopardy by over-population, whilst most of Africa suffers from chronic protein deficiency. What is required, is replenishment of wildlife populations over the vast relatively empty areas, and their sustained utilization as a food resource, thus expanding the size of productive natural areas to continental proportions.

Only by the development of an altruistic symbiosis (mutalism) between the surrounding rural people and the natural area (park, reserve, wilderness area etc.), by means of their benefitting from park products,will it be possible to obtain cooperation to regulate where people live or cultivate. In this way it will be possible to lessen the impact on resources such as water on which all are dependent. Concurrently, conservation organizations and others involved in the stewardship of parks require to be involved in demonstrating labour-saving and intensive cultivation methods (intermediate technology of Schumacher 1973), for example the use of trench cultivation in poor soils by which alternate layers of green cut grass and soil are used as trench refull. Such aid should be wholly empathetic with the life ways, cultures and religion of the tribes people, as clear on the why as on the how. Table 10.2 notes the aspects in which conservation organizations should become involved if they are to realize meaningful outward creative conservation.

TABLE 10.1

Strategy used for assessing the conservation status of ecosystems and communities in Mocambique

A. *Principal features*

1 Endemism & Rarity
2 Limits
3 Natural Processes: Dynamics & Vulnerability
4 Landscape Diversity
5 Quality
6 Danger
7 Priority

(1) ENDEMISM & RARITY

(a) Plants and/or animals endemic to a region or site.

(b) Non-endemic components occurring in small number, or confined to few sites. Determined as locally (i) abundant, (ii) common, (iii) scarce.

(2) LIMITS

Extreme limits of biogeographic or ecosystem outliers, remnants or initials (including centres of speciation). Barriers and filter bridges.

(3) NATURAL PROCESSES: DYNAMICS & VULNERABILITY

Successional status (trends, contraction, expansion), environmental dynamics and limiting factors (including geomorphic succession, storms, drought, fire, temperature changes particularly in shallow coastal waters, size and shape of community).

(4) LANDSCAPE DIVERSITY

The number of systems within a region or area.

Control: (i) topography, aspect, substrate and resultant climatic influences (interdigitation, overlap and confluence of ecosystems or their components).

(ii) continuum sequence (variation of essentially similar ecosystem due to environmental gradients).

(5) QUALITY

Intact/Disturbance Rating 1–5*

1 intact (undisturbed)
2 minor disturbance
3 medium disturbance
4 major disturbance
5 destroyed or altered beyond repair

(* including invasion or dominance by alien plants and/or animals)

(6) DANGER: FROM HUMAN ACTIVITIES

Examples include communications (roads, railways, powerlines, pipelines and canals etc), urbanisation (eg. spread in coastal areas, tourist impact through recreation facilities etc), lack of responsible land use planning, human settlement schemes, dams et. al.

(7) PRIORITY

Priority conservation for threatened species and/or natural systems including scenery.

Priority Action/Urgency Rating 1–5

1 Immediate
2 within 1 year
3 within 5 years
4 within 10 years
5 within 20 years

B. *Other features*

(1) Archeological Sites
(2) Geological Sites (unique outcrops and fossils)
(3) Historical & Cultural Sites
(4) Type localities of plants and animals
(5) Sufficient representative examples of plant or animal populations ("gene banks") on various environmental gradients (latitudinal, altitudinal etc).
(6) Breeding, nesting, roosting and resting sites (eg. seabirds).

TABLE 10.2

Seven spheres of conservation involvement

1 RURAL EDUCATION

- Change of content and emphasis to human and environmental values based on local or regional characteristics.
- Technological aids as the tools of man.

2 RURAL LAND USE

- Intensive agricultural methods introduced by way of their traditional systems (eg. VALLEY TRUST experiment in Natal using trench cultivation).
- Capital—less resource production (eg. protein from wildlife).
- Replacement of scarce resources, eg. firewood by establishment of plantations to save indigenous forests.
- Self -sufficiency in food production.

3 REGIONAL CO—RELATIONS

- Relation of the natural area to its region.
  - (a) Physical — ecosystem diversity, and the role of natural or accelerated landscape changes in the region on the dynamics of the natural area.
  - (b) Economic — in its complete sense, the maintenance and exchange of rural resources.

4 INVOLVEMENT OF RURAL PEOPLE

- Involvement with the protection and management of natural areas (a mutualism drawn from coactive benefits (3b)).

5 STATEWIDE INVOLVEMENT

- Statewide involvement in establishment of full spectrum of natural areas.
- Their relation on a state and local level.

6 MANAGEMENT OF NATURAL AREAS

- Internal management of natural areas based on geomorphic, hydrologic and ecological processes and trends determined by salient factor analysis (management based on causes not effects, using the visible responses as indicators).
- The internal dynamics must be correlated with the wider framework of changes occurring in the catchment basin or region in which the natural area occurs.

7 EXPERTISE DIVERSIFICATION

- Employment (and/or hire) of staff from the following fields unrepresented in southern African conservation organisations: Agriculture, Economics, Education, Engineering, Geography, Geomorphology, Forestry, Human Ecology (Anthropology), Hydrology, Landscape Planning, Pasture Science, Soil Science.
- Representatives from rural communities adjacent to natural areas of all kinds as local field propagandists and demonstrators (including: herbalists, beekeepers, hunters, fishermen, teachers).

