BEHAVIOUR OF LARGE MAMMALS DURING THE FORMATION OF LAKE KARIBA

By

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Frontispiece. A general view of Kariba Dam showing a number of islands formed by the Lake.
(Photo: Rhodesian Information Service)

INTRODUCTION

The success of large mammals, native to marginal areas in Africa, suggests that an understanding of their basic ecology will lead not only to their survival through correct management, but also to better conservation practices where ungulates form a part of the economy. Gaining this understanding depends to a large extent on field studies as, for obvious reasons, it is usually difficult to submit wild populations to predetermined experiments. Valuable complementary data can be expected from captive specimens, although captivity has limitations and it is often difficult to assess the effects induced by captivity on the normal behaviour of a species.

When undertaking a field study it is, however, economical to select and exploit situations which provide easy access to certain types of information which might otherwise be difficult to obtain. These often involve a striking change in the animal-environment relationship and Riney (1958 and 1963,a) has emphasised the opportunities arising from the sudden alteration of the animal aspect which results from the introduction of large mammals, while in this study, changes initially affected the environment.

The present study sought to make use of conditions during the formation of Lake Kariba, which resulted from the impoundment of the Zambezi. Three important factors led to changes in the ecology of the Kariba Basin, an area of 2,109 sq. miles, inhabited by primitive tribesmen and supporting extensive populations of large game mammals. In chronological order these were : i) the evacuation of the native inhabitants; ii) the preparation of fishing grounds; and iii) the inundation of almost the whole floor of the Central Zambezi Valley. The removal of the people resulted in large areas, especially those on or adjacent to fertile alluvium, which had been over-populated, being fallow until either cleared for fishing or submerged by the Lake. The bush clearing of selected areas designated for fishing-grounds resulted in the destruction of most vegetation, while the filling of the Lake transformed a terrestrial environment, bisected by a seasonally fluctuating river, into a large static body of water within four and a half years. The habitat thus eliminated was typical of dry marginal areas in Rhodesia, the remaining strongholds of large mammals in the territory.

This paper aims at describing some of the effects of the formation of Lake Kariba on large mammals and their response not only to flooding, but also to the over-populated conditions which arose on islands on which they became marooned. In so doing it is, however, necessary to touch on the influence of past human settlement on the distribution and abundance of large mammals and on the effects of the clearing of incipient fishing-grounds. It is also convenient to mention briefly some of the most obvious responses of other groups of animals, as they showed certain similarities with those of mammals.

Periodic droughts in marginal areas lead to a temporary reduction in essential habitat resources and consequent over-population. Animals are also subjected to occasional floods, which occur almost annually on an African wide basis. Conditions at Kariba enabled these two extremes to be observed simultaneously, with the exception that water was always readily available even when food or cover was limited.

It is obvious that when many rivers overflow their banks, the strength of the flood waters is sufficient to sweep away animals, even if they are accomplished swimmers. This mechanical effect is ignored when interpreting the observed response of large terrestrial mammals towards flooding at Kariba. Here flooding was more akin to that of lakes filling to unusual heights, of which there have been several examples in Central Africa during the past few years, or when mature rivers, such as the Luangwa or the Senegal overflow on to the flood plain seasonally. Mr. D. F. Vesey-Fitzgerald (pers comm) indicates that the abnormal high level of Lake Tanganyika in 1963/1964 generally favoured large mammals by inducing better grazing conditions (of the soak zone at Kariba p.28), although a number of zebra became cut off by rivers and eventually drowned.

The flood plain of the Luangwa River in Eastern Zambia is uneven, so that temporary islands are cut off by a slowly moving body of water during the flood season. Unfortunately, the area is not well known at this time of the year, and the only species so far reported as being marooned on islands are Impala, while Vervet monkeys have become trapped in trees in the water (Mr. M. Ronaldson, pers. comm). Mr. J. Feeley (pers. comm) reports that under abnormally high flood conditions, the Impala became isolated on termite mounds and under these conditions some would almost certainly drown or starve, suggesting a remarkably close parallel to conditions observed at Kariba. Blair (1939), Yeager and Anderson (1944), Stickel (1948), McCarley (1959) and Ruffer (1961) have observed similar behaviour in small North American mammals and Bigourdan (1948) for Wart Hog in Senegal.

The effects of flooding on large mammals will thus depend, to a large extent, on local topography and, in particular, on whether or not islands are formed. It is nevertheless reasonable to assume that animals which do tend to remain in an area regularly, or even occasionally, affected by this type of flood, would be more susceptible to violent floods, which are difficult to observe because of their very nature. Further, it is highly desirable that the effects of the construction of large dams on the fauna and flora of an area should be taken into account at the planning stages in order to minimize the disturbance to the ecology of the region flooded by the dam and down stream of the barrage. This requires, amongst other things, a basic understanding of the response of species towards large scale inundation, so that a secondary aim of this study is to record observations on behaviour and ecology of animals affected by the artificial inundation for eventual comparison with similar situations as they arise elsewhere in Africa.

Islands at Kariba, on which animals became marooned, became over-populated as the habitat decreased, unless this loss was compensated by an exodus, or the removal of the animals. Population density increased, not through recruitment, as generally occurs when numbers become too high, but through reduction in habitat. This obvious fact led to a normal population becoming over-stocked very rapidly, without a period of adjustment to declining resources. With the exception of the availability of water, this process was similar to that experienced by populations during a severe drought.

Many populations became limited to small, easily observed areas where the habitat was deteriorating. This created excellent opportunities for observing survival mechanisms in several species, in areas made marginal and finally intolerable to the species by the conditions created by the flood. This opportunity was enhanced by the fact that not all islands became over-stocked to the same extent, or with the same combination of species, or in precisely the same habitat, so that these responses could be compared between islands with differing environmental conditions.

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METHODS

Changes associated with the formation of Lake Kariba were generally so rapid that the relationship between animals and their environment could be described by less exact and time-consuming methods than might be permissible under more stable conditions. The significances of the Kariba data were not always immediately apparent when standing on their own however, so they are frequently evaluated against similar information collected by the author in suitable control areas elsewhere.

1. DESCRIPTION OF HABITAT

Step-point transects were used extensively for describing habitat. The method involved an accurate description of conditions at a series of points along a traverse. By definition, these points, which were spaced at two yard intervals along lines ranging from 50 to 600 yards, had no area.

The procedure followed was similar to that described by Evans and Love (1957) and modified by Kinsey (1963,a). Each step-point was located by lowering a point vertically from a thin line marked on the toe of the observer's right boot, each time this foot came to the ground. The sole of the boot was held at about 30° to the ground so as not to disturb underlying vegetation, and conditions at that point were described on field forms. Bare ground was recorded if there were no rooted plants. If plants were present, they were divided into annual and perennial grasses, forbs and woody species. The height of the plants was measured or, if over nine feet high, estimated, such estimates being checked against felled trees of a similar size wherever possible. Any vegetable remains protecting the surface of the soil was recorded as litter. The canopy of grasses and forbs was noted if, when undisturbed, it was judged vertically above the point. Woody canopies were treated in the same way, except that gaps through the branches were ignored. Where the canopies of more than one plant covered the point, all were recorded. Other data taken on transects included the effects of the soak zone (p.23) or bush fires and signs of the use made of the vegetation by large mammals.

Transects followed a straight line towards a distant land mark and were sited by pacing off a predetermined distance of 30 to 100 yards from a convenient starting point, such as a suitable landing place on the shore.

Evans and Love, and Kinsey both review this method favourably and found it a quick and reliable way of obtaining an objective measure of the habitat. It could be repeated by the same or different workers and yielded consistent results and Evans and Love found it quicker and more accurate than other methods commonly used.

Strip transects were used as a basis for the description of the vegetation on over populated islands. These were sited in the same way as step-point transects and involved sketching to scale all rooted vegetation within two feet of either side of a steel tape laid in a straight line along the ground. These transects were useful for illustrating hedging or browse line effects. A more objective measure of the relative use of different browse plants was obtained from the proportion of leaves removed from samples within easy reach of animals. The percentage of browse taken was determined from the number of leaves removed from a possible 100, but results were influenced, to some extent, by the growth form of different plants. Where leaves arose in clusters, it was sometimes difficult to be sure how many had been eaten, and the relative sizes of leaves were not taken into account. Preferences were usually so definite, however, that the method was useful when direct observation was not possible, the animals using the plants being determined from spoor.

2. METHODS AND RESULTS OF GAME RESCUE OPERATIONS

A high proportion of the large mammals marooned on islands were rescued and released on the mainland by Government-sponsored rescue units. One unit operated along the southern shore of the Lake in Rhodesian waters, while the other was responsible for islands in Zambian waters. The following account is based on experience gained while the author was stationed with the Rhodesian unit during the 1960 and 1961 rescue seasons. Most data extracted from official records of rescue operations apply to the period 2 December, 1958 to 30 June, 1961 as, thereafter, there was a change in policy and animals caught at Kariba were used for introduction into various Game Parks. This resulted in smaller numbers being caught and selection for particular species and sex or age classes.

The first task was to find islands on which game was marooned. These were usually situated in the broad fringe of partially submerged vegetation which, in some places, was over a mile wide. Reconnaissance work was best done from small boats, as many islands were missed from the air and it was often impossible to determine from an aircraft whether or not game was present, as most trees on islands remained in leaf throughout the year.

Animals which could be driven to the mainland from islands or incipient islands were treated first, but formed a small proportion (8.6%) of the total number rescued (Table 1). Where they had to swim, they were followed by a small boat to ensure they reached

Table 1.

Results of Game Rescue Operations

(December 2nd. 1958 - June 30th 1961)

Species	Rescued					Destroyed	Total	% of Total caught or destroyed
	Total	Driven to safety	Handled	Died During rescue	% Loss during rescue			
Monkey	175		175	6	3.4	99	274	7.2
Baboon	217	120	97	2	0.9	206	423	11.1
Hyaena	2		2	0	-		2	
Leopard	1		1	1	100.0		1	
Antbear	38		38	2	5.3		38	1.0
Elephant	3	2	1	0	-	1	4	0.1
Rhino	16		16	3	18.8		16	0.4
Zebra	60	10	50	15	25.0	1	61	1.6
Bush Pig	49		49	4	8.2		49	1.3
Wart Hog	487	17	470	31	6.4	3	490	12.9
Duiker	169	2	167	4	2.4	6	175	4.6
Grysbuck	296	11	287	5	1.7		296	7.8
Klipspringer	20		20	0	-	1	21	0.6
Waterbuck	84	51	33	3	3.6		84	2.2
Impala	1,316		1,316	133	10.1	5	1,321	34.8
Sable	60	27	33	5	8.3		60	1.6
Bushbuck	328	29	299	40	12.2	2	330	8.7
Kudu	153	30	123	7	4.6	2	155	4.1
Total	3,474	299	3,175	261	7.5	326	3,800	100.0

the mainland and did not drown or become lost among the trees. Any which showed signs of drowning were loaded into boats and were then classed as "caught" in Table 1.

