

The use of drinking sites, wallows and salt licks by herbivores in the flooded Middle Zambezi Valley

P. J. JARMAN Department of Zoology, Manchester University, and Department of Zoology, University College of Rhodesia

Summary

In the unflooded Middle Zambezi Valley, water was available for drinking in zoogenous pools in the deciduous woodlands of the escarpment hills only during, and for a short period after, the rains. For 5 or 6 months each year these pools were dry. During the dry season the majority of large mammals drank either from remnant pools in stream beds, or migrated to the Zambezi flood plain where water was available in the Zambezi River and in pools on the flood plain. In the part of the valley filled by Lake Kariba the Zambezi and its flood plain have been inundated, and the lake shore now lies permanently in the deciduous woodlands of the escarpment hills. Although the former riverine dry-scason water sources have been removed, new sources are available along the lake shore. The suitability of the shore as a drinking site is affected by its exposure to wave action, its pitch, its soil type, and the vegetation type abutting on it, as well as by the preferences of the species using it. Elephant modify drinking sites on the shore by digging water-filled holes at the water's edge in clay soil, and elephant, buffalo and rhinoceros create wallows in similar situations. The holes dug by elephant are much used by antelope, especially impala, for drinking. By analogy with elephant-created pools in the woodlands, these zoogenous pools on the lake shore may have been a source of sodium for species drinking there. Such sources were not widely available in the dry season in the unflooded Zambezi Valley.

Introduction

When the dam in the Kariba gorge was closed in December 1958 the waters of the Zambezi River rose to fill the upper part of the Middle Zambezi Valley, forming Lake Kariba. In the process about 5500 km² of land were flooded, along 240 km of the valley, and some thousands of BaTonga people and tens of thousands of large mammals were displaced from all or part of their former ranges. The lake reached full storage level in late 1963. From December 1963 to March 1967 I carried out a study of the large mammals living in the Chete Game Reserve on the southern shore of the lake. The study was based at the Nuffield Kariba Research Station, between

Present address: c/o P. O. Box 45079, Nairobi, Kenya.

17°08' to 17°18' S and 27°40' to 27°54' E, and its purpose was to study the effects of the creation of the lake upon the large mammals (Jarman, 1968). Comparative studies were carried out in the Mana Pools Game Reserve in the unflooded, lower part of the Middle Zambezi Valley, around 15°44' S and 29°22' E. One of the major effects of creating the lake was to remove the habitats which had been used in the dry season by several herbivores, notably impala (Aepyceros melampus Lichtenstein), elephant (Loxodonta africana (Blümenbach)), zebra (Equus burchelli Gray), buffalo (Syncerus caffer Sparrman) and warthog (Phacochoerus aethiopicus Pallas) and which had been used throughout the year by hippopotamus (Hippopotamus amphibius L.) and the majority of the population of waterbuck (Kobus ellipsiprymnus Ogilby). These dry season habitats which were removed by flooding were the complex of vegetation types on the Zambezi flood plain.

The seasonal use of this region has been described elsewhere (Jarman, 1972). where it was suggested that at least part of the reason for the annual movement to the flood plain of the populations of the major species might be their need to find water in the dry season. These parts of the valley receive some 650 mm of rain annually during a restricted wet season from October or November to April, the rest of the year being quite dry, Plant growth generally ceases in the dry season (Jarman, 1971). the moisture content of plants falls, and the majority of herbivores then need to drink to supplement their intake of moisture in food. Even species such as greater kudu (Strepsiceros strepsiceros Pallas), klipspringer (Oreotragus oreotragus Zimmermann) and black rhinoceros (Diceros bicornis L.), which were found not to use the flood plain as a normal, dry season feeding area (Jarman, 1972) apparently need to drink in the dry season, and kudu and rhinoceros were recorded crossing the flood plain to drink at the Zambezi.

With the obliteration of the Zambezi River and its flood plain above Kariba dam the riverine water sources were removed, but a completely new water source, the lake shore, became available. This paper considers the use of this, and alternative water sources by various herbivore species in the study area on the shore of Lake Kariba, and describes the factors which apparently affect their choice of site. The ways in which species modify drinking sites, and two related activities, wallowing and saltlicking, are discussed.

