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The effect of drought on the large mammal populations of Zambezi riverine woodlands

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(With 16 figures in the text)

Large mammals were counted in Zambezi alluvial woodlands and on the adjacent ecotone in the north of Mana Pools National Park, Zimbabwe, from April 1981 until October 1989. Densities of all large herbivores on the alluvium in the daytime increased during the dry season. Year-to-year variation was studied by comparing end-of-dry-season densities. Flooding of the Zambezi River, controlled by Kariba Dam 100 km upstream, ceased in 1981 and the densities of all species on the alluvium declined in 1982. Rainfall was low in 1982 and very low in 1983 and 1984. The density of buffalo in the study area declined, owing to high mortality and a change in habitat utilization (buffalo herds spent more time in the south of the park). Densities of other species were high during the drought, but the densities of waterbuck, kudu, eland, bushbuck and warthog declined in 1985. Zebra density declined on the ecotone, but not on the alluvium. The densities of eland and kudu increased in 1986 and 1988, respectively, but the densities of the other species were still low in 1989. Impala density on the alluvium in October was related to rainfall during the preceding wet season and was high in drought years. Elephant density declined after a management cull. Rhinoceros density decreased by > 90% during the 1985/6 wet season, as a result of poaching and captures. The long-term decline in the densities of grazers was probably due primarily to the cessation of flooding by the Zambezi River, rather than to low local rainfall in some years. During the drought, the large grazers (e.g. buffalo) died before the smaller grazers (e.g. warthog). Waterbuck density declined less than the density of other grazers, because waterbuck could cross to vegetated sandbanks in the Zambezi River.

Contents

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Introduction

The riverine woodlands in the Middle Zambezi Valley are an important dry season concentration area for numerous large mammals of a wide variety of species, ranging from warthog to elephant. (Latin names are listed in Table I.) Many animals in the area between the Zambezi River and the Zambezi escarpment, 50 km to the south, move towards the river in the dry season. Jarman (1972) described how, during the 1960s, the density of all large herbivores in the Zambezi alluvial woodlands increased as the dry season progressed. At the start of the rains, these animals dispersed back into the woodlands to the south. The extent of these seasonal movements is largely unknown, except for elephant and buffalo. Elephant cows which used the Zambezi riverine woodland in the dry season usually stayed within 20 km of the Zambezi River during the rains (Dunham, 1986), but buffalo moved further, towards the base of the escarpment (Swanepoel, 1989).

The ecology of the valley was changed in 1958 when completion of the Kariba hydroelectric dam altered the flooding regime in the downstream riverine vegetation. It has been claimed that the habitats in the eastern Middle Zambezi Valley were degraded by large mammals and too frequent fires even before 1958 (Savory, 1961, 1965), although it is now known that these claims were exaggerated (Dunham, 1989*a*). Nevertheless, they led to the culling of thousands of large mammals. Large herbivores using the Zambezi riverine woodlands were first counted with repeatable methods in 1965, prior to the culls (Jarman, 1972).

Insecurity during Zimbabwe's pre-independence war prevented both management and research in the Zambezi Valley throughout the late 1970s. By 1981, large mammals had not been culled for several years. The purpose of this study was to record the densities of large mammals using the Zambezi alluvial woodlands during the 1981 dry season; to compare these densities with the densities recorded during 1965, before culling commenced; and to record annual changes in the densities from 1981 until 1989.

Study area

Mana Pools National Park (between 15° 40′ and 16° 20′S and 29° 08′ and 29° 45′ E) in northern Zimbabwe experiences a single rainy season which extends from November to April. Mean

TABLE I

Truncation distances used in the line transect analyses. Animals were excluded from the analyses when the perpendicular distance of the group from the transect exceeded the truncation distance