10.3 MANAGEMENT

HABITATS

The entire thesis has focused down to a single point — the fundamental role of soil moisture balance in all ecological relations. In addition it has traced the evolution of the ecosystem to the present and these data have provided a template from which it is relatively easy to predict future changes. The areas undergoing the most rapid flux are where the canalization of floodplains is changing the soil moisture balance, permitting active invasion of woody plant communities. Whilst hippo and frugivores are the prime movers accelerating these processes, they would occur inexorably over the longer term anyway due to erosional lowering of landsurfaces to various base levels under the force of gravity.

Since its origin the Rift floor has been gradually drying out; aridification of a floodplain system and its replacement by a dry to mesic savanna-thickt-dry forest mosaic. The near extinction of the floodplain ecosystem as a natural process is destined in the near future (within several decades) unless remedial measures are taken. The final phases of woody predominance of the entire Rift floor is depicted in Fig 6.4. This stage will undergo further change but the processes are likely to be slow. Floodplain conditions will not return unless local, secondary or primary base levels are raised to cause renewed flooding and die back of woody cover.

There is thus a management dilemma — do we accept the elimination of floodplain grassland ecosystem and its replacement by wooded cover ecosystem (ie. exchanging hippo habitat for impala, and then bushbuck habitat) or do we 'stick our finger in the breached dyke' and damp down the inexorable process? Evidence presented in Ch. 6 (Process & Response) shows that in Gorongosa the greatest diversity of habitats and life occurs under present circumstances, but from now on the area will become more homogenous physiognomically and structurally (Fig 6.4).

In order to maintain this diversity a two-pronged strategy is required in mangement — habitat modification and maintenance, concomittantly with reduction, on a sustained yield basis (park product), of ungulate overpopulations. To only cull animal species is dangerous as the demise of one may change the pasture structure with far reaching results on the population trends of other animals. That culling alone is pointless, is easily demonstrated by trying to save Lichtenstein's hartebeest, for example, by culling any other ungulate species which may be competing with it for food, or by drastically reducing its predators. The preferred dambo ecotone habitat of this species may, however, be on the verge of extinction by natural geoecological successional processes, and this, not reduction of the other herbivores or predators, is what is required to be re-established, if the process has not already gone too far. Occlusion of habitats is a normal landscape process and where this occurs, mobile animal species can move further afield except in fenced-off areas. In the latter situation therefore, certain species are liable to extinction under the inexorable landscape changes, whilst others opportunistically take advantage of them and a build up in their populations result.

The control of a floodplain system is relatively easy compared to hill country, as the smallest blockage can restore the flood and ebb regime (Fig 10.1). The key sites are the local base level sills or "critical heights" which earlier formed the convexities enclosing each slack-basin, until they were breached (had the plug pulled out) releasing the water and thus resulting in loss of inundations. Several kinds of practical problems require careful attention as otherwise they would nullify any attempt to save the floodplains and slacks.

(1) Where possible dykes should be built across the top of nickpoints, with an overflow sluice course for flood waters to pass around the weir and enter the incised stream course from a lateral position.

(2) In places where the nickpoint has already eroded a gully into a slack, for example the Mucodza Marsh (Fig 10.2) and Chizunguzungu ***tando***, it is useless putting the weir at its head as the point is to restore the entire slack basin. Thus the weir must be constructed at the old local base level sill on the rim of the depression. Most important is that the section of gulley cut off above the weir must be filled with water or levelled with soil brought in from elsewhere, and packed in. Unless the nickpoint sites are smothered, active headward erosion will continue. If filled by water or soil, the nickpoint is effectively drowned and stopped.

(3) In slack-basin areas where floodwaters enter at one end and exit at the opposite side (eg. the Pungue new course through the Dingedinge slack Fig 10.3), it is wasted effort to close off the entrance as this will naturally seal itself off in flood periods,(if the ***exit*** is closed downstream)which will pond the waters in the slack basin. The entrance becomes a site of splay deposition, aggrades, and is fixed by reedbeds. Hence, the effective course of action is to close the exit by massive infill from adjacent banks using a bulldozer.

(4) A special case is the restoration of the plug action of alluvial deposits from the Muaredzi stream at the exit of the lake (Fig 10.3). Here a weir is required to completely close off the present Urema course to force the water level up sufficiently to flow out along an adjacent flood channel (a natural spillway). In this site a low slotted weir should be built into the ground so that its crest is close to the present spillway surface. The weir should be slotted in such a way that sufficiently high floods result followed by a gradual lowering of the lake — a slow ebb through the autumn and dry season.