Sources of water

In its unflooded valley the Zambezi River formed a permanent water source for large mammals, but was probably an important source only in the dry season. Then it was at its lowest, flowing fairly fast, some 3 m below the level of the flood plain, and often separated from the flood plain by extensive sand banks. Although elephant and baboon (Papio ursinus Kerr) were regularly observed on the sand banks, most species did not cross the open sands to drink at the river, preferring sites where, in its meandering, the river ran close to the flood plain bank. Paths were developed cutting through the flood plain bank to the water's edge, usually where the adjacent vegetation type was Acacia albida Del, sayanna or grassland rather than gallery forest. These paths to drinking sites were used by a variety of species and, once established, gave animals an easier gradient to descend and climb than that offered by the rather precipitous river bank.

Animals feeding in the deciduous woodlands inland from the flood plain would have had to cross the full extent of the flood plain, about 2 km, to reach the river bank. However, several small tributary streams crossed the flood plain to join the Zambezi at intervals along its course; perhaps one every 5 km. These provided an alternative water source which was heavily used by species such as impala which relatively infrequently drank on the rather exposed Zambezi banks. Also on the flood plain were many pools filled with flood water in old channels and ox-bows of the Zambezi. In terms of their extent of land-water margin these pools were much more heavily used by all species than the Zambezi itself, perhaps because an animal located at random on the flood plain would usually find itself closer to a pool than to the main river. These pools generally had less steep banks than the Zambezi.

Each year before the dry season movement to the flood plain the populations of the most numerous herbivore species were dispersed in the deciduous woodlands of the escarpment hills and ancient river terraces (Jarman, 1972). During the wet season and for a short while after rains ceased water was available in these woodlands in tributary streams, in natural pools, and in zoogenous pools. These last were pools which had been created through the removal of soil by elephant and other species. They are discussed below (p. 204). Water remained in pools in tributary streams and in a few of the very largest zoogenous pools throughout the dry season, but it became in that season a scarce resource with a markedly clumped distribution.

Of all these formerly available water sources only some of those in the deciduous woodlands of the escarpment hills have survived the filling of Lake Kariba. However, for the animals living in its vicinity the lake now forms a new water source, whose landwater interface has several novel characteristics. Because the lake has penetrated the faulted, tilted, eroded topography of the escarpment hills the water's edge now abutts on a diversity of shore types quite unknown along the Zambezi, and the length of the land-water margin has trebled. The lake shore varies in pitch from nearly level to 50° above horizontal, but perpendicular banks, so common along the Zambezi, have formed in very few places. Shores of alluvial silt are now almost totally absent and sandy shores are rare, while these types formerly predominated along the Zambezi. They have been replaced by shores on woodland soils of clays, sandy clays, grits and rocks, of the cluvial and co-luvial sections of the catena. The type of erosion has changed, since water flow along the shore is now minimal, but wave action, which was very slight on the Zambezi, is now in places very heavy. Thus the extent of the land-water contact, the motion of the water at that contact, the soils and the vegetation types at the water's edge have all changed with the flooding of the valley. The choice made by the mammals between various combinations of available shore and water characteristics reveals some of the factors which govern the selection of drinking sites in general.

Seasonal use of sources after flooding

In the study area adjacent to the shore of Lake Kariba data on densities and habitat associations of species were collected during regular foot patrols of three transects. These were aligned so that one sampled a strip near or along the open lake shore, the second a strip near or along first the flooded valley and then the unflooded valley of the Sinamwenda River, a minor tributary of the Zambezi, and the third a strip in the woodlands between the other two. Although neither the transects nor the patrols were designed to investigate drinking activity or selection of drinking sites, the records can be used to show the pattern of seasonal use of the different water sources, and to some extent preference for one type of source.

Figure 1 shows the proportion of all sightings of groups of animals, in appropriate transect sectors in each month, which were recorded as drinking. Appropriate sectors were those containing a sample of that type of water source. Rainfall is also indicated in the figure. Despite the records being collected between 07.30 and 10.00 hours, a time of day when few species drink (Weir & Davison, 1966; Jarman, 1971), drinking records were obtained in all months. The main feature of the seasonal pattern is that zoogenous pools were used only during the rains, since that is the only time when they held water. While zoogenous pools were available the other two water sources were

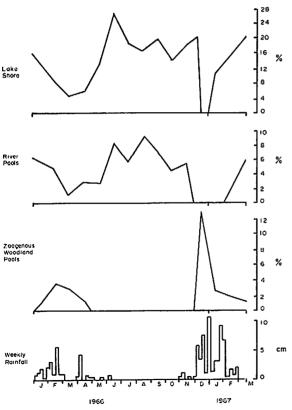


Fig. 1. Animal groups which were drinking when seen, expressed as a percentage of all groups seen. in appropriate sectors of transects. Appropriate sectors were ones containing the particular type of drinking site. At the bottom of the figure is a histogram of weekly rainfall totals for the same period.