Species	Truncation distance (m)
Elephant *Loxodonta africana* Blumenbach	400
Buffalo *Syncerus caffer* Sparrman	400
Black rhinoceros *Diceros bicornis* L.	400
Eland *Taurotragus oryx* Pallas	400
Zebra *Equus burchelli* Gray	400
Waterbuck *Kobus ellipsiprymnus* Ogilby	400
Lion *Panthera leo* L.	400
Spotted hyaena *Crocuta crocuta* Erxleben	400
Impala *Aepyceros melampus* Lichtenstein	250
Warthog *Phacochoerus aethiopicus* Pallas	250
Greater kudu *Tragelaphus strepsiceros* Pallas	200
Baboon groups *Papio ursinus* Kerr	200
Bushbuck *Tragelaphus scriptus* Pallas	150
Side-striped jackal *Canis adustus* Sundevall	150
Vervet monkey groups *Cercopithecus aethiops* L.	150
Leopard *Panthera pardus* L.	50

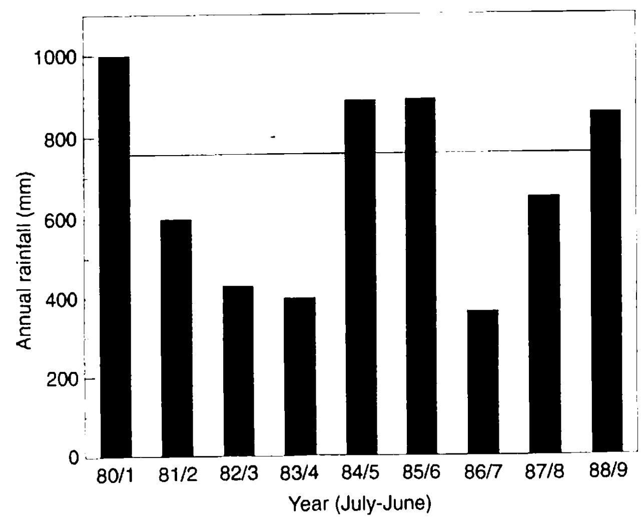


FIG. 1. Annual rainfall from July 1980 to June 1989 in the Zambezi alluvial woodland in Mana Pools National Park, Zimbabwe (Recording Station: Mana Pools, Zambezi). > 90% of rain falls during November to March inclusive. The horizontal line indicates the 21-year-mean annual rainfall.