The next phase was to plan the removal of animals which could not be driven to safety. Here the size and shape of an island and the species on it had to be taken into account, but the procedure was generally as follows :-

Dangerous game was removed first. In most instances, Elephant swam away from islands, but this had to be prompted on several large islands between 1961 and 1963 by shooting a few, and there were three Elephant prior to this which proved difficult to move (p.50). The small number of Lion and Buffalo trapped before June 1961, left of their own accord, but later numbers of both species were caught or destroyed. Leopard usually disappeared without trace and probably swam to the mainland; the only attempt at catching a Leopard failed when the animal drowned under the influence of an immobilising drug. Black Rhinoceros were immobilised with drugs before being moved to the mainland, as has been described elsewhere (Child and Fothergill, 1962).

Animals which could be driven into the water were dealt with next, as it was easier to catch them from small motor boats than on land. Here the size of an island was important for, as shown in Table 2, most species took to the water more readily from small islands. Animals which were too powerful to be caught in the available game nets were then run down. Men were distributed over the island and the animals were kept running until they could be caught on foot. This method was used for Zebra in particular, and usually led to chases lasting over four hours, by which time the animals were exhausted, so that the method was not satisfactory. It was, therefore, delayed wherever possible on large islands, where the bigger or more dangerous animals could be chased to one portion of an island while smaller species were caught elsewhere.

Game nets, of quarter inch rope woven into a nine to 12 inch mesh, were very satisfactory for Impala and Wart Hog, the two most common species on islands. The nets were erected as an enclosure (fig. 1), preferably across a narrow neck of the island, so that animals were funnelled towards the entrance. Beaters drove animals towards the nets, but these drives often had to be repeated several times as animals broke and doubled back before entering the enclosure. Wart Hog that tangled in the nets well ahead of a drive had to be removed quickly by men hidden behind the nets, as their squeals alarmed other game. Once a group of animals was in the enclosure, the entrance was raised by men concealed near the gate.

Table 2.

The Readiness with which Ungulates Entered the Water from Large and Small Islands.

	Islands Under 5 Acres			Islands over 5 Acres		
	Sample	Entered	%	Sample	Entered	%
Zebra	7	5	71	40	5	13
Bush Pig	10	10	100	4	2	50
Wart Hog	45	37	82	74	8	11
Duiker	31	31	100	4	0	0
Grysbuck	20	17	85	10	5	50
Klipspringer	5	3	60	7	0	0
Waterbuck	16	16	100	4	4	100
Impala	17	9	53	472	13	3
Sable	2	2	100	2	1	50
Bushbuck	45	43	96	12	5	42
Kudu	18	13	72	17	16	94
Total	216	186	86.1	646	59	9.1

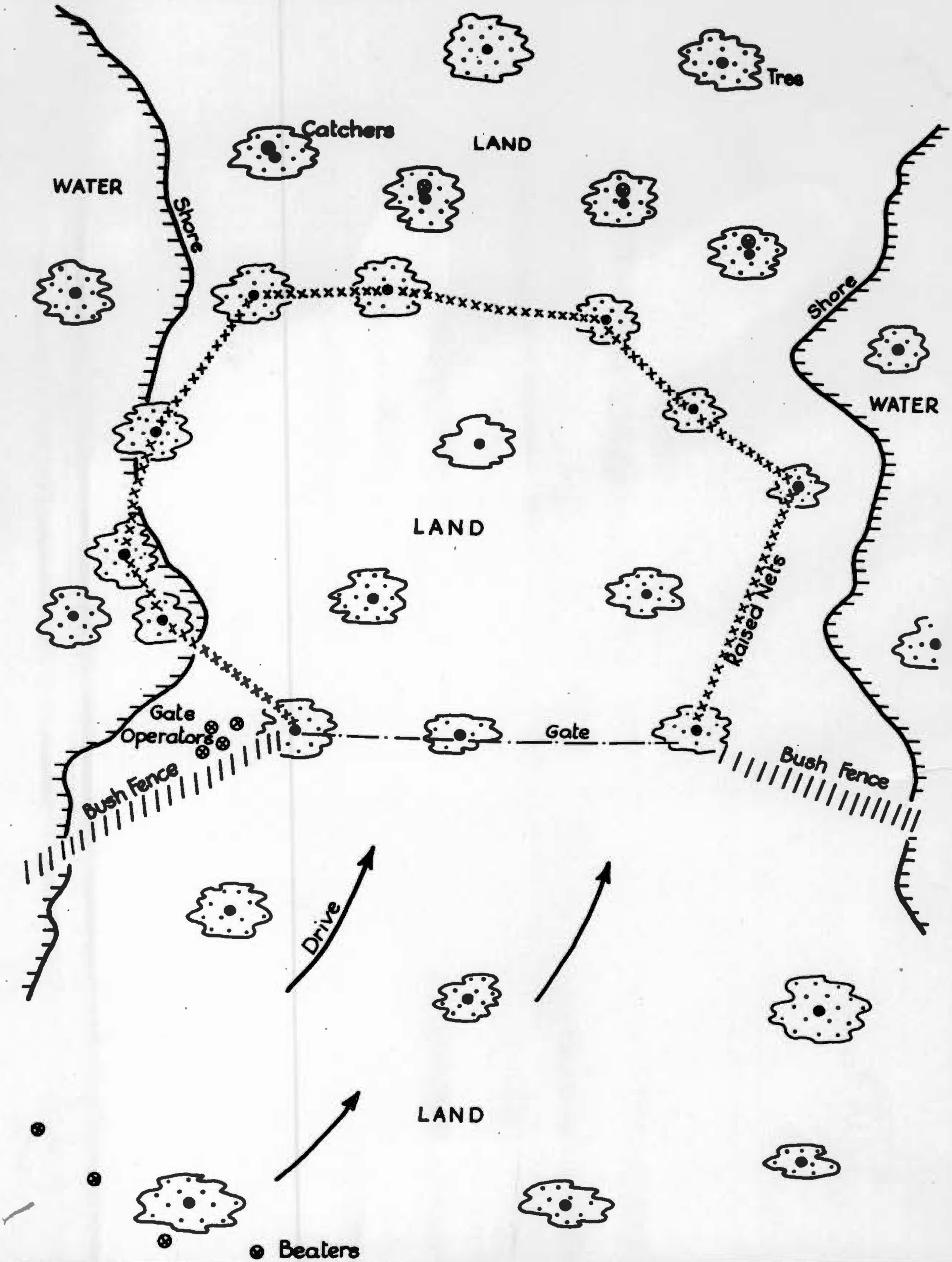


Fig. 1. The arrangement of game nets on Island 17, used on 8th. June, 1960, when over 70 head of Impala and Wart Hog were caught.

The success of this method with Wart Hog and Impala, of which up to 70 could be caught at a time, showed that, with modifications, nets would have been suitable for most species. They needed to be of stronger material for bigger animals and to have had a finer mesh along the lower margin to prevent the escape of the smaller species.

The efficiency of netting was increased if the drive took place from up wind and the enclosure was within the home range of such species as Impala (see p. 81). It was also advisable to pay particular attention to the concealment of the side lowered as a gate. This was done by covering it in a shallow trench and reproducing game trails over the disturbed earth.

Animals which escaped the nets were usually left until an island had diminished in size and they could be driven into the water. Any that took shelter in burrows were then dug out. Primates were left longer, until the island submerged and they were marooned in partially submerged trees, but even then the difficulty of catching them necessitated the destruction of many.

When caught, the smallest animals were placed in grain sacks. Larger species had their legs tied with plaited ladies' nylon stockings, which were elastic and did not chafe, but rope had to be used for the biggest animals. The snouts of Wart Hog and Bush Pig were bound securely and anchored to a firm object, to prevent the wounding of other animals, Zebra had to be stopped from biting or kicking and Ant Bears from kicking. The horns of Sable were held, as this was the only antelope which attempted to use its horns in self-defence.

Small animals caught on land were carried (Plate 1) to a holding point before being loaded into boats for transport to the mainland, while larger species were carried on netting stretched between two poles. All were kept as quiet and in as natural position as possible, and the held was held up, as this reduced losses, possibly caused by the disturbance of the rumen. Animals were seldom in captivity for over three hours, which probably accounted for the low casualties experienced (Table 1). Van Zyl (1961 and pers comm) reports that losses of up to nearly 40% are to be expected where large samples are caught and held for considerable periods in the Transvaal, unless tranquilising drugs are used. Largactil was tried at Kariba, but seemed an unnecessary expense as, in most species, losses were under 10%. The high figure for Zebra (30% of those handled) arose from the unsatisfactory way in which they had to be caught. Grzimek and Grzimek (1960), van Zyl (1961) and Davidson (in press) reported lower losses, but