very little used. This suggests that the zoogenous pools contributed more than the other sources to satisfying water requirements while they held water; however, it is a time of year when water requirements are in any case low. Like the flood-water pools on the Zambezi flood plain these zoogenous pools were relatively well scattered throughout the feeding habitats, and would usually constitute an animal's nearest water source. However, the records showed that, in a situation where animals had a direct choice between drinking at the lake shore and drinking from a zoogenous pool, they displayed a significant (P < 0.001) preference for the latter. The zoogenous pools apparently have some property which adjacent lake water lacks.

After April the zoogenous pools were nearly all dry and animals made the choice between drinking from the Sinamwenda River, now reduced to a series of pools, or from the lake. Perhaps because of its greater availability, in terms of land-water margin and in proximity to the studied feeding areas, the lake appeared in the records as the more important source. Thus for the whole of the dry season, when it is assumed that drinking was of the greatest importance to most species, the lake shore, an entirely novel water source, seemed to meet the requirements of most animals.

Distribution of drinking sites on the lake shore

Surveys of parts of the shore of Lake Kariba in the vicinity of the flooded valley of the Sinamwenda River were carried out in June and August 1966. The object of each survey was to plot the location of drinking sites, which were identified as places where tracks could be found leading to the water's edge in such a manner that the animal might have drunk there. The location of each site, the species that had used it, and various characteristics of its environment were recorded. The June survey covered 27-35 km of coast west of the confluence of the unflooded Sinamwenda River and the lake. One flooded creek had been particularly heavily used and a second, more detailed survey of this creek was made in August. These two stretches of shore and the distribution of drinking sites along them are shown in Fig. 2. which also indicates the direction of the prevailing wind at that season and the area of water covered by a semi-permanent mat of the aquatic fern Salvinia auriculata Aubl. It is obvious that drinking sites were neither evenly nor randomly distributed along the shore, and some of the factors affecting their distribution can be considered.

(i) Wave action

For much of the dry season (May-October or November) the southern lake shore experiences rather constant north-easterly winds which are capable of producing strong wave action where they have sufficient fetch (i.e. distance travelled over open water). By 1966 the effects of this wave action were apparent, various forms of erosion being well advanced on exposed shores, in contrast to a lack of erosion on sheltered shores. From Fig. 2 it can be seen that drinking sites were almost entirely confined to shores that were sheltered from this north-easterly wind and the waves it produced. It has been suggested that animals might have been avoiding drinking in situations where a predator could stalk them from down-wind. This does not seem to be true here, since at many sheltered sites animals would still have to approach the shore into the wind. It seems more likely that the distribution of drinking sites was affected by something related to the wave action; either the movement of the water, or the noise of breaking waves, or the eroded nature of the shore. Table 1 compares the number

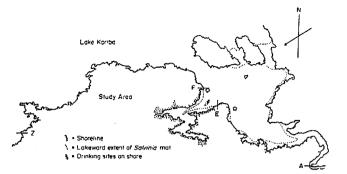


Fig. 2. A map of the shore of Lake Kariba in the vicinity of the study area, showing the location of drinking sites recorded during the June (A along to Z) and August (E along to F) surveys of the shore. Each dot corresponds to a drinking site on the shore at the point closest to it. The line at A marks the junction of the lake and the unflooded Sinamwenda River. The lakeward limit of semipermanent Salvinia mat is shown by the dashed line. The prevailing wind direction is indicated by the arrow across the line indicating true north.

Table 1. The effects of wind and wave action on the distribution of drinking sites on the lake shore. The numbers of sites recorded, in the June and August surveys, on shores exposed to. and on shores sheltered from, wind and waves are compared with the numbers that would have been expected on the sampled lengths of each shore type if exposure had no influence on drinking sites

	I areach ac	No. of	drinking sites
Shore type	Length of shore (km)	Observed	Expected
Exposed	3-1	2	27-2
Sheltered	24.3	238	212.8
Total		240	240.0
		χ* 26·	33; <i>P</i> <0·001.

of drinking sites found on exposed and sheltered shores with the number that would have been expected on each if their distribution were unaffected by exposure. The result shows that exposure had a significant effect on distribution of drinking sites.