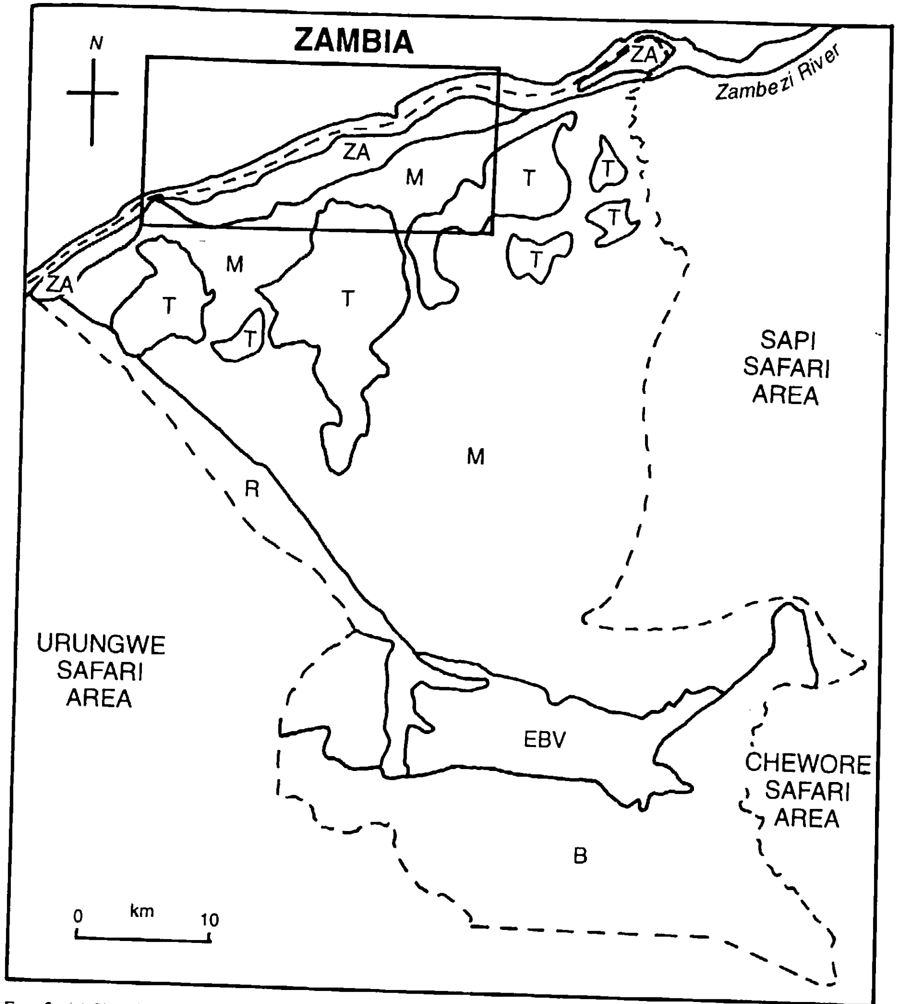


FIG. 2. (a) Simplified vegetation map of Mana Pools National Park, Zimbabwe. The dashed line indicates the park boundary. The Zambezi River forms the international boundary with Zambia. The principal vegetation types are: Zambezi alluvial woodland (ZA); *Combretum* deciduous thickets (T); mopane woodland (M); escarpment base vegetation (a complex mixture which includes *Acacia-Lonchocarpus* wooded grassland and dense stands of *Combretum* bushes) (EBV); riverine woodland (R); and *Brachystegia* scrub woodland (B). The northern limit of the *Brachystegia* scrub woodland is the Zambezi escarpment. The study area is boxed and shown in more detail in Fig. 2 (b). (b) Map of the study area, the Zambezi alluvial woodland in the north of Mana Pools National Park. Dashed lines indicate tracks used for counting. The southern-most solid line is the boundary between the alluvial woodland, and the mopane woodland and sodic grassland. The dotted lines approximately divide the alluvial woodland into the three sections used in the study of habitat selection.

annual rainfall is 758 mm, but this study included three successive years of below-average rainfall (Fig. 1). July is the coldest month (mean minimum temperature 10·7 °C) and November the hottest (mean maximum temperature 39·6 °C). The park covers 2196 km^2 (Fig. 2a), but is part of a larger block of Parks and Wild Life land covering over 10 000 km^2. Outside the park, this area is used mainly for sport hunting of large mammals.

The alluvial woodland (about 55 km^2) in the north of the park constituted part of the floodplain and river terraces of the Zambezi River until completion of Kariba Dam 100 km upstream of the park. The extent and duration of flooding are now controlled mainly by water release through floodgates in the dam. There were annual floods from 1962 to 1981, except in 1973. Floodgates were last open from February to June 1981. Flooding occasionally occurs due to runoff into rivers which enter the Zambezi below Kariba Dam. This happened once during the study, in January 1989.

The composition of the woodland varies along the alluvium. *Acacia albida* Del. trees characterize the alluvial woodland, but their contribution to the tree layer increases towards the east (Fig. 2b). The eastern alluvium is low-lying (relative to the level of the Zambezi River) and covered by '*A. albida* woodland' (Dunham, 1989*b*). The herbaceous layer includes more perennial grasses than elsewhere on the alluvium. '*A. albida* dominated mixed woodland' or 'mixed riverine woodland' cover the higher, central alluvium. Here, the trees include *Kigelia africana* (Lam.) Benth., *Lonchocarpus capassa* Rolfe, *Trichilia emetica* Vahl, *Combretum imberbe* Wawra and *Ficus zambesiaca* Hutch. The herbaceous layer is dominated by annual grasses and, in years of high rainfall, forbs. 'Mixed riverine woodland', often with abundant shrubs, covers the highest, western section of alluvium. Throughout the alluvial woodland, there is little regeneration by tree species. Often, the alluvium is locally called the floodplain (e.g. Jarman, 1972). The frequency of grass fires on the alluvium declined after 1958, when people resident in the area were removed, and there were no fires during this study.