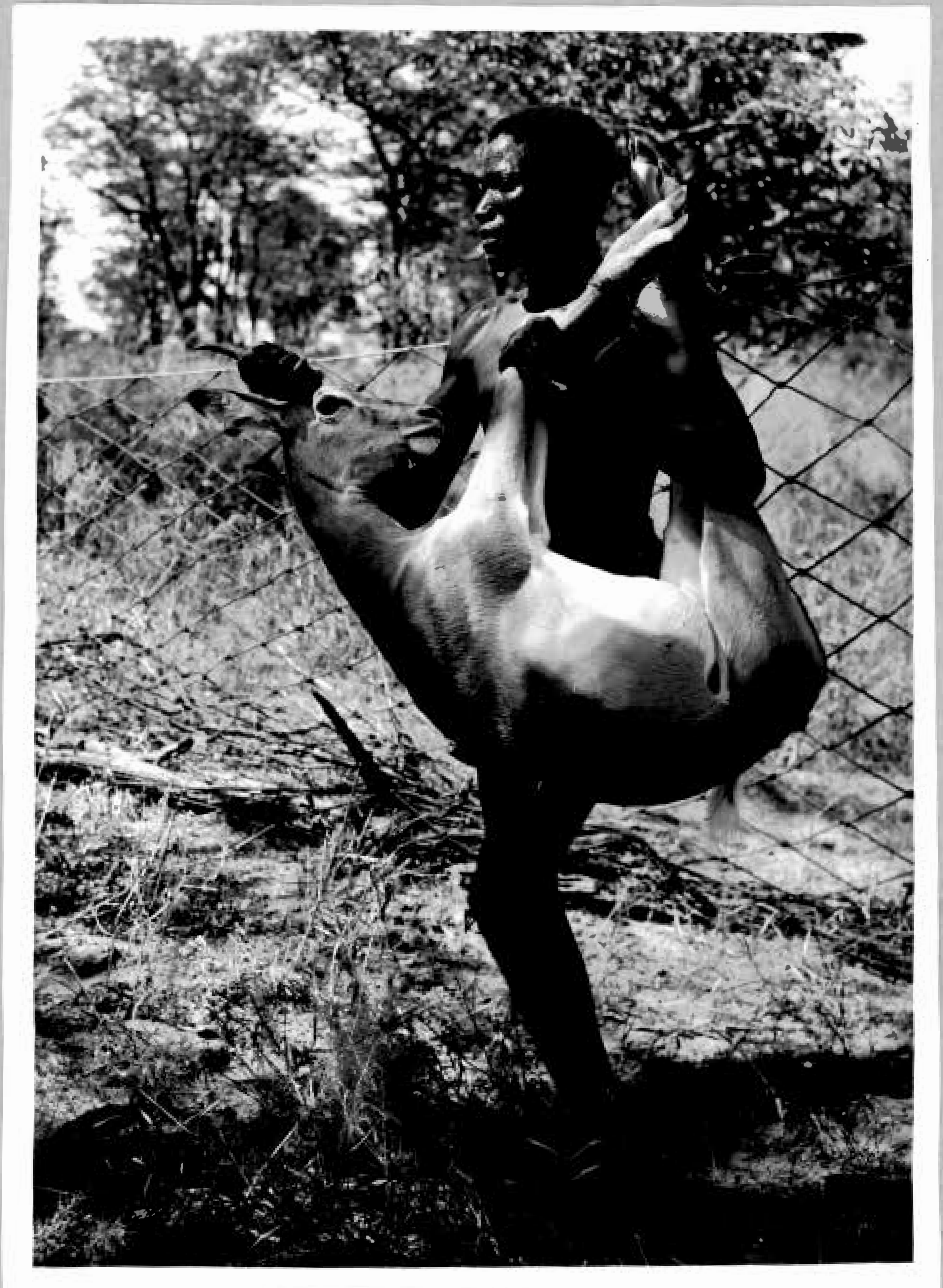


Plate 1. Shows the method used for carrying small ungulates.
Note that the head is held up.

(Photo: Rhodesian Information Service).

had the use of jeeps or horses and only caught animals which could be captured before they were too tired.

Other species with high losses at Kariba were Bushbuck (12.2%) and Impala (10.1%), both of which were prone to shock. This was characterised by high body temperatures, rapid, shallow respiration and a rapid, irregular heart beat, accompanied by a tensing of the muscles, so that the neck acquired a rigid, shallow "S" shape. Some animals with these symptons were saved by pouring water over them to reduce the temperature and so help restore normal respiration and heart beat. For example, a male yearling Impala had a temperature of 106.4°F (the normal temperature in five calves used to being handled, averaged 103.7, range 103.5 to 103.9°F) when caught. This was reduced to 103.4°F in 12 minutes and was accompanied by a rapid fall in the respiratory and pulse rates and a strengthening of the heart beat.

Shock acted quickly and a struggling animal often died within a minute. It seemed to affect animals in better physical condition, possibly because they were stronger and more alert. A curious property of shock in Impala was the way it seemed to be communicated through a group, in much the same way as mass panic. On several occasions, a number of parties of Impala were caught under similar conditions and in one group mortality was higher than in preceding or succeeding groups. The same sort of thing happened in different boatloads of animals loaded simultaneously, where convenience determined which animals were put into any particular boat. An example of this occurred on 28 May, 1961, when eight of 10 Impala died in one boat, although only four of 29 died in three other boats.

Animals were marked for future recognition with numbered ear tags before being released. These metal tags were very efficient in species where the incidence of torn lobes is normally low, but tended to tear out in species like Wart Hog and Rhinoceros, which frequently have damaged ears. Routine records were made at this stage. These included the sex, weight (where possible) and estimated age of each animal, but during this study the following additional data were sought: hind foot length, status of the udder or obvious signs of pregnancy, scrotal length and physical condition, and a few animals were mouthed to obtain the tooth formula.

3. DETERMINATION OF BREEDING STATUS

Breeding data from Kariba was compared, wherever possible, with information collected in other parts of Rhodesia. At Kariba, dead animals were autopsied in the field and this information was augmented by observations of living animals, although elsewhere this was not always possible and men stationed in the field preserved reproductive tracts in 10% Formalin.

A careful macroscopic search was made for foetuses and corpora lutea in dead females, the udders of all females were tested for milk and obvious cases of pregnancy in living animals were noted. In males, testicles were removed by a tangental cut along the proximal edge of the corpus testis, and weighed. In addition to this, a scrotal length was obtained for a few living Bushbuck and Impala at Kariba. The scrotum of bound animals was drawn horizontally along a tape and allowed to relax before measuring it to the nearest half centimeter. This measure was useful for live animals, as it correlated with the testis weight. In seven Impala calves, where the testis was under five grams, the length averaged 3.8 cm (range 3 to 4.5 cm), in 10 yearlings, with testes weighing 15 grams, it was 8.4 cm (range 6 - 11 cm), while in 20 adults, with testes over 35 grams, the scrotum was never less than 11.5 cm. and averaged 13.5 cm.

4. DETERMINATION OF PHYSICAL CONDITION IN LARGE MAMMALS

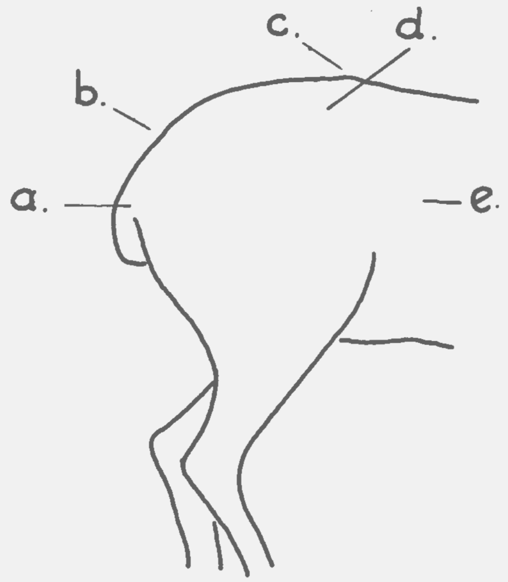
The physical condition of individuals indicates a population response to the status of the environment. Conditions will demonstrate the relative suitability of a given habitat at the current stocking rate and can also be used to predict the effects deterioration of resources will have on population structure. A differential loss of condition between different sex or age classes, for example, shows which groups will be most sensitive to a further decline in environmental conditions.

The condition of animals was determined by the technique developed by Riney (1960), and the results from this method have been checked against the extent of fat reserves.

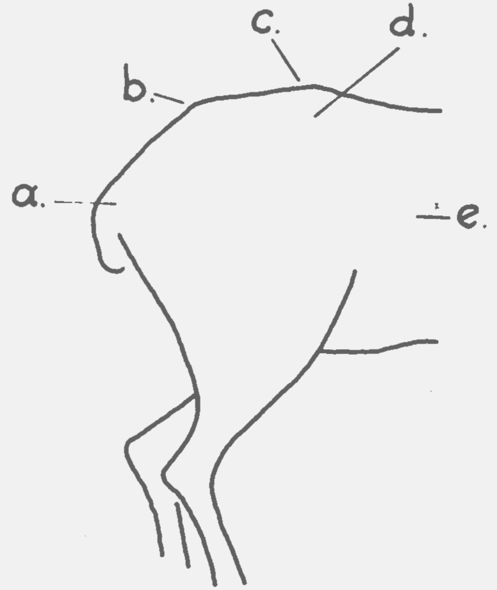
Riney showed that an objective assessment of condition in deer and some African antelope was possible, if individuals were assigned into one of three condition classes, based on the features show in Fig. 2. In animals in good condition (i), the points 'a' to 'c' are not angular and 'd' and 'e' are not readily visible. Animals in poor condition (iii) have 'a' to 'c' clearly angular, the lateral processes of the lumbar vertebrae are visible as a shelf 'd', and the ribs, 'e', are clearly defined. If, after a critical examination of these features, animals were neither good nor poor, they were classed as fair, as represented by (ii).

This method was tested on antelope in the Wankie National Park, and elsewhere in Rhodesia, and worked well, but different sets of criteria were necessary for other taxonomic groups and could only be developed if reasonable samples were available.

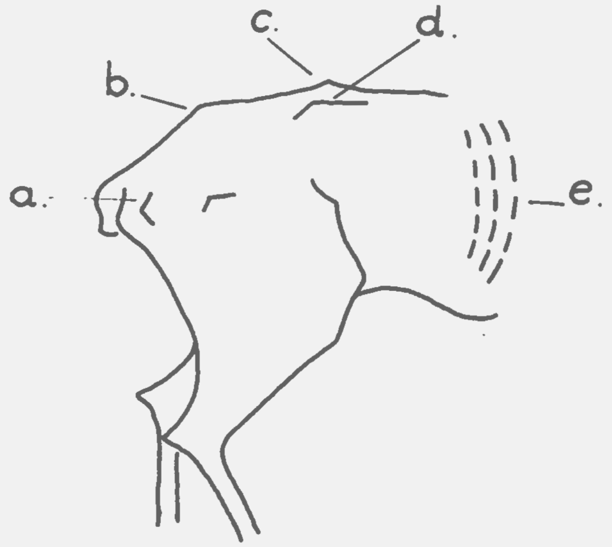
Baboons were divided into two categories. If the limb



(i).



(ii).



(iii).

girdles showed clearly and the abdomens protruded, they were classed as poor and all others were called fair.

Zebra classed as thin had well defined rib cages and vertebral platforms, but these tended to be obscured by the disruptive effect of the animals' stripes and were difficult to detect at over 25 yards, even when using 10 x 50 binoculars. This probably accounts for the widely held belief (see for example Shortridge, 1934) that Zebra are seldom thin. Zebra in poor condition were not confined to islands at Kariba, as most samples observed on a cropping scheme in the south of Rhodesia during the latter half of the dry season contained a few (5 to 10%) thin individuals.

Wart Hog, with the ribs and points of the pelvis showing, with slack skin over the abdomen and often with the dorsal processes of the vertebrae in the lumbar region forming a definite ridge, were classed as poor. Where none of these features showed, they were classed as good and all intermediates were called fair. These criteria were developed at Kariba and have been maintained throughout the present study, although preliminary results from elsewhere suggest some Wart Hog and, to a lesser extent other species, classed as fair were actually in poor condition.

Other species were divided into poor or fair condition on more subjective estimates.

The measurements of fat reserves is being investigated as a means of determining condition of large mammals in Rhodesia, but preliminary results show a good correlation with the visual assessment method. This work is based on Riney (1954) who showed that the size of fat deposits gives a reliable index for the condition of free-ranging Red Deer, <u>Cervus elaphus</u>, Linn, but establishing criteria for Rhodesian species depends on the availability of suitable material ranging from good to poor. Riney based his work on over 1,000 Red Deer carcasses alone, and there were over 300 other autopsies involving six additional species. It is neither economic nor practical to kill sufficient animals for this purpose alone, so that data has been taken from animals shot for other purposes. Unfortunately, most hunting schemes are in over-populated areas and take place mainly in the dry season, so that, although data from animals in poor condition is available, few animals in better shape are shot. Enough work has, however, been done to show that the method will work with most species.