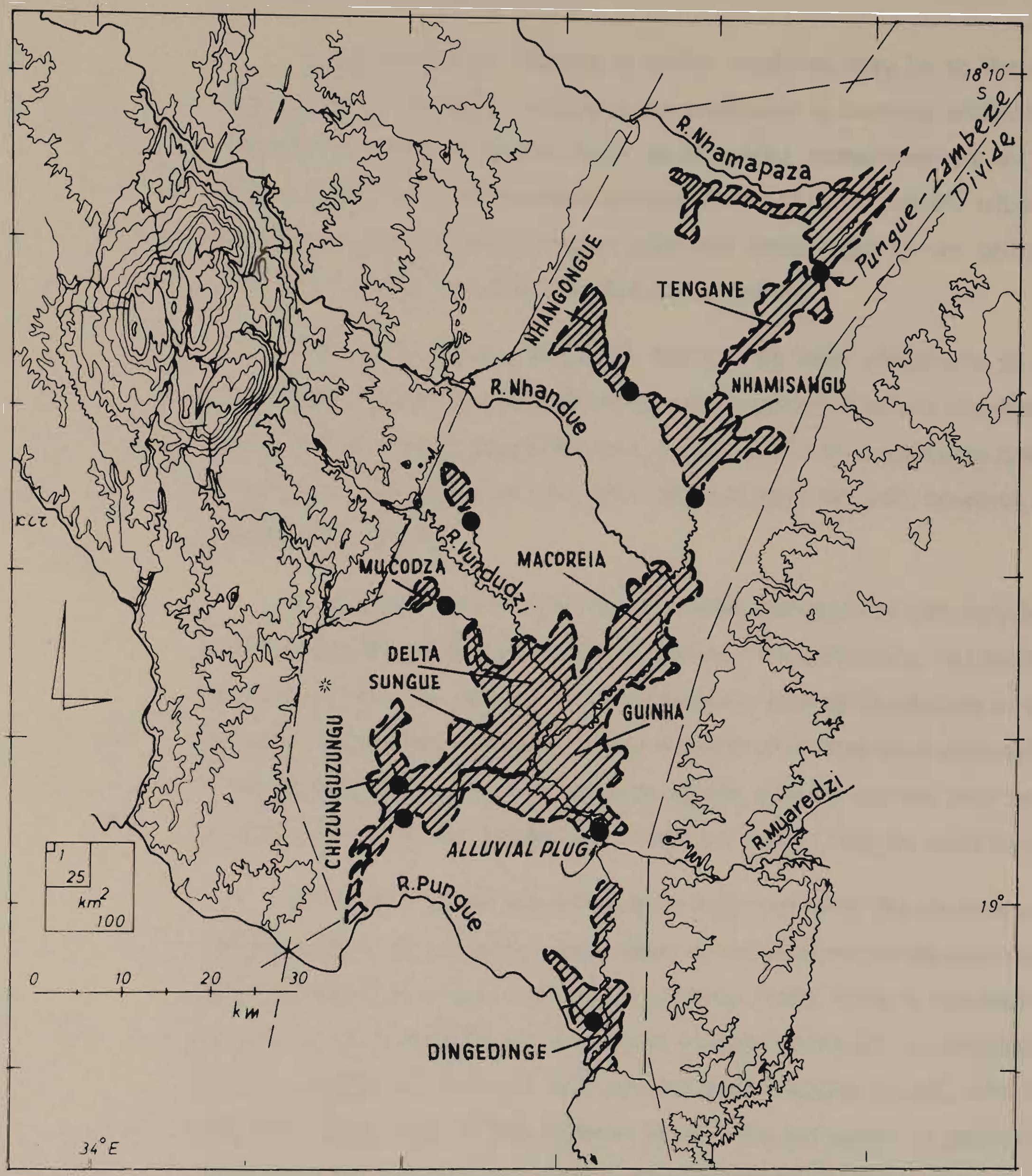


FIG 10.1 MANAGEMENT OF FLOODPLAIN GRASSLANDS BY REINSTATING THE CONVEXITES RESPONSIBLE FOR THEIR EXISTENCE

▨ FLOODPLAIN GRASSLAND AND SLACKS (TANDOS)

● CONVEXITIES FORMING CRITICAL HEIGHTS OR BASE LEVELS. SOME INCISED OTHERS THREATENED BY HEADWARD EROSION OF NICKPOINTS. THESE SITES TO BE RESTORED BY PERMANENT WEIRS.

The maintenance of a flood-ebb sequence is essential. Immediately west of the present Muaredzi confluence is another much deeper channel which requires total sealing off.

(5) Finally, the erosive power of the smallest drainage lines in flat country is usually grossly underestimated, resulting in washaways of all constructions. Where possible these constructions should be built in such a manner that they emulate as closely as possible the appearance of natural splay or bar deposits. Straight line should be avoided.

A first result of a restored higher flood level will be the die-off of areas of marginal floodplain woodland and expansion of the aquatic pasture grasses ***Echinochloa stagnina*** and ***Vossia cuspidata***. Chemical analysis of these grasses should help determine the length of inundation permissable in order to maintain pasture quality (vide Section 9.5).

These are some of the factors to be taken into account when a longer lasting flood and ebb sequence is required, and in this an ideal management tool would be a weir with a simple vertically adjustable notch.

UNGULATES AND PRIME MOVERS

The present management approaches in national parks either ignore the habitat problems and concentrate on culling over-populations of particular species, or attempt random bush clearing programmes although there is no hope of restoring grassland because of changed soil moisture balance. Effort has to be directed at restoring a high soil moisture as well, if cutting, fire or other methods are used in bush clearing. Unless this is done deep rooted savanna trees must, as a natural process, become the dominant cover.

Restoring the soil moisture balance in many sites particularly in plainsland, and old vlei or dambo areas, will by itself kill the scrub encroachment. Thus scrub clearing must be selectively applied in the field to land facets and soil profiles where effective hydromorphism can be restored. A valuable quick aid in delineating such sites is the use of air photos from twenty or thirty years ago in which natural distribution patterns of grassland, forest and savanna can be seen,as it was then as yet little changed by poor land use practises.

Other management approaches such as culling the top of the food pyramid, predators for example, is possibly justifiable to protect rare or endangered species. However, it is impossible to predict what subsequent chain of events may follow such a move as new interactions are superimposed over the natural processes and responses at play, and habitat restoration may well be all that is required in any case.