(ii) Salvinia mat

It can also be seen in Fig. 2 that a large number of drinking sites were recorded on shores adjacent to Salvinia mat. This aquatic fern can form a thick, floating blanket of dead and living material, often more than 10 cm thick in places where it has persisted for several months. Since the weed is driven by the wind, and its mat is broken up by wave action (Mitchell, 1970), the distribution of mat is closely correlated with shelter from wind and wave action. Hence the correlation between the distribution of Salvinia mat and the distribution of drinking sites was probably fortuitous, each of them being associated with shelter. However, the mat of Salvinia does dampen wave amplitude, thus producing calmer water and less erosion on the shores against which it floats, possibly enhancing the value of those shores as drinking sites.

(iii) Pitch of shore

It was apparent in the June survey that drinking sites were generally not found where a steep hillside fell directly into the water. The topography of this part of the southern shore is largely dominated by the scarp and dip slopes of the blocks of grits, sandstones, shales and clays of the Karroo sediments. Tilting has in general been slight, so that slopes are readily classified as steep or gentle. Since much of the steep shore surveyed in June was also exposed to the wind and waves of the open lake, the records of the August survey of the sheltered creek have been used to investigate the influence of steepness of shore, uninfluenced by exposure, on the distribution of drinking sites. Table 2 shows that significantly fewer drinking sites were found on steep shores than would have been expected if drinking sites were distributed irrespective of pitch of the shore. Table 3 shows that the six most common species differed in their reaction to pitch of shore. Elephant, buffalo, rhinoceros, impala and greater kudu avoided steep shore to varying extents, while klipspringer preferentially used drinking sites on steep shores. Of the five species that avoided steep shore, buffalo did so most completely, elephant and kudu least.

(iv) Shore vegetation type

The August records also showed that, to some extent, species drank on shores whose landward side most resembled their feeding habitat at that season. Elsewhere (Jarman, 1968 and in prep.) I have described the distribution of species in this study area in relation to vegetation types. In all seasons klipspringer were associated with rocky hillsides, which were avoided by buffalo; the same association and avoidance were found in the two species' choice of drinking site. Table 3 considers the incidence of drinking sites used by the six most common species, recorded in the August survey, in the three major vegetation types abutting on the lake shore. Hillside is equivalent to steep shore. Although all species except kudu appeared to make significant selection between the three vegetation types, only buffalo made a significant distinction between shores backed by mopani (Colophosphermum mopane Kirk) and by Combretum woodlands, choosing to drink where the shore was adjacent to the latter. Elephant and impala

Table 2. The occurrence of drinking sites on steep and nearly flat shores, as recorded in the August survey, compared with the distribution that would be expected if occurrence were not affected by pitch of the shore

	Length of	No. of	drinking sites
	sampled shore (km)	Observed	Expected
Flat shore	6.08	135	117
Steep shore	3.82	55	73
		$X_{s^{\pm -}}$	7·21; <i>P</i> <0·05.

Table 3. The observed occurrence of drinking sites used by the six most common herbivore species on various shore types, compared with the expected distributions if the attributes of those shore types were not affecting distribution. Records from the August survey of the sheltered creek only have been used

Shore types

	F	lat she	re			ep shor (hillside				
Species	Obs.	E	.p.	% Shift	Obs.	Exp		N	χ.*	Sig. (P⊄)
Elephant	74		61	← —13	26	3	9	100	7-1	0.05
Buffalo	49		32	←32	4	2	i	53	22.8	0.00
Rhinoceros	25		18	24	4	1	1	29	7-2	0.05
Impala	40		29	← 23	7	1	8	47	10.9	0.01
Kudu	59		48	←- 14	19	3	0	78	6.6	0.05
Klipspringer	. 2		7	42>	10		5	12	8.6	0.05
					Veg	etation	types			
	-									
% of sample			i types 44·1%	Combretun	types 17:4%		lillside 38·5%			
% of sample Species								N	χ.*	(Sig. P<)
Species		re	44-1%		17.4%		38.5%	<i>N</i>	Х. [‡]	(Sig. P<)
Species Elephant		Obs.	44·1% Exp.	Obs.	17·4% Exp.	Obs.	38·5% Exp.			
Species Elephant Buffalo		Obs.	44·1% Exp.	Obs.	17·4% Exp.	Obs. 26 4 4	38-5% Exp. 39 21	100	10·7 45·9 11·7	0.05
Species Elephant Buffalo Rhinoceros		Obs. 60 23	44·1% Exp. 44 23	Obs.	17-4% Exp. 17 9 5 8	Obs. 26 4 4 7	38-5% Exp. 39 21 11 18	100 53 29 47	10·7 45·9 11·7 11·6	0·05 0·001
		Obs. 60 23 14	44·1% Exp. 44 23 13	Obs.	17·4% Exp.	Obs. 26 4 4	38-5% Exp. 39 21	100 53 29	10·7 45·9 11·7	0·05 0·001