Riney found that the order in which fat is laid down or resorbed from given centres in the body is constant in several distantly related taxonomic groups, and data from Rhodesian species follows the same pattern. This applies only to the beginning and ending of the process in each deposit, as fat may continue to change in one centre after changes have started in another. In Red Deer in very poor condition, for example, the first easily observed deposit to respond to improvements in the environment is the bone marrow. This is followed by abdominal fat, including fat around the kidney, and finally subcutaneous fat is laid down. Loss of fat is in the reverse order.

Kidney fat gives the best index for a wide range of physical condition and was measured by removing the kidney with the fat around it, using the cuts shown in Fig. 3, and weighing this. The fat was then expressed as a percentage of the weight of the kidney with the fat removed in order to standardise readings from different sized animals. The relationship between kidney weight and live weight in Impala is shown in Fig. 4. in which fat animals are excluded because of the obvious influence this fat has on an animal's weight.

Changes in the depth of subcutaneous fat overlap changes at the upper extreme in the kidney fat and are useful for determining the condition of individuals high on a theoretical scale extending up from death to animals in peak condition. The depth was measured to the nearest millimetre near the root of the tail by making a cut at 45° to the dorsal processes of the lumbar vertebrae. The greatest depth was taken, but if under one millimeter it was ignored and if between one and three millimeters, it was described as a trace and taken as two millimeters when calculating averages.

Changes in the marrow fat indicate condition at the opposite end of the overall scale and overlap the lower limits of changes in kidney fat. The femur bone was broken and the fat was assigned into one of three classes. If whitish in colour and waxy in texture, it was good, if red and gelatinous or watery or oily, it was poor, and all intermediates were fair. The condition of the bone marrow could also be assessed in carcasses which had been dead for some time. This was very useful in cases where decay was fairly well advanced or where other deposits had been damaged by scavengers. It is necessary to stress, however, as some authors have overlooked this point, that although poor marrow does show an animal to have been in poor condition, better marrow does not necessarily mean it was in fair or good condition.

These three indices can be combined to cover a wide range of physical condition similar to that described by Riney (1954) which show a satisfactory relationship to visual assessment of condition. Work at Kariba dealt mainly with animals classified

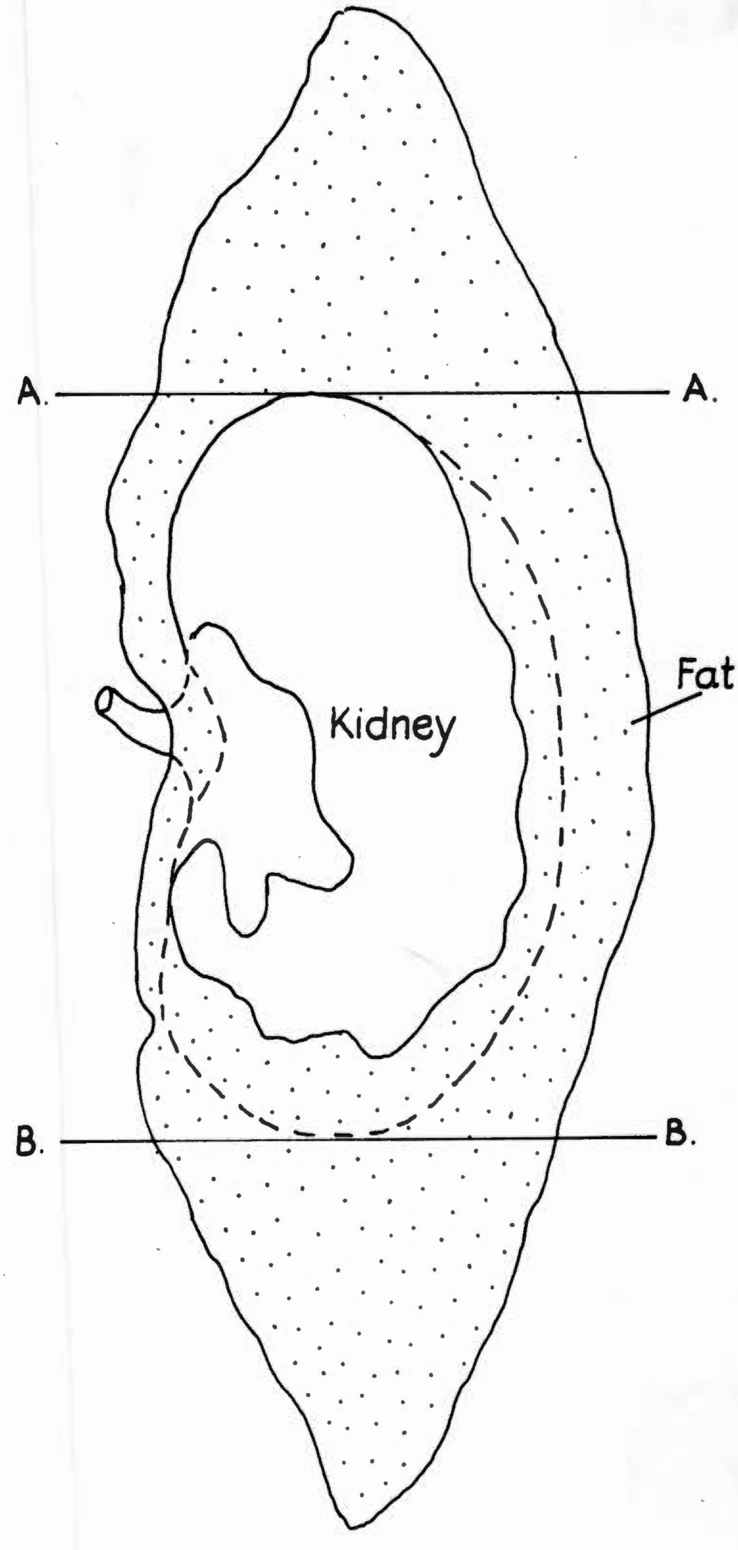


Fig. 3. Shows the standard cuts AA and BB used to remove the left kidney and a uniform quantity of the surrounding fat, shaded, which was expressed as a percentage of the weight of the kidney.

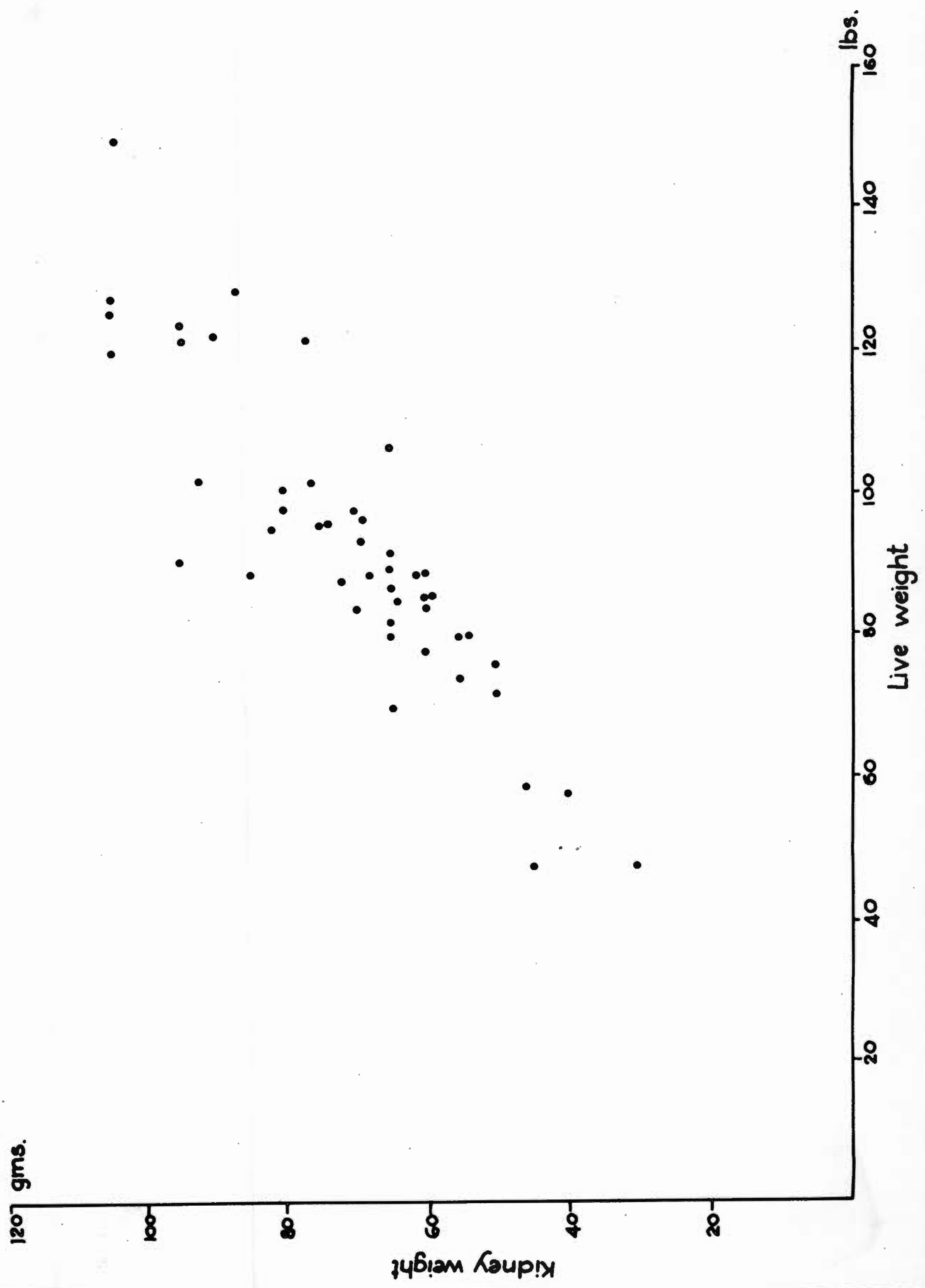


Fig. 4. Shows the correlation between body weight and kidney weight in Impala ($r=0.701$, $P>0.001$).

as poor and it was important to be sure that these had depleted fat reserves. The preliminary results in Table 3, show that this was in fact the case, and indicate the correlation between the extent of various fat reserves for a number of species for which adequate measurements are available.

It has been suggested that large fat reserves are seldom developed in African game because it never has to face critical winters, similar to those experienced by deer in ranges with winter snow. The five animals classified as good (Table 3) did, in fact, have well developed reserves and at the beginning of the flood season on the Kafue flats, Lechwe, Kobus leche Gray, had large deposits. Back fat ranged between a trace and 30 mm (mean 12 mm) in 41 females over a year old, while the kidney index ranged from eight to 120 (mean 53.3) in 36 specimens, four of which had indices of over 100. These measurements were taken at a time when the Lechwe were becoming limited to a small portion of their range (Robinette and Child, 1964). The use of condition indices, as suggested and elaborated by Riney for ungulates in temperate regions, seems equally applicable in principle to most ungulates in tropical regions, but much more work is needed to explore further the uses and limitations of the technique as an index to the suitability of specific environments for each species.