A band of sodic soils separates the alluvium from the dry, deciduous *Combretum* spp. thickets on deep aeolian sands to the south. *Colophospermum mopane* Kirk ex Benth woodland is the principal vegetation on the sodic soils, but, in places, the soils are so highly sodic that no woody

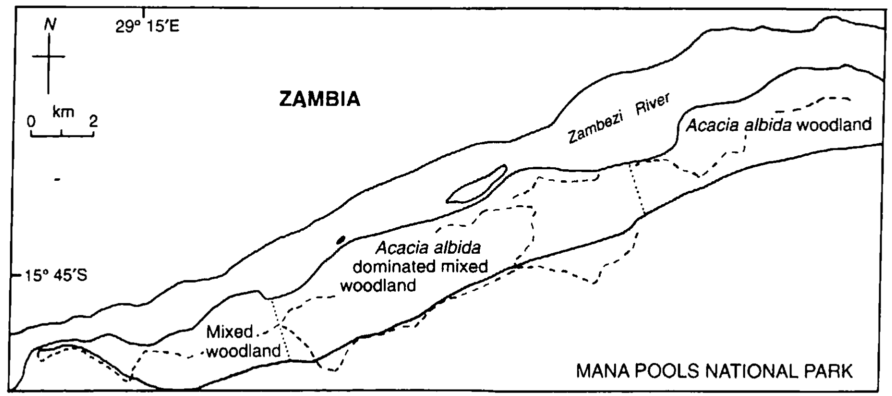


FIG. 2b

TABLE II

Sampling intensity during road strip counts on Mana Pools floodplain and alongside it. The total distance driven in each habitat is given, together with the numbers of times the routes were replicated (k). Except where indicated, the distance was equally divided between mornings and afternoons. The numbers in parentheses refer to impala replicates for those months. (Although impala were counted along all routes, the numbers of groups seen along eight replicates occasionally exceeded the capacity of the program DISTANCE and therefore densities were calculated using data from only six replicates during these months)

Year	Month	k: Floodplain	k: Ecotone	Total Distance (km): Floodplain	Total Distance (km): Ecotone
1981	April	9	7	170·70	89·19
1981	July	8	8	168·39	128·95
1981	October	6	6	135·24	99·90
1982	October	8	8	176·48[a]	133·20
1983	July	10	10	225·40	166·50
1983	October	10	10	225·40	166·50
1984	July	8	8	180·32	133·20
1984	October	8 (6)	8	180·32 (135·24)	133·20
1985	October	8	8	180·32	133·20
1986	October	6	6	135·24	99·90
1987	October	8 (6)	8	180·32 (135·24)	133·20
1988	October	8	8	180·32	133·20
1989	October	8	8	180·32	133·20

[a] Mornings 90·16 km, afternoons 85·32 km

plants can grow and only short grasses survive. In the thickets, little grass grows and the shrubs are leafless throughout the dry season, with leaf flush following the start of the next rains. South of the thickets grows *C. mopane* woodland on slightly sodic or non-sodic soils. Here, woodland structure and grass growth are spatially variable, dependent on soil depth, texture and sodium concentration. All rivers in the park, except the Zambezi, are dry soon after the rains end.

Over 12 000 large mammals (> 11 000 impala, > 900 buffalo, > 350 waterbuck, > 330 elephant, > 180 zebra and 36 kudu) were culled in the park from 1969 to 1976 inclusive. Elephants were culled on the alluvium during 1985 (Dunham, 1988) and in the south of the park in 1988, but otherwise few animals were culled during the 1980s.

Methods

Data collection

Large mammals were counted by 1 or 2 observers standing in the back of a 4-wheel-drive vehicle which was driven at about 15 km $hour^{-1}$ along existing vehicle tracks. Counts were made in 2 habitats: the Zambezi alluvial woodland; and the mopane woodland and sodic grassland alongside the alluvium. The mopane woodland and grassland were called the 'mopane ecotone' by Jarman (1972) (although the border between the riverine woodland and adjacent vegetation types is distinct). Nevertheless, for the sake of brevity, the term ecotone is also used here. The ecotone is about 30 km long (Fig. 2b). For the purpose of comparing densities on the floodplain and ecotone, the area of the ecotone can be taken as about half that of the alluvium, i.e. about 25 km^2.