% of (mopani + Combretum		ni types 71.7%	Combretui	n types 28·3%			
Species	Obs.	Exp.	Obs.	Exp.	N	χ,*	Sig. (<i>P</i> <
Elephant	60	53	14	21	74	3.3	n.s
Buffalo	23	35	26	14	49	14-4	0.00
Rhinoceros	14	18	11	7	25	3.2	n.s
Impala	31	29	9	11	40	0.5	n.s
Kudu	42	42	17	17	59	0.0	n.s

showed insignificant preferences for mopani, and rhinoceros for Combretum, woodland on the landward side of their drinking sites. These correspond to the species' choices of vegetation types as feeding habitats at that time of year. This suggests that the commoner herbivores were moving directly from feeding habitat to adjacent shore to drink. It also appeared in the field that animals feeding further inland tended to drink where paths met the coast. This was suggested by the clusters of drinking sites, many of them very heavily used, where minor valleys or terraces met the shore; well marked paths ran along these valleys and terraces to the shore, and some of these paths could be traced for over 2 km inland. The use of such path-determined drinking sites may have obscured the influence of feeding habitat on choice of drinking sitc.

Separation of species at drinking sites

Of the 190 drinking sites recorded in the August survey of the sheltered, heavily used creek, ninety-three (49%) carried the tracks of only one species, the other ninetyseven having been used by two or more species. If we assume that the frequency of occurrence of extra species at a drinking site, that is of species in addition to the one required to identify the place as a drinking site, would follow a Poisson distribution if species were not seeking to associate or dissociate, then we can test the observed distribution of numbers of species at drinking sites with this expected distribution. This has been done in Table 4, where it can be seen that the two distributions are very similar. However, this close approximation to a Poisson distribution may be the result of combining the tendencies of some species to use the same drinking site as others, and of some species to drink where other species were not drinking. Table 5 suggests that elephant and klipspringer were each recorded as being the only species using a

Table 4. The occurrence of numbers of species at drinking sites in the August survey only. The expected number of species at each site has been calculated as a Poisson distribution of extra species at each site in addition to the initial species required to identify it as a drinking site

No. of species		No. of sites
(maximum possible 6)	Obs.	Exp.
1	93	91
2	63	67
3	21	25
4	12	6
5	1	1
6	0	0

Table 5. The tendency shown by species to be the only one using a drinking site. The fourth column figures are derived by dividing the second column figures by 93, and the last column figures are derived by dividing the first column figures by 319. The values in the fourth and last columns have been compared and the significance of differences between them is indicated

Species	Total no. of sites used by that species	No. of sites used by that species alone	% of that species' sites used by that species alone	% of all one-species sites used by that species	Significance of difference P<	% of all records which were of that species
Elephant	100	36	36	38-7	0.001	31.3
Buffalo	53	10	19	10.8	0.001	16-6
Rhinoceros	29	8	28	8.6	n.s.	9.9
	47	9	19	9.7	0.002	14.7
Impala	78	21	27	22.6	n.s.	24.5
Kudu Klipspringer	12	9	75	9.7	0.01	3.8
Totals	319	93				

difference in the distribution of elephant records between the two periods. This suggests that, in certain circumstances, these two species may under natural conditions avoid using the same drinking site.

Modification of drinking sites, and the creation of wallows and salt licks

Drinking sites were recognized as such by the presence of tracks, in themselves a minor modification to the site. Repeated use of sites led to more extensive modifications in that an obvious path leading to the water's edge would be formed, wet soil would become trampled, and a certain amount of soil would be removed. In places where there was a mat of Salvinia this weed might be pushed out from the shore, leaving a clear water surface next to the land. The presence of these effects of repeated use were recorded in the survey to classify sites as 'heavily' as against 'lightly' used. This distinction was clearly arbitrary, but the records did suggest that rhinoceros and impala tended to use only a few sites, but to use them heavily, while elephant and kudu used a scatter of sites, most of them being used lightly.