If culling is to be taken to its ludicrous conclusion, it would be to mount a campaign against all frugivores as they are the prime movers in afforestation and thus in the extinction of grasslands!

As distasteful as mowers or cutter machines may be to the wilderness atmosphere of a national park, cutting is far preferable to burning, which depresses valuable soft leaved, sensitive grasses, such as ***Urochloa mosambicensis*** in favour of coarse thatch grasses, and it compounds encroachment of scrub. Ideally tribal people ***en masse*** should be employed to cut thatch grass and encouraged to use, sell or barter this product for other requirements (another park product).

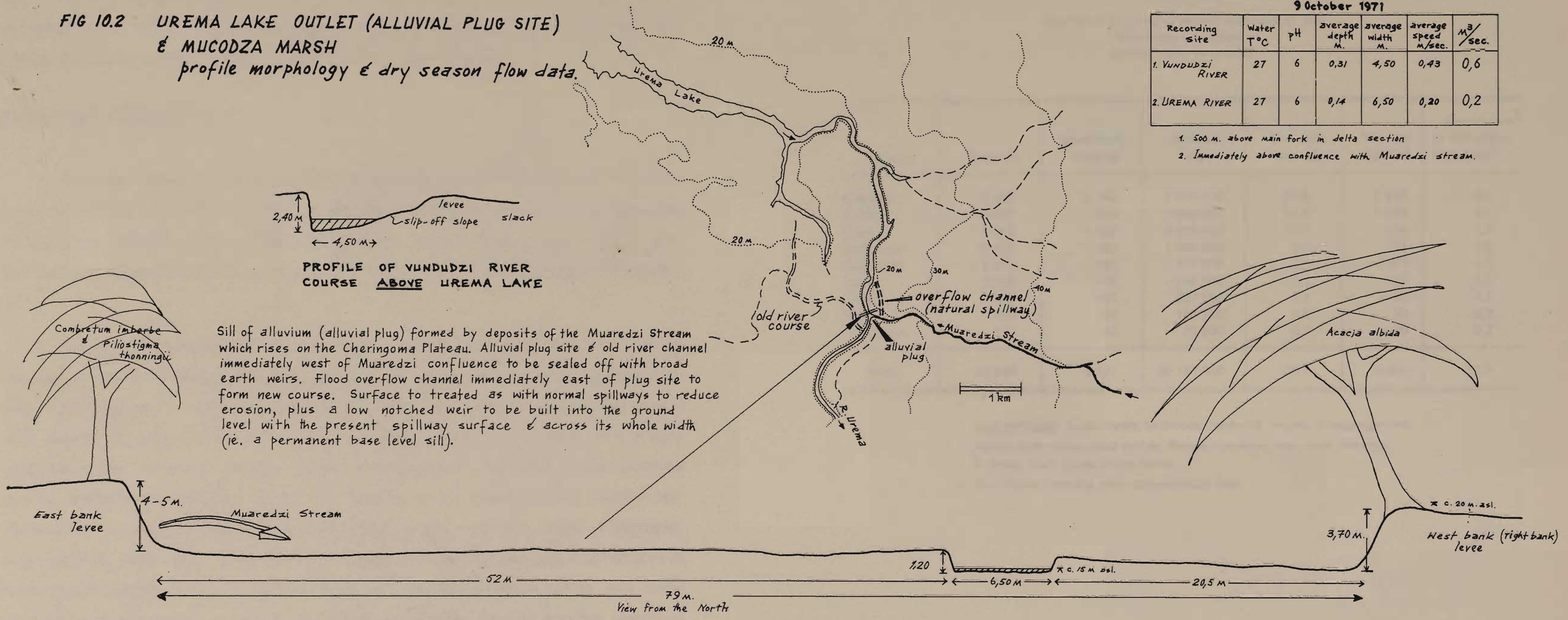
The only manner in which fire can be used effectively to open up heavily wooded savanna, or to maintain an existing grassland is where ungulate populations are sparse, so that there is adequate rank regrowth and thus adequate fuel for another, late season, fire. The selection for rank fibrous pastures will, however, further mitigate against most grazers.

In the final count meaningful habitat management can only be effectively carried out where ungulate populations are low. Thus diversity, not quantity, is a primary requirement in areas where no buffer systems, such as floodplains or slack pastures are available. Where this habitat,or its equivalents on a small scale such as pans, are present in abundance, large numbers of single species such as buffalo may be maintained, according however to the capabilities of the dry season riverine conditions.

All wild ungulate stocks must be balanced with the riverine zones available in the dry season, ie. stocking rates related to dry season riverine carrying capacity, which does not result in undue destruction of these zones. What is required then is for a pan system in the hinterland to be restored (where breached), or deepened to hold water for the duration of the rains and autumn until midyear (June), and then dry out,forcing the herds back to the riverine zones. The provision of permanent waterpoints away from the riverine zones effectively spreads the 'riverine zone' allowing for greater build up of species which are forced back to the natural riverine areas anyway, due to lack of suitable pasture,where they multiply the impact by adding to the populations already dependent there.

Hence, in any landscape,ungulate populations must be kept at the level at which natural riverine zones can support them in the dry season without massive destruction of these sites. This requires geohydrological analysis of the drainage in slack pastures on either side of the actual stream or river beds. If slacks are connected at the lower end by drainage channels then these pastures are on their way to becoming (if not already) only seasonally productive in the rains instead of through the "worst" time of

FIG 10.2 UREMA LAKE OUTLET (ALLUVIAL PLUG SITE) & MUCODZA MARSH
profile morphology & dry season flow data.