I was always the principal observer. When an animal or a group was seen, the vehicle was stopped: the

animals in the group were counted, always using binoculars; the habitat in which the animals were present was noted; the distance from the vehicle to the geometric centre of the group (sighting distance) was measured with a Wild TMO rangefinder (operating range 35–500 m); and the angle between the centre-front of the vehicle and the line from the vehicle to the geometric centre of the group (sighting angle) was measured with a large compass rose mounted behind the vehicle cab. All records referred to the position of the animals when they were first seen. The perpendicular distance of each group from the road was calculated as the product of the sighting distance and the sine of the sighting angle. A few groups which were clearly more than 400 m (perpendicular distance) from the road were not recorded. For the purposes of this study, a single animal was regarded as a group with a size of one.

The age and sex composition of each group was noted when possible, except in 1982. Juveniles were animals aged under 1 year. The composition of impala groups was not recorded: during October, when most counts occurred, juvenile female impala were nearly 1-year-old and not readily distinguishable from adult females. Warthogs noted as yearlings in October were born during October or November of the previous year. Following Jarman (1972), individual monkeys and baboons were not counted, but groups were recorded. The length of each track was measured with the vehicle odometer and a mean length was calculated for each road at the end of the study. Counts were conducted over 2–3 weeks during April, July and October 1981; July and October of 1983 and 1984; and October of 1982, and 1985 to 1989. From October 1981, a standard set of tracks was driven, with each road covered usually 8 times (Table II). For each road, the number of drives was equally divided between mornings and afternoons. During October, counts were usually made between 06:00 and 10:30 h, and 15:00 and 18:00 h.

The accuracy of the rangefinder was checked before each survey by sighting 10 times on a pole at the end of a 100 m tape. No rangefinder was available during July and October 1981 and so sighting distances were estimated. Later, a test showed that there was no significant difference between estimated distances, up to 500 m, and those recorded with a rangefinder ($n = 21$, $r = 0{\cdot}96$, slope $b = 1{\cdot}01$, intercept $a = -2{\cdot}1$; b not significantly different from 1·00, $t = 0{\cdot}209$).

Using existing tracks as transects is not ideal, but it was undesirable to establish new, randomly-placed roads in a national park solely for this study.

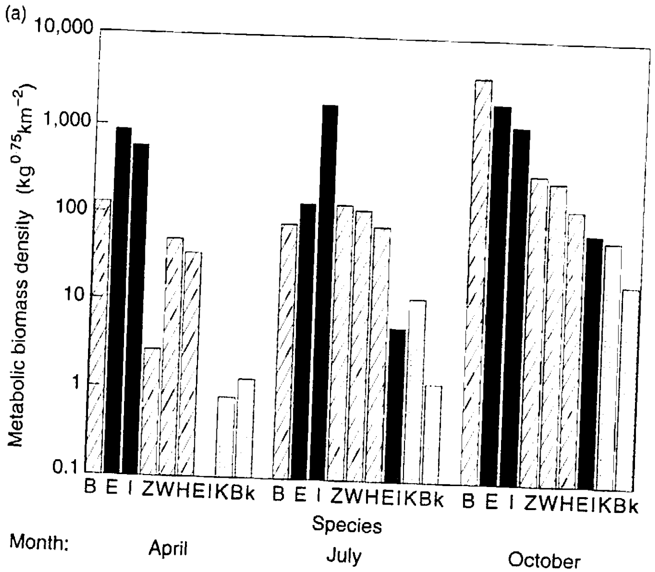
Data analysis

Densities were calculated separately for 2 habitats: the alluvial woodland; and the mopane woodland and sodic grassland alongside the alluvium (= ecotone).

For each survey month, data collected along the different tracks in a single habitat were combined to produce replicated samples (equivalent to transects). Transect 1 was formed by combining the data from the first morning drive along each road (disregarding the day of the month when the roads were counted). Transect 2 was formed by combining the data from the first afternoon drive along each track. Transect 3 was formed by combining the data from the second morning drive along each track and so on. This procedure is equivalent to sampling one long transect several times.