Apart from the incidental effects of repeated use of a site, some species, most importantly elephant, acted so as to modify the structure of a drinking site. Examples of modification were found in the unflooded woodlands and in river beds as well as on the lake shore. Several holes dug by elephants were found in sand banks in river beds during each dry season. These holes were up to 2 m across and 1 m deep, and were often situated close to pools of open water in the river bed which were obviously accessible to the elephants. The holes had been dug down into the sand to below the local water table so that water seeped into them. Similar behaviour has been reported by Lamprey (1962) from the Tarangire Game Reserve in Tanzania. The water that gathers in the hole looks cleaner than that in the adjacent river pool, but Weir has suggested (pers. comm.) that it may be the low temperature of water in such holes that is preferred by the elephants, particularly if environmental conditions are such as might lead to heat stress.

More widespread examples of excavation of holes by elephants occurred throughout the study area on clay soils. These holes varied from shallow scrapes in the surface soil to pits up to 5×10 m in area and 1 m deep. Some of these were known to have had their origins as salt licks, and others were used as wallows, but during the rains many functioned for a few months as pools collecting rain water. These were the zoogenous pools referred to earlier. Their distribution, both in the woodlands away from the shore and on the shore itself, was closely linked to soil type and hence to vegetation type. They typically occurred on clay soils, especially where emergent ridges of rock impeded surface run-off. Table 10 lists typical densities of zoogenous pools in various woodland types, and numbers of pools recorded on different shore types in the August survey. Meiostemon woodland grows upon fairly deep sandy soils. and pools were not formed there. Combretum woodland grows on a mixture of sandy and sandy-clay soils shallowly overlying flat-bedded rocks, and pools were formed there infrequently. Mopani woodland grows on clay soils, and was the typical habitat of zoogenous pools.

Formation of zoogenous pools as drinking sites must be considered in conjunction with wallowing and salt licking, two other activities performed at similar sites by some herbivores. Weir (1960) recognized that pits which were originally excavated when dry as salt licks might be used as wallows when wet, and finally develop into pans, which would then develop through stages of expansion and in-filling. This

Table 10. The location of zoogenous pools or wallows in vegetation types, in the woodlands and on the shore

Vegetation type	Density of pools/km²
Hillside	0
Meiostemon woodland	0
Pure Combretum woodland	96
Combretum and rock ridges	184
Coppiced mopani scrub	197
Light mopani woodland	270
Mopani and rock ridges	993

(b) Zoogenous pools and wallows on the lake shore. Records from the August

	Length of		No. of pools and wallows		
Vegetation types	sampled shore (km)	% of sample	Observed	Expected	
Hillside	3.82	38.5	0	18	
Mopani types	4.36	44.1	43	22	
Combretum types	1.72	17-4	6	9	
Totals	9.90	100-0	49	49	

Comparison of mopani and Combretum shore types only

No. of pools and wallows

	Observeü	Expected
Mopani types	43	35
Combretum types	6	14
	½° ← 6.4	0; <i>P</i> < 0·05.

concisely describes the earlier stages of some zoogenous pools as observed in the Kariba study area; but by no means all salt licks became wallows in the wet season since many were excavated in the sides of termitaria, under boulders, or in clay or shale cliffs, in situations where they could not form water-holding pits. Equally, wallows were sometimes formed in the woodlands, and often on the shore, on places that had not previously been used as salt licks. The requirements for salt licks and wallows are at least partly different; a salt lick requires mineral rich soil, often rich in water-soluble sodium salts (e.g. Weir, 1969), while a wallow requires a clay which will puddle well. Clays in the Kariba study area are generally sodium-rich and also puddle well, so wallows may readily be evolved from some salt licks. Weir (1971, 1972) has indicated that elephant, and perhaps other herbivores, prefer sodium salts in aqueous solution when they are available in that form, and the puddling of clay with water by elephants in the Kariba study area may have resulted in such a solution of sodium salts.

Although no direct measurements of sodium content of soil samples were made, conductivity of soils from different sites in the woodlands of the study area was measured. Weir (1969) has illustrated the correlation between conductivity and sodium content of soils from the Kalahari sand area of Wankie National Park. The results in

Av Source of sample	erage conductivity (µmhos/cm²)	Range	No. of samples
Combretum woodland	16.5	16-5	1
Sand from stream bed	40	29-60	:
	80	18-540	21
Mud of natural pools Woodland surface soils	169	20-480	13
	2360	160-8500	13
Termitaria	625	550700	2
Lightly used salt licks Salt licks	2490	650 - 7000	

Table 11 suggest that soils from termitaria and salt licks carried higher sodium concentrations than soil from other woodland sites, if one accepts that sodium is the major reason for high conductivity in African soils.