PROFILE OF VUNDUDZI RIVER COURSE ABOVE UREMA LAKE

Sill of alluvium (alluvial plug) formed by deposits of the Muaredzi Stream which rises on the Cheringoma Plateau. Alluvial plug site & old river channel immediately west of Muaredzi confluence to be sealed off with broad earth weirs. Flood overflow channel immediately east of plug site to form new course. Surface to treated as with normal spillways to reduce erosion, plus a low notched weir to be built into the ground level with the present spillway surface & across its whole width (ie. a permanent base level sill).

PROFILE OF UREMA RIVER COURSE IMMEDIATELY ABOVE THE MUAREDZI STREAM CONFLUENCE

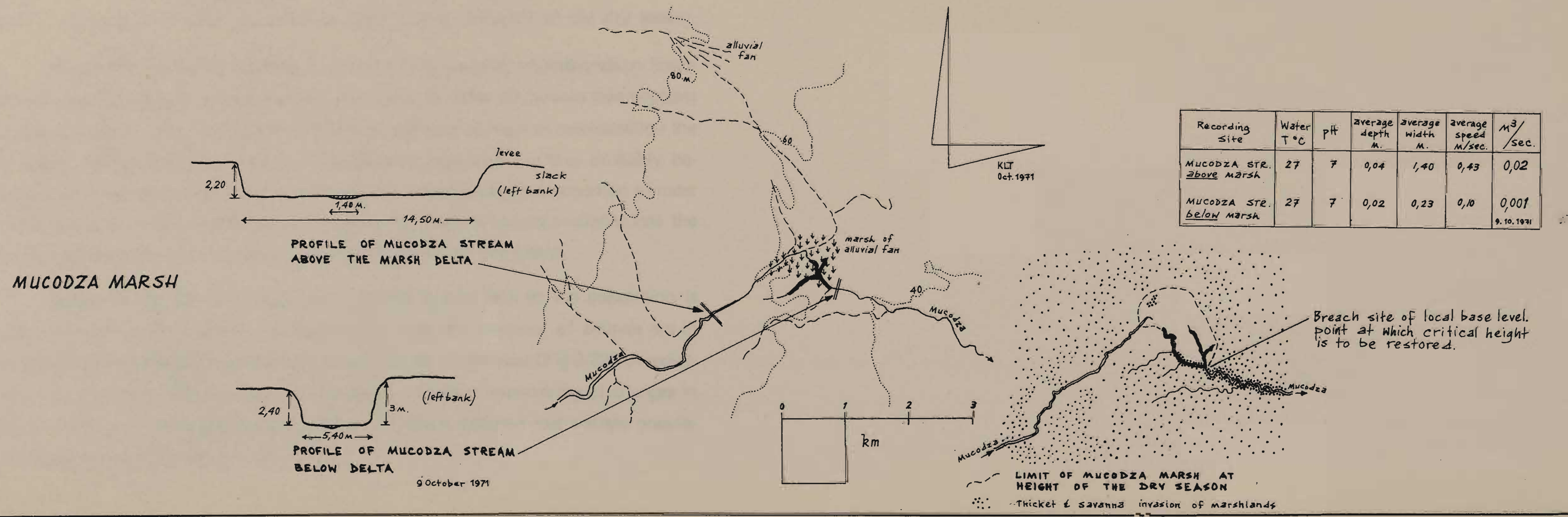
9 October 1971

STREAM VOLUMES AT PEAK OF DRY SEASON PERIOD
9 October 1971

Recording site	Water T°C	pH	average depth m.	average width m.	average speed m/sec.	m³/sec.
1. VUNDUDZI RIVER	27	6	0,31	4,50	0,43	0,6
2. UREMA RIVER	27	6	0,14	6,50	0,20	0,2

1. 500 m. above main fork in delta section
2. Immediately above confluence with Muaredzi stream.

MUCODZA MARSH



PROFILE OF MUCODZA STREAM ABOVE THE MARSH DELTA

PROFILE OF MUCODZA STREAM BELOW DELTA

9 October 1971

Recording site	Water T°C	pH	average depth m.	average width m.	average speed m/sec.	m³/sec.
MUCODZA STR. above marsh	27	7	0,04	1,40	0,43	0,02
MUCODZA STR. below marsh	27	7	0,02	0,23	0,10	0,001 9. 10. 1971

LIMIT OF MUCODZA MARSH AT HEIGHT OF THE DRY SEASON

Thicket & savanna invasion of marshlands year. The crux of all management therefore rests on an appreciation of geomorphic processes, in particular the fluvial aspects which provide (slacks) or eliminate (by nickpoint breaching) high primarily productivity in the dry season.

CARRYING CAPACITIES

Biomass figures of the principal large ungulates is given in Table 10. 3. Using a standard stock unit (SSU) of 454 kg mass, the stocking rate at the time of study was of the order 1 SSU/6–8 ha on the 3650 km^2 area of Rift Valley floor. If the dry season carrying capacity is as much as half of this, then the Rift floor is grossly overstocked.