Animal densities were calculated using the computer program DISTANCE (version 1.12) (Laake *et al.*, 1993). During any survey, some groups are undetected and DISTANCE uses the distance data from the groups which are seen to develop a model which estimates the proportion not seen. Buckland *et al.* (1993) describe the theory and assumptions behind the use of line transects to estimate density and they detail the analytical methods used in DISTANCE. The principal advantage of DISTANCE over earlier programs (e.g. TRANSECT (Burnham, Anderson & Laake, 1980)) is that the density estimation models in DISTANCE are constrained to decrease monotonically as a function of perpendicular distance.

Preliminary analyses using DISTANCE to calculate the densities of animal groups revealed that the uniform and hazard-rate key functions more often provided a closer fit to the data than other key functions, as judged by Akaike's Information Criterion (Buckland *et al.*, 1993). The analyses were repeated using cosine and simple polynomial adjustments for both these key functions. The uniform key function more often provided a closer fit



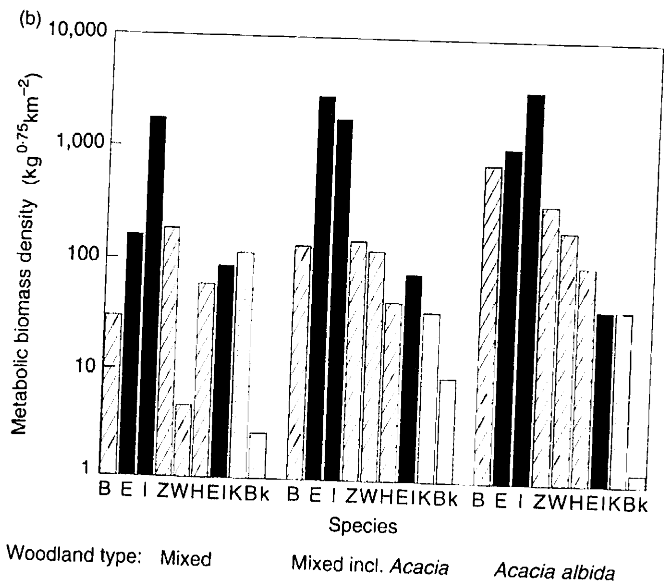


FIG. 16

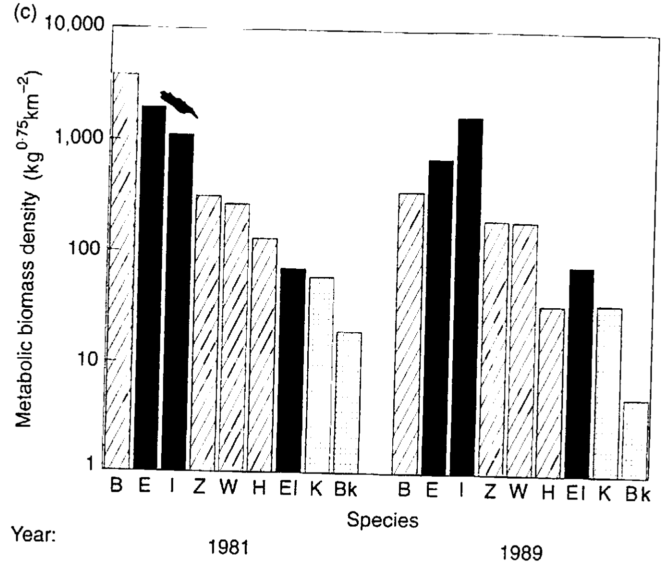


FIG. 16. (a) The changes in the metabolic biomass density of individual species in Zambezi alluvial woodland during the 1981 dry season. (b) The differences in the metabolic biomass density of individual species in three types of Zambezi alluvial woodland during October 1988. (c) The changes in the metabolic biomass density of individual species in Zambezi alluvial woodland between October 1981 and October 1989. Cross-hatching (▨) indicates grazers, dots (▩) indicate browsers and black (■) indicates mixed feeders. B = buffalo; E = elephant; I = impala; Z = zebra; W = waterbuck; H = warthog; El = eland; K = kudu; Bk = bushbuck.

season (Fig. 14). In 1983, density declined during the late dry season, but in 1984 it was constant in this period. Density on the ecotone during October 1981–89 averaged 0·04 (0·01) groups km^{-2}.