5. AGE DETERMINATION

The absence of established ageing criteria and growth rates for all species, except Duiker, proved a serious handicap when determining the age structure of populations marooned on islands. As a result, less precise methods had to be developed on the study, and several species could only be divided into arbitrary age classes, based on stages of development. The fact that changes in the age composition of these populations could still be detected further strengthens the conclusions reached in this paper.

Baboons were divided into infants, juveniles, sub-adults and adults. Infants were dark in colour and judging from a known age captive specimen included all individuals up to at least three months old. Juveniles had predominantly adult coloration, but were less than half the size of adult females. Animals larger than juveniles, but not yet full grown, were classed as sub-adults, but the separation from adults was made difficult by the possibility that young males may grow more quickly and would have been termed adults, while the same aged females may still have been called sub-adult. Changes in population structure were, however, so clearly defined that this problem did not alter the results obtained at Kariba.

Table 3.

Comparison of The Visual Method of Assessing Physical Condition with the Extent of Fat Reserves

Visual Assessment	Species	Sample	Fat Measurements						
			Back Fat mm.		Kidney Index		Marrow i)		
			Spread	Mean	Spread	Mean	G.	F.	P.
Good	Impala	3	14-17	16	72-148	101	3		
	Wart Hog	1	-	11	Over 50 not weighed		1		
	Klipspringer	1	-	8	-	63	1		
Fair	Impala	11	Tr-11	7	20-50	36	4	1	
	Wart Hog	1	-	7	-	13		1	
	Grysbuck	1	-	3	-	65	1		
	Bushbuck	1	-	2	-	52		1	
	Kudu	1	-	3	-	30		1	
	Reedbuck	1	-	0	-	36	1		
	Zebra	1	-	8	-	3			
Poor	Impala	83	0-6	1	0-39	7	5	15	45
	Duiker	72	0-0	0	0-20	0			72
	Wart Hog	37	0-10	3	0-50	7		37 ii)	
	Steenbuck	14	0-0	0	0-Tr	0			14
	Bushbuck	7	0-Tr	1	0-89	24 iii)			7
	Zebra	7	0-0	0	0-0	0			6
	Kudu	6	0-2	0	3-15	7			6
	Klipspringer	6	0-0	0	0-Tr	2	2	2	2
	Baboon	4	0-0	0	0-0	0			4
	Sable	4	0-0	0	0-20	11			4
	Grysbuck	3	0-0	0	0-Tr	0			3
	Tsessebe	3	0-Tr	1	0-2	1			3
	Rhino	2	0-0	0	0-0	0			2
	Reedbuck	2	0-0	0	1-13	7		1	1
	Buffalo	2	0-0	0	0-0	0			2
	Roan	1	-	3	-	7		1	
	Total	275							

G = Good, F = Fair, P = Poor

i) **The marrow was not checked on a few skeletons retained as specimens**

ii) **Additional investigation needed for assigning condition of Wart Hog Marrow**

iii) **Average influenced markedly by a Bushbuck with no back or marrow fat which died of starvation, with a kidney index of 89.**

by the state of tooth eruption and it was not possible to check the teeth of many living Impala at Kariba. They were usually caught in groups which needed to be released quickly to avoid losses from shock. The cheek teeth are difficult to see because of the narrow muzzle and Child has shown that the incisor form teeth are replaced by the age of 20 months in most specimens, whereas yearlings at Kariba in May to July were 19 to 21 months old. Wear of these teeth might have been a guide, but was considered unreliable because of the harsh feeding conditions on some islands. All casualties and carcasses found on islands were, however, aged according to the method described by Child.

Small antelope, including Klipspringer, Grysbuck and Bushbuck, but not Duiker caught in 1961, were aged from size. This was not satisfactory for Grysbuck, except as a means of distinguishing young calves, because they probably grow rapidly as Riney and Child (1960 and 1964) showed that Duiker over six months old were all about the same size. The average weight of five Grysbuck with adult dentition was 20 lbs. (range 18 to 24 lbs) compared with an average of 34.9 lbs. (range 31 to 40 lbs) in 16 male and 38.5 lbs (range 27 to 47 lbs.) in 15 female Duiker, with the same dentition, from the Cewali area and Doddieburn Ranch, so that Grysbuck probably grow even more quickly.

In a sample of 31 Grysbuck, there was one which was smaller than the range covered by specimens with all adult dentition. It had a hind foot of 175 mm. compared with two adult males with a hind foot of 194 and 214 mm. and four adult females, where it ranged from 202 to 209 mm. (mean 206 mm). Live weight was also of little value in ageing these small antelope.

Bushbuck are bigger than Grysbuck and compare in size with Impala and, as in Impala, females, which mature earlier than males, reach maturity at about one and a half years (Wilson and Child, 1964). It therefore seems probable that visibly smaller Bushbuck included all those up to a year old, and these were classed as calves.

Large antelope, such as Kudu, Sable and Waterbuck, were handled in relatively small numbers and were difficult to age as little is known of their rate of growth and tooth eruption, or of their age at maturity. The order of tooth eruption follows the usual sequence in deer and antelope (excepting Duiker) so that where the tooth formula could be obtained, age was expressed in terms of the state of tooth eruption, or in animals with fully adult teeth as wear, recorded as either light, moderate or heavy. Two known age two year old Kudu helped in the assessment of age in this species.

Buffalo were also divided into age classes based on the tooth formulae, in this case obtained from a collection of jaws and supplemented by flesh measurements.

The Author's own records of the age composition of populations of large mammals trapped on islands is augmented by departmental records of Game Rescue operations. These records are used cautiously, as ages were estimated by several observers using different standards. It is safe to assume that animals recorded as juveniles were very young, although "adults" may have included many immature animals. This meant that a decline during the year in the proportion of juveniles, in species with a marked peak in calving, could mean either a juvenile mortality, or that the calves had grown too big to class as juveniles. This fact was not taken into account by Dasmann and Mossman (1962c) although there is little doubt that the trends they described were correct.

THE CENTRAL ZAMBEZI VALLEY

1. SITUATION

Lake Kariba lies between 16°25' and 18°5'S, and 25°45' and 29°5' E, (Fig. 5). It resulted from the flooding of most of the Central Zambezi Valley, which is defined by Bond (Ms) as lying between the Victoria Falls gorges and Kariba gorge, when the river was dammed at Kariba. The river here formed the boundary between Rhodesia and Zambia.

Field work took place all along the southern shore, but on the north bank was limited to within 20 miles of Binga (Fig. 6). The area on the east bank of the Bumi River is mapped in greater detail in figure 7, as it is discussed later in the paper.

In order to avoid confusion with other published work, it is necessary to point out that there has been considerable alteration of place names in this region during the last few years. The most important of these was the renaming of Northern Rhodesia as Zambia and the Sanyati river as the Umniati. It should also be mentioned that there are two Mwenda rivers flowing into Lake Kariba, one from the north above Binga and one from the south below Chete. Islands were allocated arbitrary numbers during the course of field work and these are retained in Figure 6.

2. GEOLOGY AND TOPOGRAPHY

Gair (1959) recognised the Zambezi Valley as an area of subsidence overlaid by Karoo sediments, upon which alluvia were later deposited. He considers major geological change ceased in early tertiary times and that the topography of the valley arose from erosion.

Around the southern and eastern shores of the Umniati basin, at the eastern end of the Lake, there is an abrupt escarpment formed by the Matuzadonna and adjacent ranges (Fig. 6). These mountains reach 4,068 feet and are over 2,300 feet above the valley floor. Elsewhere, the descent to the valley from the Rhodesian or Zambian plateaus is down a series of rough sandstone ridges resembling giant terraces. The last of these ridges varies from under a mile to over 20 miles from the Zambezi river. It skirts the valley floor, which is flat or undulating with occasional isolated hills, and slopes gently from the foot of the ridge (see cross sections Fig. 8). Flooding covered most of this area, so that the shores of the Lake are along the ridge. The main exception is a broad apron of flat land at the base of the Matuzadonna range, between the Umniati and Bumi rivers.

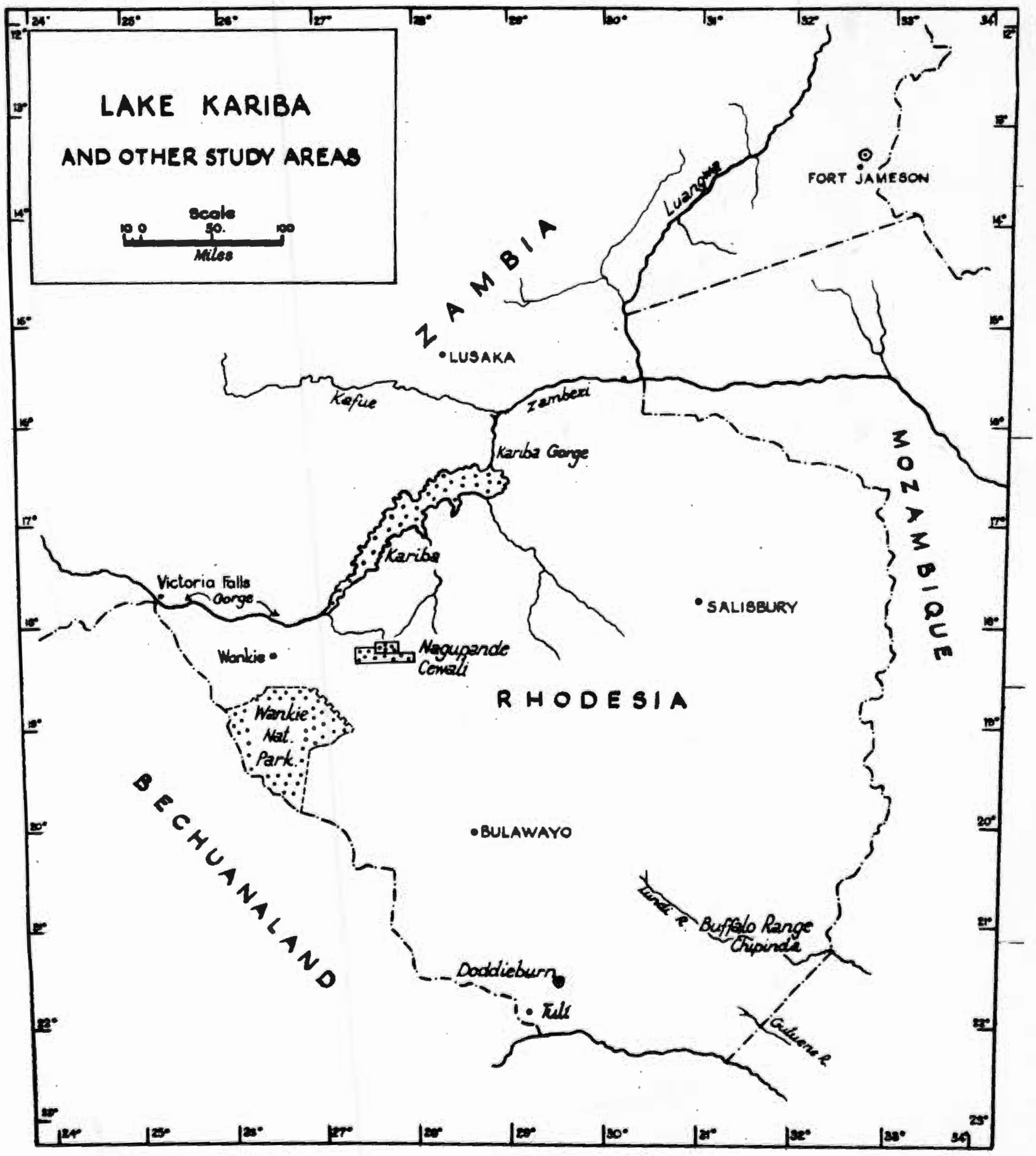


Fig. 5. Shows the position of Lake Kariba and other important areas mentioned in the text.