As should be clearly evident from the plexus of pasture responses and influences explored in Section 9.5, this aspect remains the most glaring gap in the necessary knowledge for the formulation of a meaningful management programme, as pasture quality at various times of the year and under different circumstances is totally unknown. The prevalence of poor physical condition in the three largest biomass species, elephant, buffalo and hippo, is indicative of the inadequacy of suitable pastures in the dry season, despite its superabundant cover. The restoration of hygrophilous pastures, which are the primary food base throughout the year, over extensive areas would greatly alter the picture from the present situation where only some 40 km^2 of green pasture is left at the height of the dry season. Another unknown factor is the total area occupied by the tall thatch grasses that are prevalent in many sectors. Together with the dried out (salinized) floodplain pasture, these too, would have to be subtracted from the effective total carrying capacity of the dry season.

Myre & Antão 1972) estimate that the carrying capacity of grasslands on floodplain alluvium is between 3 and 5 ha/SSU. Reference to Table 10.2 shows that elephant are already close to 1/km^2 on the entire Rift floor, without taking into consideration the dry season riverine carrying capacity. The elephant population is thus probably beyond the safe carrying capacity, as emphasized by the poor physical condition of most of the matriarch herds. Restoration of green slack pastures would probably tide the present elephant population, in better condition, through the dry season.

Hippo are obviously overpopulated, as the greater part of the population is confined to the grazing around the Urema lake, and the majority of animals are in chronically poor physical condition for three-quarters of the year (Fig 9.22). A reduction of at least half the population is indicated. However, monitoring of changes in grass structure and possible differential impact on the wildebeest and buffalo populations in particular would have to be recorded.

TABLE 10.3

Biomass of principal large wild ungulates in the Gorongosa ecosystem.
(derived from air counts)

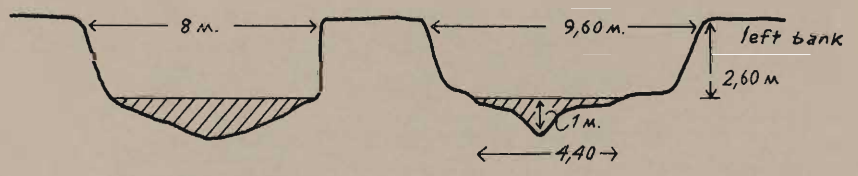
Species	Total No.	Mean body mass kg	Biomass kg	% of total biomass	Biomass kg/km^2	Density/km^2 in Rift Valley (3659 km^2) *
Elephant	2 200	3 182	7 000 400	34,6	1 918	0,6
Buffalo	14 000	500	7 000 000	34,6	1 918	4,0
Hippo	3 000	1 136	3 408 000	17,3	934	1,0
Wildebeest	5 500	182	1 001 000	4,9	274	1,5
Waterbuck	3 500	205	717 500	3,5	197	1,0
Zebra	3 000	216	648 000	3,2	178	1,0
Eland	500	455	227 500	1,1	62	0,1
Sable	700	159	111 300	0,5	30	0,2
Hartebeest	800	92	73 600	0,3	20	0,2
Totals	33 200	6 127	20 187 300	100,0	5 531	10,6

(not included: Kudu, nyala, bushbuck, reedbuck, impala, klipspringer, red duiker, grey duiker, blue duiker, Sharpe's grysbok, suni, oribi, warthog, bushpig, black rhino, white rhino)

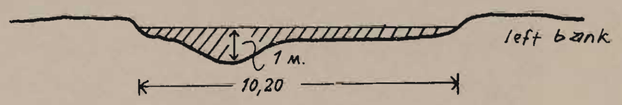
- Rift Valley floor the main concentration area

FIG 10.3 DINGEDINGE SLACK MARSHES AT THE UREMA-PUNGUE CONFLUENCE.

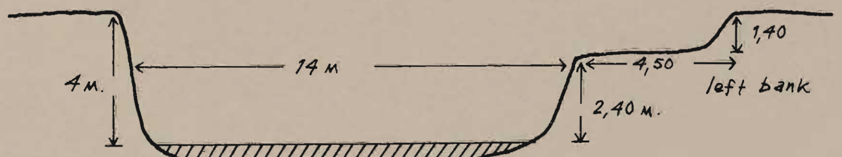
profile morphology & dry season flow data of Pungue 'new course' incising the marshlands through a breached levee.