Group density on the floodplain during October declined from 1·5 km^{-2} in 1981 to 0·4 (0·06) km^{-2} in 1982–83. It increased in 1984, but thereafter averaged 0·4 (0·05) km^{-2}.

During October 1987/8, the density of groups was highest in the mixed woodland of the central alluvium (Table IV).

Uncommon species

The density of black rhinoceros on the floodplain during October averaged 0·05 (0·013) km^{-2} in 1981–85. This was equivalent to 2·43 (0·27) rhinoceros seen per 100 km driven. Between October 1985 and October 1986, the mean number seen decreased to 0·14 (0·28) per 100 km (Fig. 15). Only seven rhinoceros were observed along the ecotone: six before the end of July 1983 and the last during October 1986.

The number of lions seen per 100 km driven on the floodplain in October did not vary during the study (number vs. year: r = 0·24 for individuals, r = 0·29 for groups, $n = 9$, ns). The mean density of lions was 0·09 (0·026) km^{-2} on the floodplain and 0·05 (0·023) km^{-2} on the ecotone. The density of lions on the floodplain was higher in the morning (0·15 (0·056) km^{-2}) than in the afternoon (0·02 (0·011) km^{-2}).

The mean density of spotted hyaenas on the floodplain during October was 0·03 (0·013) km^{-2}. Hyaenas were commoner in the morning (0·05 (0·021) km^{-2}) than in the afternoon (0·01 (0·012) km^{-2}). Only three lone hyaenas were seen on the ecotone during October.

Nine sightings of side-striped jackal on the alluvium during October gave a mean density estimate of 0·02 (0·007) km^{-2}. Only one jackal was observed on the ecotone. Leopards (eight animals in five groups) were occasionally seen on the floodplain during October: mean density was 0·05 (0·025) km^{-2}. None was seen on the ecotone. Two groups of seven and nine wild dogs (*Lycaon pictus* Temminck) were seen on the ecotone during April and October 1981, respectively.

Sable antelope (*Hippotragus niger* Harris) were rare in the 1980s: groups of 11, five and one sable were seen along the ecotone during October 1982, July and October 1983, respectively. A lone bull was observed on the floodplain during October 1988. In the early 1970s, Guy (unpubl.) recorded few sable on the central alluvium (Table III), but they were commoner on the eastern alluvium.

Nyala (*Tragelaphus angasii* Gray) were seen on the alluvium during October of 1983 and 1987 and on the ecotone during October 1982, July 1983, July 1984 and October 1987 (1, 1, 1, 2, 1 and 2 groups, respectively). Antelope which were rarely seen included: a puku (*Kobus vardonii* Livingstone) on the floodplain during July 1983; a grey duiker (*Sylvicapra grimmia* L.) on the floodplain in October 1983; and a grysbok (*Raphicerus sharpei* Thomas) on the ecotone during July 1984.

Hippopotamus (*Hippopotamus amphibius* L.) were seen in pools on the floodplain and along the ecotone. Most of the population lived in the Zambezi River and were not counted during this study, although hippopotamus fed in the study area at night.

Community structure

Metabolic biomass density (MBD) on the alluvium (calculated using the herbivore masses given by Coe, Cumming & Phillipson (1976) and Cumming (1982)) increased 6·5-fold during the 1981 dry season, to reach 7780 $kg^{0.75}$ km^{-2} by October. Mixed feeders formed 80% of MBD during the first half of the dry season, but the MBD of grazers increased by an order of magnitude during the second half, mainly as a result of the increase in buffalo density (Fig. 16a). In the mixed woodland, browsers formed 5% of MBD at the end of the dry season, but total MBD and the MBD of mixed feeders were half that elsewhere on the alluvium (Fig. 16b). The MBD of grazers was 3–5 times greater in the *A. albida* woodland than elsewhere.