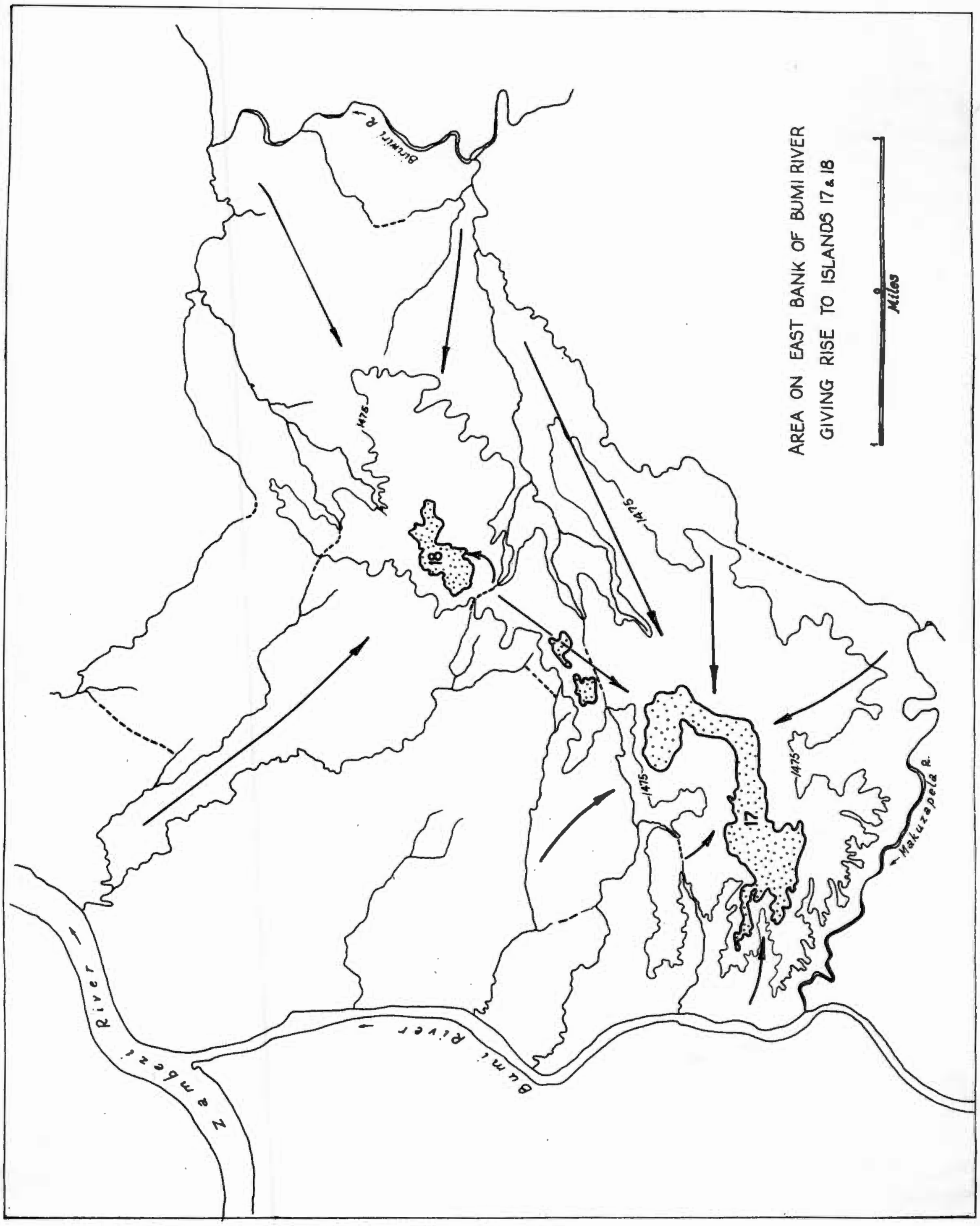


Fig. 7. The position of this area is shown in Fig. 6. Dotted lines indicate where water cut through between rivers or streams and the arrows indicate the pattern of flooding towards Islands 17 and 18 which are shaded.

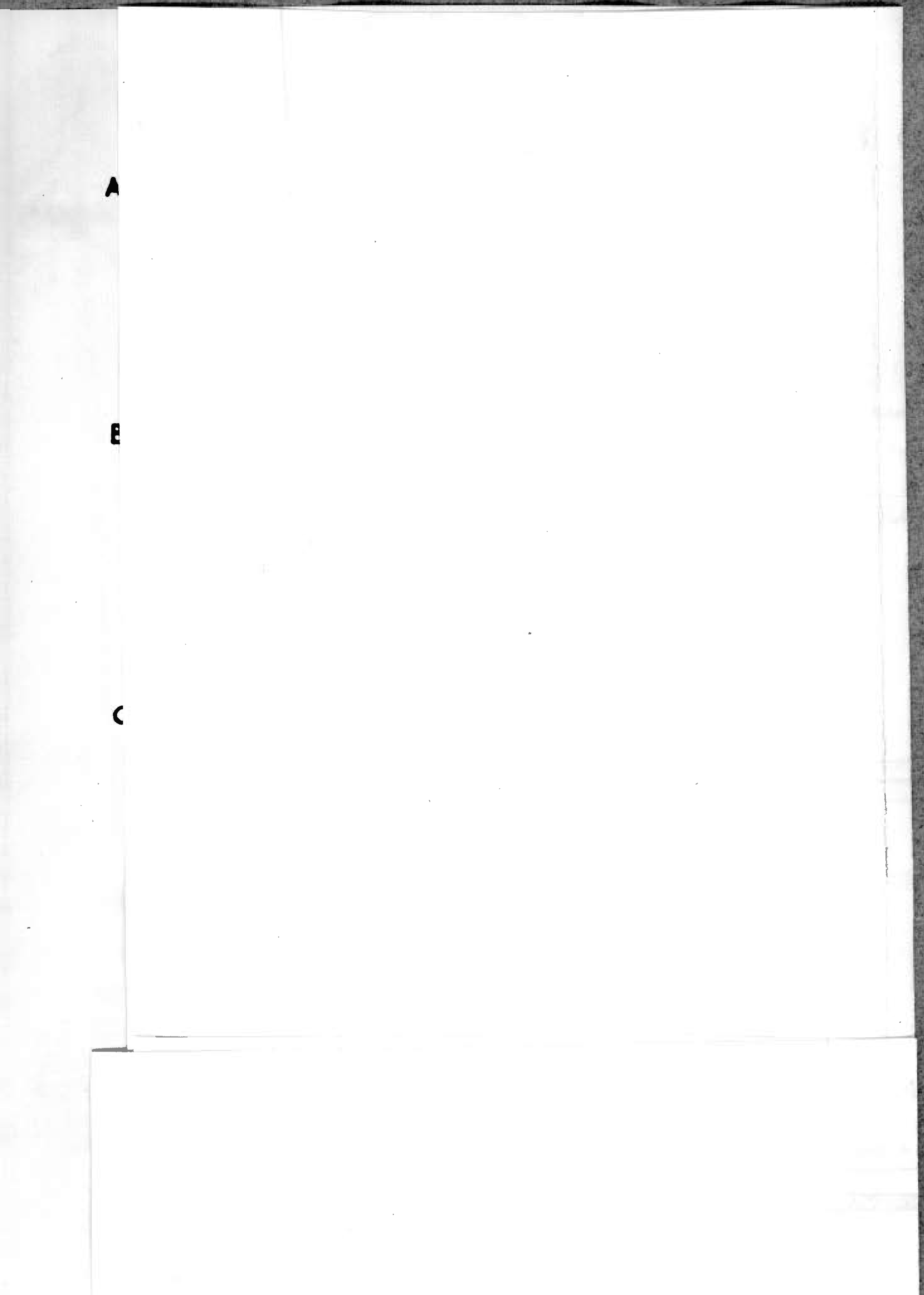


Fig. 8. Cross sections of the Kariba Basin showing the flat valley floor surrounded by rocky escarpments. The positions of these sections are shown on Fig.6.

Generally the soils of the valley floor were derived from Karoo deposits, but there were areas of fertile alluvium along rivers, and old eroded alluvial terraces formed a band some distance from the Zambezi, between the Sengwa and Umniati valleys. The most extensive deposits of fertile alluvium were between the Masumo and Sebungwe rivers, where the Zambezi meandered through a plain up to five miles wide.