1 ENTRANCE OFF THE MAIN RIVER OF NEW PUNGUE COURSE BISECTING THE DINGUEDINGUE MARSHLAND. VIEW UPSTREAM. 9 October 1971



2 NEW COURSE IN MARSH SECTOR.



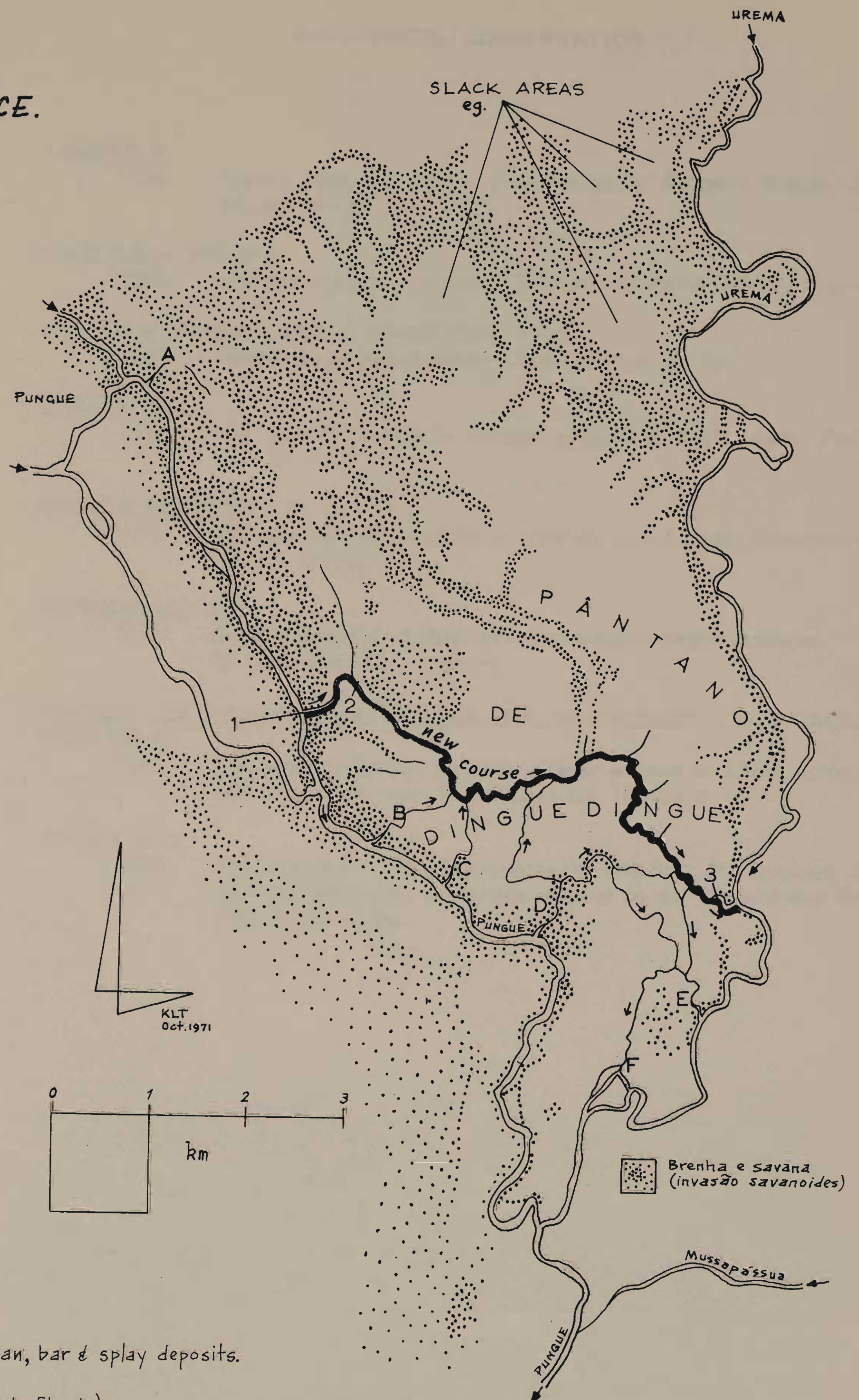
3 JUNCTION ZONE OF NEW COURSE WITH UREMA RIVER.

Recording Site	Water T °C	pH	average depth m.	average width m.	average speed m/sec.	m³/sec.
NEW COURSE IN MARSH SECTOR [see 2 above]	27	6	0,48	10,20	1,0	5,0 10.10.1971

▨ savanna & thicket invasion of slacks on faintly convex surfaces formed by fan, bar & splay deposits.

A-D Breached levee sites now sealed by splay deposits (functional only during high floods).

3, E, F Sites to be sealed off by earth weirs, damming the slacks which will result in natural plugging of upriver levee breaches by splay & bar deposits during floods.



THE DINGUE DINGUE MARSHLAND IN THE PUNGUE-UREMA CONFLUENCE AREA OF GORONGOSA NATIONAL PARK.

Buffalo is the third species which show extremely decimated physical condition, accompanied by die-offs during the torrid pre-rains period between August and October. Though elephant are mixed feeders, utilizating a large proportion of browse in the Gorongosa ecosystem, they and buffalo are heavily reliant on the last green zones of slacks and riverine strips during the dry season. From large scale maps it is estimated that a maximum of 40 km^2 of green pasture is left at the height of the dry season in the entire Rift floor area within the ecosystem limits (ie. only 1%, due to canalization of slack pastures). The major grazing population is confined largely to this 1% base at the height of the dry season. If unseasonal rain or fire brings a flush of regrowth to other pastures, the herds move out to these and return to the green zone base once withering occurs.

Until the hygrophilous pastures have been restored by blocking off the breach sites, and a through-the-year chemical analysis is made of the browse foods and the important pasture grasses listed in Table 9.3 under different conditions, it is vital that reduction of hippo and buffalo numbers is commenced and their products utilized before crashes in their populations results in a large scale waste of animal protein. It would be in vain to make recommendations on carrying capacities of these and other ungulates without a periodic monitoring programme of the response in condition of the animals and pasture to the effects of culling and habitat manipulation, as well as their influences on other species. In this, the use of a helicopter for accurate air coverage of animal populations and habitats is fundamental.

REFERENCES / CONSERVATION

ARNOTT, B.
1974 There's meat for Africa, if you're game. ***Farmer's Weekly*** Sept. 4th. pp. 16–19.

DARLING, F. FRASER
1960 Wild life husbandry in Africa. ***Scientific American*** 203 (5): 123–134

LAWS, R.M., PARKER, I.C.S. & JOHNSTONE, R.C.B.
1975 ***Elephants and their habitats.*** Clarendon Press, Oxford.