The MBD on the alluvium at the end of the dry season declined by more than half between 1981 and 1989, to reach 3384 $kg^{0.75}$ km^{-2} during 1989. Buffalo, elephant and impala contributed more than 80% of MBD in both years (Fig. 16c). The MBD of grazers, mixed feeders and browsers decreased by 82%, 20% and 41%, respectively (but these figures take no account of hippopotamus). The MBD of mixed feeders declined because of the elephant cull and would have increased without the culling.

Comparing MBD in the 1980s with that in 1965 is complicated by the differences in methods, but the MBD of large herbivores on the central alluvium increased by 36% between 1965 and 1981. This rise was entirely due to the apparent increase in buffalo density: the total MBD of all species except buffalo halved between 1965 and 1981.

Discussion

Seasonal variation in density

Food availability was a major attraction of the alluvium during the dry season, because plant growth continued here long after the rains ended. *Acacia albida* trees have an unusual phenological cycle, being leafless in the wet season, but growing new leaves towards the end of the rains and bearing leaves and fruits during the dry season (Dunham, 1991). The trees at Mana have an elephant-induced browse line and the leaves are inaccessible to most other species, but ripe fruits drop for several months during the mid-dry season. Fruit-fall may be as high as 300 kg per tree and the fruits are eaten by a range of herbivores, including grazers (Dunham, 1990*a*). In drought years, fruit production was reduced because warm dry weather during March–May encouraged a rapid increase in the numbers of caterpillars and these defoliated the trees. Defoliation was followed by a second leaf flush, which diverted the trees' resources from fruit production. The abundance of ripe fruits available to ungulates in drought years was further reduced by baboons, which picked more unripe fruits than in other years.

Perennial grasses were also an important dry-season food and they often continued growing after the end of the rains (Dunham, 1990*b*). Until 1981, floodgates in Kariba Dam were opened almost annually, causing the Zambezi River to flood at Mana. When one gate was closed at the end of June 1981, flooding ceased and the river level dropped 1 m immediately. It declined another metre during the next four months. Production of perennial grasses such as *Panicum coloratum* L., *P. repens* L., *Paspalum scrobiculatum* L., *Hemarthria altissima* (Pior.) Stapf & Hubbard and *Cynodon dactylon* (L.) Pers. was high in lower lying areas, because the moisture content of the soil was high. Since 1981, however, rainfall throughout southern Africa has been low and water flows into Lake Kariba have been too small to require floodgates to be opened. The frequency of perennial grasses has declined since 1981 (unpubl. data) and grass growth during the dry season is now confined to low-lying areas close to the Zambezi River.

Large mammals were also attracted to the alluvium because of its proximity to water, in the Zambezi and in alluvial pools. There is no surface water in the well-drained thickets and, in most years, pools in the mopane woodland evaporate during the dry season. Water is then available only at the alluvium or near the base of the escarpment, 50 km away. Water was important not only for drinking: some animals on the alluvium, e.g. warthogs and buffalo bulls, cooled themselves by wallowing in wet mud. Shade may be a third attraction of the alluvium and an additional means of reducing heat stress. *Trichilia emetica* trees were common and their low branches cast deep shade, except for a few weeks during the mild dry season, when the old leaves dropped and new ones grew. Animals often rested under these trees, especially in the early afternoon, the hottest time of day.

In a typical year, only impala, baboon and a few bushbuck, waterbuck, warthog, buffalo and elephant were on the alluvium at the end of the rains. By the mid-dry season, densities of impala, waterbuck, warthog and baboon had increased and zebra and a few kudu and eland had moved on to the floodplain. There were big increases in the numbers of browsers (bushbuck, kudu and eland—the latter a mixed feeder, but preferential browser (Hofmann, 1973)), buffalo and elephant on the alluvium during the second half of the dry season. In drought years, warthog and zebra numbers increased sooner, during the early dry season, and the same happened for bushbuck, eland, waterbuck and buffalo in 1984, the second successive year of drought. Even in drought years, kudu and elephant densities did not increase until the late dry season.