3. CLIMATE

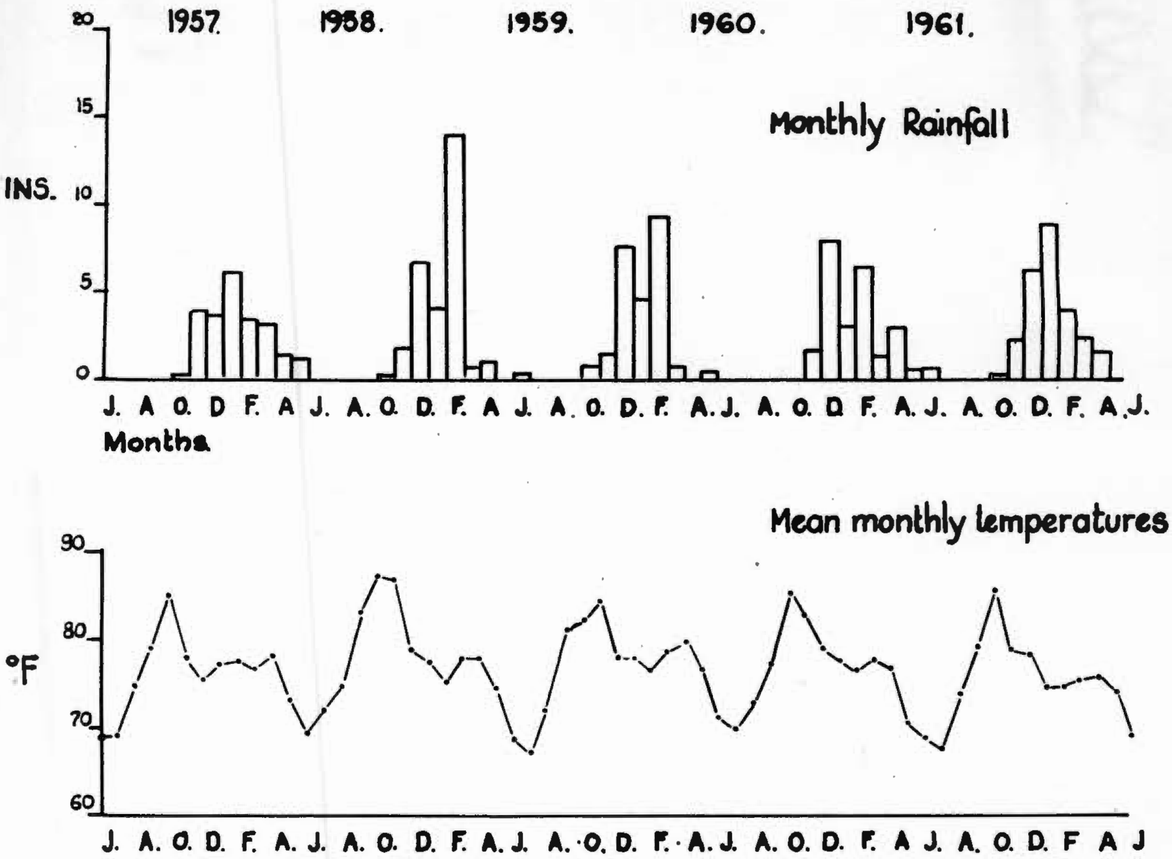
The Central Zambezi Valley has mild dry winters, leading to a hot dry season before the rains, which are characterised by sporadic heavy falls over a period of six months. Rainfall and temperature figures from 1957 to 1961 for Kariba and Binga, the only two meteorological stations on the south bank, are graphed in Figure 9. A more detailed account of the climate is given by Scudder (1962).

The coolest months are June and July, with average temperatures around 70°F. From then, mean temperatures rise to a maximum of 85 to 90°F. in October or November, before the rains begin in earnest. The annual rainfall at Kariba and Binga is c 25 and c 26 inches respectively, and during the rainy season mean temperatures remain around 80°F, before declining to the winter minimum.

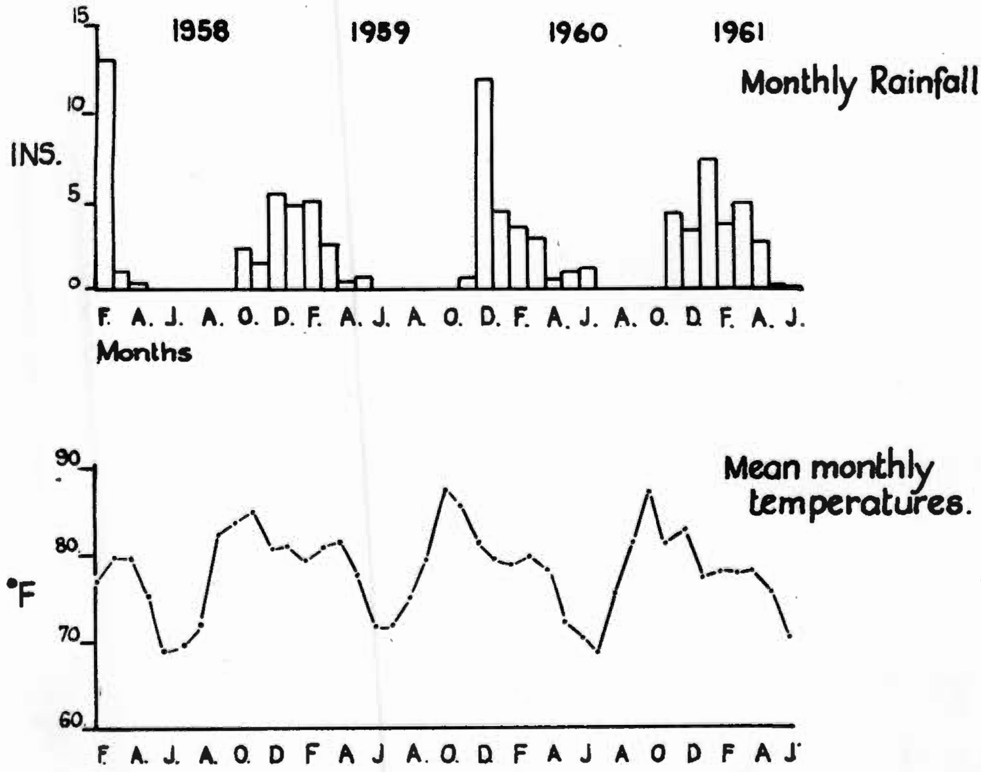
This climate is not as severe as that associated with semi arid regions, although in common with them it has a very dry season lasting two to three months. Riney (1963) and others have referred to this type of situation as "marginal" or "dry marginal", implying it approaches semi-arid conditions and is unsuited to conventional agriculture, except on a very extensive scale. This term is appropriate for many of the game areas in Rhodesia, including the Central Zambezi Valley, and has been adopted here for areas with fluctuating climatic conditions which periodically experience poor rainy seasons.

4. VEGETATION

The vegetation was characteristically deciduous except for the narrow fringe of evergreen trees on fertile alluvium along rivers and is described by Keay and Aubreville (1959) as predominantly savannah woodland dominated by mopane, Colophospermum mopane. The mopane was not homogeneous as scattered through it there were thickets, while in rocky areas there was a mixture of other trees. East of the Sengwa river there was a broad belt of open savannah with scattered small



KARIBA.



BINGA.

Fig. 9. Monthly rainfall and mean monthly temperature figures for Kariba and Binga.

trees and tussock grassland on the old eroded alluvial terraces.

A. Riverine Vegetation

The riverine vegetation had been greatly modified by the dense human settlement on fertile alluvium, so that limited areas retained a closed canopy which had generally been reduced to scattered big trees, with scrub or native cultivation between them. The species composition of 450 evergreen trees in an area near Binga is given in Table 5, which shows how the natives saved those trees most useful to them (see Scudder, 1960). The general nature of the vegetation between the trees is analysed in Table 6, based on point-line transects. In the most fertile areas, the scrub was mostly *Acacia* spp. with some *Dicrostachys cinerea* (*glomerata*) but even here grasses were poorly developed. *Diospyros quiloensis* became very conspicuous in less fertile areas, while on the oldest alluvium, where large trees were rare, the scrub was more varied and included *Combretum* spp., *Commiphora* spp., *Terminalia* spp., some *Grewia* spp. and a few stunted mopane.

This vegetation type supported few large mammals apart from monkeys, as its distribution coincided with that of the densest human settlement. Most of it was submerged so that it is now represented by isolated, poorly developed pockets along some of the tributaries leading into the Lake.

B. Mopane Veld

Mopane occurred in almost pure stands over most of the valley floor between the riparian fringe and the rocky ridges in the area described as (A) in the cross-sections of the Lake (Fig.8). These attenuated trees up to 60 ft. tall, formed an open canopy and grasses, mostly short annuals, were sparse. Usually there were occasional baobabs, *Adansonia digitata*, and in some areas a few *Commiphora* spp. trees or *Terminalia prunioides*. In one area sampled, *Commiphora* accounted for 7% and mopane 51% of a total woody canopy of 69% along two step-point transects. On another transect, *T. prunioides* contributed 14% and mopane the remaining 30% of the woody canopy. The differences in the actual number of trees was greater than these results suggest, as both *Commiphora* and *T. prunioides* have spreading forms which frequently covered several points on a transect, whereas this was unusual for mopane.

Thompson (1960) attributes the widespread occurrence of mopane in the Central Zambezi Valley to soil conditions, with a shallow top soil overlying an impervious sodium-dominated subsoil. Here the shallow rooted mopane competes favourably with deeper rooted plants. He also found that mopane does not become established where there is a good grass cover, but that once established

Table 5.

Species composition of large trees on fertile alluvium near Binga. i)

Species	Number Counted	% Total Sample
Lonchocarpus capassa	159	34.87
Phyllogeiton discolor	105	23.02
Diospyros mespiliformis	47	10.31
Triplochiton zambesiacus	26	5.70
Acacia albida	21	4.61
Cordyla africana	18	3.95
Trichilia emetica	17	3.73
Tamarindus indica	17	3.73
Azanza garckeana	7	1.54
Kigelia pinnata	6	1.32
Combretum imberbe	5	1.10
Kirkia acuminata	3	0.66
Unidentified (5 species)	25	5.48
TOTAL	456	-

i) Nomenclature follows Boughey (1964)

Table 6.

Vegetation on Fertile Alluvial Deposits

Transect	No stations	% old cultivation	% bare ground	Ground cover			Woody cover			
				% grass + canopy	% forbs + canopy	% total	% *Diospyros quiloensis*	% Thorn scrub *	% other spp.	% total
1.	100	0	90.0	43.0	18.0	61.0	45.0	27.0	4.0	64.0
2.	500	26	92.8	38.2	9.8	45.0	4.6	39.8	8.0	48,0
3.	100	0	90.0	34.0	10.0	33.0	0.0	64.0	18.0	78.0

* Thorn scrub in this area consisted mostly of *Acacia* spp., especially *A. tortilis (hetracantha)*, with some *Dichrostachys cinerea (glomerata)*

it suppresses grass growth. This was borne out by the improved grass cover observed in bush clearings. For example, at the height of the growing season there was 40% grass and grass canopy averaging 20 inches in height in a clearing, compared with 19%, averaging six inches, in uncleared mopane veld 20 yards away. The significant improvement in the grass cover (standard error difference of proportion = 0.0644, $P=0.001$) was accompanied by an increase in other woody species at the expense of mopane, and this probably favoured browsing and grazing animals.

C. Scrub Thickets

There were patches of dense scrub scattered through mopane veld, most of which were dominated by jesse, *Combretum elaeagnoides*, which seldom exceeded 15 ft, or *Commiphora* spp. or *Terminalia prunioides*, which were small trees about 30 ft. tall. Thickets in the Umniati basin contained most of the species characteristic of open savannah, while in disturbed areas, they were mostly *Acacia* spp. and *Dichrostachys cinerea*.

Thickets provided good cover and often contained palatable browse plants, but the ground cover was negligible.

D. Mixed Woodland

Markedly deciduous woodland containing many different species occurred in rocky areas, especially on the ridges forming much of the Lake shore. Conspicuous trees were: *Sclerocarya caffra*, *Kirkia acuminata*, *Strychnos* spp., *Combretum* spp., *Commiphora* spp., *Sterculia quinqueloba* and baobabs. This vegetation had more perennial grass than any so far described, but was relatively unimportant in the present study.

E. Open Savannah

The commonest of the small trees in open savannah are listed in Table 7. *Diospyros kirkii* predominated in some areas while elsewhere *Terminalia randii* and *Combretum apiculatum* were common. The greatest mixture of species occurred along the many water courses draining this undulating country. *Andropogon gayanus* and *Loudetia flavida* were widespread among the tall rank perennial grasses which grew in most areas.