Nearly all the common herbivores except warthog were recorded salt licking (eating soil) during the study. Only elephant, rhinoceros, warthog and buffalo were recorded wallowing, either rolling in mud or muddy water, or, in the case of elephant, also daubing and spraying muddy water upon themselves. Of these species elephant are the largest and most persistant users of wallows, and are largely responsible for the creation and expansion of most of the wallows and water-holding zoogenous pits found in the woodlands. As an example of their excavating power, I recorded elephants in the woodlands of the study area turning a salt lick which was originally no more than a shallow surface scrape into a pool 2×3 m in area and over 50 cm deep in 1 year, and in 3 years they created a woodland pool $6\!\times\!9$ m in area and over 1 m deep. Without knowing how many elephants used each site how often, the rate of removal per elephant cannot be calculated, but judging by the thick smears of mud left on trees around the pools an elephant might carry away a layer of mud over 5 mm thick on much of its back and flanks. The actions of an elephant in obtaining this covering of mud, stamping in the pool to puddle the clay, scooping it up and applying it with the trunk, inevitably deepen the hole as well as expanding it sideways, and it thus becomes a water-holding pool. Wallows used by buffalo and rhinoceros, however, may consist simply of an area of churned up, damp mud, insufficiently deep to act as a pool. Both these species apply mud to themselves by rolling and wallowing, and have no effective means of scooping it up onto themselves. Among buffalo it is mainly the adult males which wallow. For these males wallows act as focal points for social interactions, and many of their activities at wallows, such as horning the soil at the side of the wallow and urinating into the wallow, may have as much social as physical or physiological significance. Rhinoceros, too, will horn the soil at the side of the wallow. In this way both species' wallows tend to expand sideways faster than they deepen.

These differences between the three major wallowing species in the type of wallow they create and use were particularly apparent on the lake shore. Before the creation of the lake these species would have been unable to find wet wallows in the present study area after about June in each dry season. The constant presence of the lake water abutting on the woodlands and their soils enabled these species to create wallows that were wet throughout the dry season. Along the shore sampled in August were found forty-three holes and wallows created by elephant, four by buffalo, and two by rhinoceros. The clear distinction between which species had created each wallow could be made because there had been almost total separation of utilization by the three species; buffalo tracks crossed three of the forty-three elephant wallows, and elephant tracks crossed one buffalo wallow. Rhinoceros did not cross either of the other two species' wallows, and none of the species appeared to have wallowed at either of the other species' wallows. Moreover the form of the elephant wallows was specifically distinct from those of the other two. None of the rhinoceros or buffalo wallows was deep enough to hold much water, even though one buffalo wallow measured 3×10 m in area. By contrast the majority of elephant-dug holes were deep enough to hold water, but, because of a gradual drop in lake level over the months preceding the survey, many of them were dry and disused. The forty-three elephantdug holes occurred in twenty-four clusters, some of which contained as many as six holes distributed as a series down the shore. The most recent ones were all at the water's edge, or actually under water in one case, and it was clear that elephant had had to create new holes lower down the shore each time the water had receded from a previously dug hole. Elephant tended to create these clusters of holes wherever a drinking site was scored in the survey as heavily used by them; by contrast both rhinoceros and buffalo might use a drinking site heavily without creating wallows.

Although these three wallowing species were infrequently recorded crossing each others' wallows, impala and kudu were recorded at wallows frequently. Since neither antelope wallows, they must have visited wallows either to obtain water or salts, or accidentally. Neither species was recorded at the dry elephant-dug holes, but of the twenty which contained water kudu were recorded at nine and impala at eleven. If we take the expected level of coincidence calculated for Table 8, kudu would have been expected to occur at eight and impala at five. So impala seem to have been significantly attracted by these elephant-dug holes while they contained water.

Elsewhere on the shore termitaria at water level, whose soil was wet, were heavily eaten into by all species, especially impala. In at least two recorded cases termitaria which had stood over 1 m high were reduced to low mounds a quarter of that height in the few weeks when they were at water level. On more extensive flat clay shores outside the study area (e.g. Sengwa West tree-cleared area), large numbers of termitaria were similarly degraded. There were no signs that any species avoided using, or tended preferentially to use, the salt licks on the shore that were used by any other species.