LEDGER, H.P.
1964 The role of wildlife in African agriculture. ***E.Afr. Agric. For. J.*** 30: 137–141.

MYRE, M. & ANTÃO, L.R.
1972 Reconhecimento pascícola ao Vale do Save. ***I.I.A.M. Comunicaçoes*** No. 75, 180 pp.

SCHUMACHER, E.F.
1973 ***Small is beautiful: A study of economics as if people mattered.*** Blond & Briggs Ltd., London.

TALBOT, L.M., PAYNE, W.J.A., LEDGER, H.P., VERDCOURT, L.D. & TALBOT, MARTHA H.
1965 ***The meat production potential of wild animals in Africa.*** Commonwealth Agric. Bureaux Techn. Com. No. 16, 42 pp.

TINLEY, K.L.
1969 The ecological limits of Gorongosa National Park, Mocambique: And the maintenance of wilderness. ***Report to the Mocambique Govt.*** Mim. 93 pp. 45 figs.

PLATE IX MIOMBO AMBIENT – *BRACHYSTEGIA* SAVANNA WOODLAND

Pre-rain spring aspect with post-fire flush of grass stratum and mosaic red leaf flush of canopy trees.

PLATE XI ECOLOGICAL INTERDEPENDENCE & DYNAMICS OF THE GORONGOSA ECOSYSTEM

Mountain rains shed to Rift Valley (water in foreground), floodplain grasslands dependent on seasonal flooding, ungulates dependent on grasslands and water; incision, drying out and savanna invasion along levees and other convexities (foreground).

Showing headward eroding donga which has incised the local base level sill responsible for the genesis and maintenance of the marsh.

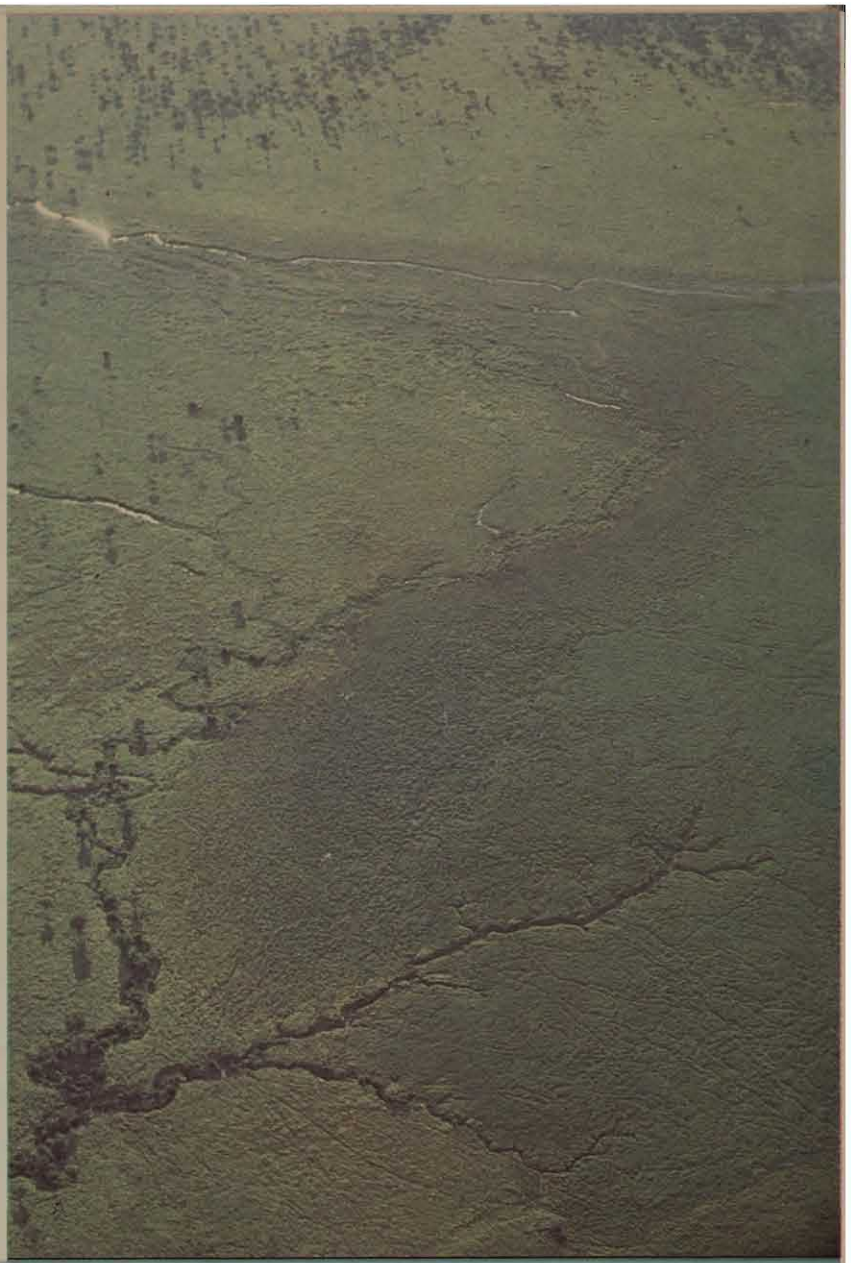


PLATE XII NORTHERN WOODED SECTOR OF UREMA PLAINS.

Depicting savanna invasion of drained slack basins, their original outlines still discernable, (ie. later stage of process shown in Plate X). View to the southwest of the Bunga Inselbergs and Gorongosa Mountain.