Discussion and conclusion

In the unflooded Zambezi valley animals were apparently not attracted to the river as a water source while other sources were still available. Because animals clearly tended to use water sources near their feeding habitats, which were largely in the deciduous woodlands of the escarpment during the rains, it is not surprising to find that they used woodland zoogenous pools and streams as water sources in that season, rather than making long daily movements to the Zambezi. In the study carried out in the flooded valley the data showed that species strongly preferred drinking from zoogenous pools while these contained water. This preference was expressed even where zoogenous pools were the least abundant source. Because of their development from salt licks and wallows, some of these pools probably contained concentrations of sodium ions. Weir (1971, 1972) has shown that such water is highly attractive to elephants, and I suggest that the same property appeals to many ruminants as well, at least in the conditions of the Zambezi valley. In the unflooded valley these zoogenous pools usually dried up in the dry season, as they did in the woodlands around Lake Kariba; but along the shore of the lake water remained in contact with sodium-rich, clay soils throughout the dry season. In these circumstances elephant were able to create zoogenous pools at the water's edge throughout the year, and most other species enjoyed this resource which had been seasonally unavailable in the unflooded valley.

In their selection of drinking sites on the lake shore species generally chose places which resembled their feeding habitats. This resemblance between drinking and feeding environments has been remarked elsewhere (Jarman & Mmari, 1971; Weir, 1971, with respect to zebra). All species avoided drinking on shores exposed to wave action, probably because of the presence of waves rather than of any secondary effect they produced. With one exception species showed no tendency to separate at drinking sites which could not be explained by separate selection for habitat factors. This contrasted with the marked tendency of elephant, buffalo and rhinoceros to avoid using others' wallows.

The effects that the creation of Lake Kariba had upon the large mammals of the Zambezi valley were clearly not all detrimental. Although the community lost much space and a set of habitats which had been extensively utilized in the dry season by the more numerous species, it gained a water source which was permanently available adjacent to feeding habitats which were now, for lack of anything better, in use throughout the year. Moreover as long as elephant continued to create pools in clay soil at the water's edge, the other species would have a perennial source of various ions, including, I suggest, sodium, in solution. Although a large proportion of the lake shore was unavailable as a drinking habitat for most species, because of exposure to wave action or steepness, the acceptable stretches more than equalled the length of land-water margin of the former Zambezi. So, in diversity of drinking site environments, in total availability of shore, and in the quality of water at some modified sites, the herbivores appear to have benefitted from the creation of Lake Kariba. It is, however, quite possible that they are only now expressing a need for sodium and an increased need for water in the dry season because of their exclusion from the flood plain habitats which they would formerly have occupied in the dry season.

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References

- JARMAN, P.J. (1968) The effect of the creation of Lake Kariba upon the terrestrial ecology of the Middle Zambezi Valley, with particular reference to the large mammals. Ph.D. thesis, Manchester University.
- JARMAN, P.J. (1971) Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. Oecologia, 8, 157-178.
- JARMAN, P.J. (1972) Seasonal distribution of large mammal populations in the unflooded Middle Zambezi Valley. J. appl. Ecol. 9 (1), 283-299.

- Jarman, P.J. (in prep.) Seasonal distribution of large mammal populations in the flooded Middle Zambezi Valley.
- JARMAN, P.J. & MMARI, P.E. (1971) Selection of drinking places by large mammals in the Serengeti woodlands. E. Afr. Wild. J. 9, 158-161.
- LAMPREY, H.F. (1962) A study of the ecology of the mammal population of a game reserve in the Acacia savannah of Tanganyika, with particular reference to animal numbers and biomass. D. Phil. thesis, Oxford University.
- MITCHELL, D.S. (1970) The autecology of Salvinia auriculata on Lake Kariba. Ph.D. thesis, University of London.
- Weir, J.S. (1960) A possible course of evolution of animal drinking holes (pans) and reflected changes in their biology. Proc. 1st Fed. Sci. Cong., Salisbury, Rhodesia, 5 pp. Mardon & Co.
- Weire, J.S. (1969) Chemical properties and occurrence on Kalahari sand of salt licks created by elephants. J. Zool., Lond. 158, 293-310.
- Weir, J.S. (1971) The effect of creating additional water supplies in a Central African National Park. In: The Scientific Management of Plant and Animal Communities for Conservation. 11th Symposium, British Ecological Society, pp. 367-385. Blackwell Scientific Publications, Oxford.
- posium, British Ecological Society, pp. 367-383. Blackwell Scientific Fundaments, Goldin. Well, J.S. (1972) Spatial distribution of elephants in an African National Park in relation to environmental sodium. Olkos, 23, 1-13.
- WEIR, J.S. & DAVISON, E. (1966) Daily occurrence of African game animals at water holes in dry weather. Zool. Afr. 1 (2), 353-368.

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