F. Vegetation of main study areas

The areas in which most field work took place were all characterised by mopane veld. There was an intrusion of the open savannah element associated with it in the Nyamuni River area on the west bank of the Umniati River, where small trees and bushes and tall perennial grasses were more abundant than usual. The mopane in the Bumi east area was well developed and homogeneous with scattered patches of jesse. The greatest variation occurred on Island 17, whose vegetation is shown in Figure 10. The map

Table 7.

Important Trees in Open Scrub Savannah

Species	Status
Diospyros kirkii	Very common
Terminalia randii	Common
T. brachystemma	Locally common
T. stuhlmannii	Very common
Combretum apiculatum	Locally common
C. ghasalense (turnifolia)	Common along some water courses
C. imberbe	Scattered along water courses
Acacia nigrescens	
A. tortilis (heteracantha)	Locally common
Piliostigma thonningii	Scattered along water courses
Kirkia acuminata	Scattered some distance from water courses.
Sclerocarya caffra	Scattered some distance from water courses
Commiphora spp.	Locally common in more broken areas
Croton sp	Sparse
Colophospermum mopane	Widespread relatively sparse
Tamarindus indica	Scattered along water courses
Diplorhynchus condylocarpon (mossambicensis)	Limited distribution
Pterocarpus brenanni	Locally common
Hyphaene crinita	Scattered near water courses

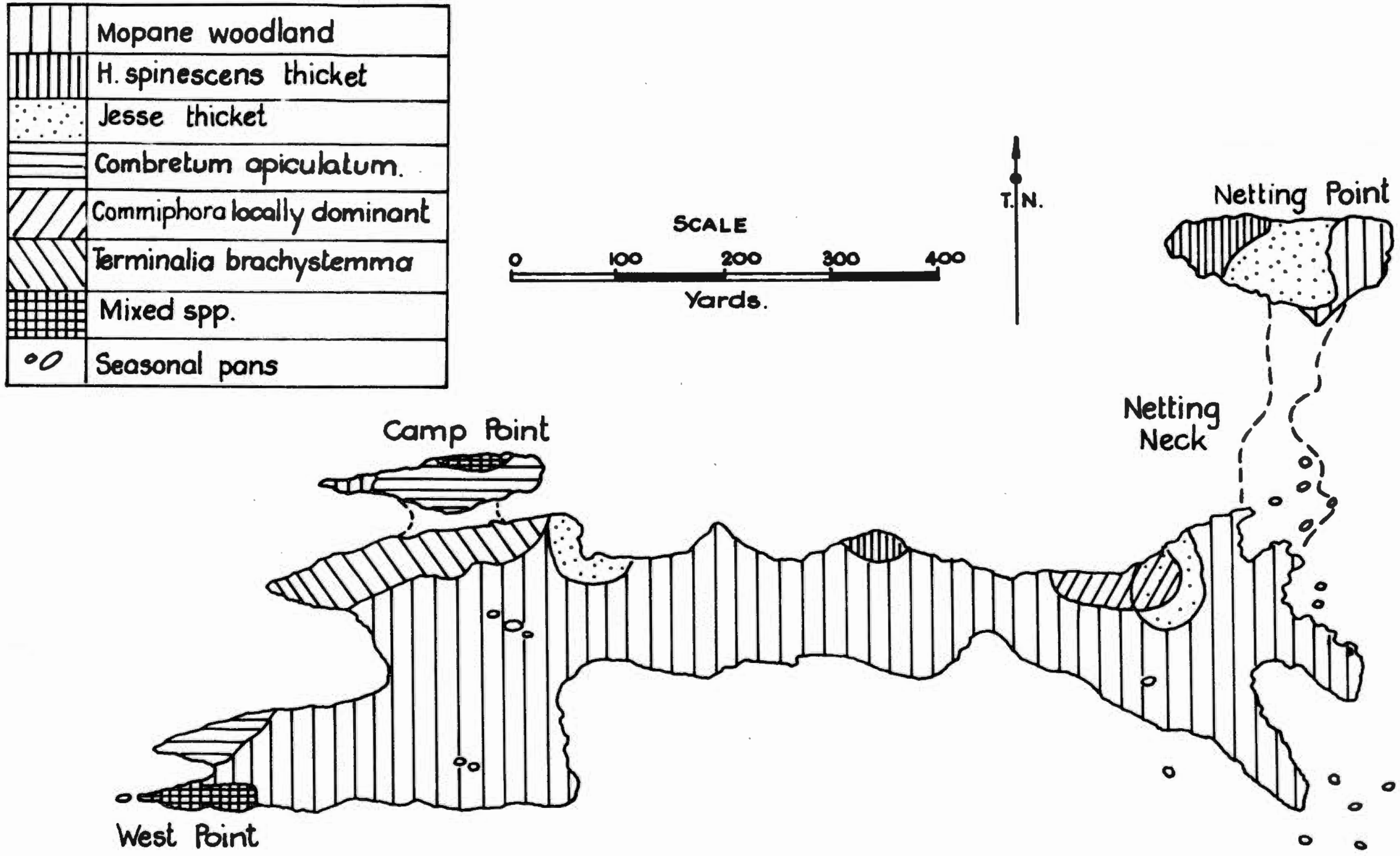


Fig. 10. Vegetation map of Island 17 showing more or less pure mopane woodland and areas where other woody plants were dominant associates with it.

was drawn at the end of June, 1960, by packing off key distances and estimating others in relation to these. By this time, the island had a somewhat different shape from that shown in Figure 7, taken from the 1,500 ft. contour on Federal Survey maps. Topography and past human disturbance, associated with a light shifting agriculture, were the chief causes for the greater complexity of the vegetation on the island. There were a number of marula trees, Sclerocarya caffra, Kirkia acuminata and Lonchocarpus capassa trees on outcrops, and Holmskioldia spinescens with some Dichrostachys cinerea, Terminalia brachystemma and Combretum apiculatum thickets marked old patches of cultivation.

Most of the island had had an annual grass cover, but neither these nor the scattered perennials associated with T. brachystemma or C. apiculatum could be identified in June 1960 because of trampling by the concentration of game on the island. Portions of the island, not submerged by early 1961, supported the annual Digitalia sp.

Most of the Bumi west area had been bush cleared but had consisted chiefly of mopane veld with patches of jesse. Thickets of T. prunioides and Commiphora spp. were fairly numerous along the Bumi river and Islands 201 and 210 consisted of a ridge, where there were other species, including Combretum imberbe, C.apiculatum, Kirkia acuminata, T. prunioides, Commiphora spp. and fair amounts of jesse, associated with the mopane. Perennial grasses were only plentiful on Island 201 and in parts of the clearing.

In the region of Island 7, there was typical open savannah dominated by Terminalia randii, and the uncleared crest of Bumi Island had savannah woodland similar to that found on rocky areas.

5. MAMALIAN FAUNA

Concentrations of game in the Central Zambezi Valley have attracted hunters since before Rhodesia was colonised in 1890 (Gale, 1960), but it was not until Game Rescue Operations started on the Lake in December 1958, that there was any sort of survey of the Mammalian fauna. Even then Game Rescue dealt mainly with large mammals, so that much work remains to be done on the smaller species. Table 8 lists the mammals so far recorded from the area. Remarks on distribution are general and abundance is indicated by "rare", "common" or "abundant", as judged against nearby areas. The scientific nomenclature and arrangement follows Ellerman et al (1953), unless otherwise stated, but common names are those in general use in Rhodesia. Remarks on distribution in Zambian waters are based on records kindly supplied by Mr. W. F. H. Ansell.

Table 8.

A Systematic List of Mammals Recorded from the Kariba Basin

Common Name	Scientific Name	Abundance	Remarks on Distribution
Short-snouted Elephant Shrew	*Elephantulus brachyrhynchus* A. Smith	?	Kariba, Umniati R., Binga, Sebungwe R.
Four-toed Elephant Shrew	*Petrodromus tetradactylus* Peters		Kariba Area, Zambia
Night-ape	*Galago senegalensis* E. Geoffroy	C	Throughout E of Sengwa R.
Bush Baby	*G. crassicaudatus* E. Geoffroy	R	One specimen caught - Bumi R. area, also known from Zambian waters.
Vervet Monkey	*Cercopithecus aethiops* Linn	C	Throughout
Baboon	*Papio ursinus* Kerr	A	Throughout
Pangolin	*Manis temmincki* Smuts	R	Bumi/Umniati areas on both sides of Zambezi
Side-striped Jackal	*Canis adustus* Sundevall	R	Bumi R. and Binga
Wild Dog	*Lycaon pictus* Temminck	?	One pack recorded Sengwa R. (Rescue Reports)
Honey Badger	*Mellivora capensis* Schreber	?	Bumi R. and Sampakaruma area and Zambian waters in this area.
Civet Cat	*Viverra civetta* Schreber	R	Kariba, Bumi area, Binga area. Also in Zambia in this area.
Genet Cat	*Genetta* sp. (?all *tigrina* Schreber)	C	Throughout
Large Grey Mongoose	*Herpestes ichneumon* Linn	?	E.Umniati Basin (Smithers *pers. comm*)
Slender Mongoose	*H. sanguinsus* Rüppell	R	Kanchirdu Mission area and opposite Sebungwe estuary.
Dwarf Mongoose	*Helogale parvula* Sundevall	?	Umniati/Zambezi confluence. Sinazongwe, Zambia.
White-tailed Mongoose	*Ichneumia albicauda* G. Cuvier	R	Zambia, opp. Bumi R. also Rhod. Island no locality recorded.
Selous Mongoose	*Paracynictis selousi* de Winton	?	Binga/Sebungwe R. area
Aardwolf	*Proteles cristatus* Sparrman	?	Bumi R. Sinazongwe (Ansell 1964
Spotted Hyaena	*Crocuta crocuta* Erxleben	C	Throughout
Wild Cat	*Felis libyca* Forster	C	Throughout
Serval	*F. serval* Schreber	?	Bumi R.
Caracal	*F. caracal* Schreber	R	Kota Kota area, Zambia
Leopard	*Panthera pardus* Linn	C	Throughout
Lion	*P. leo* Linn	C	Throughout E of Masumo R.
Antbear	*Orycteropus afer* Pallas	C	Throughout
Elephant	*Loxodonta africana* Blumenbach	A	Throughout
Dassies	*Dendrohyrax brucei* Gray	A	Throughout
Black Rhinoceros	*Diceros bicornis* Linn	C	Between Mwenda and Umniati Rs. Rhod.
Zebra	*Equus burchelli* Gray	C	Between Sengwa and Umniati Rs. Sinazongwe Area, Zambia.
Bush Pig	*Potamochoerus porcus* Linn	?	Throughout
Wart Hog	*Phacochoerus aethiopicus* Pallas	C	Throughout E. of Masumo R.
Hippopotamus	*Hippopotamus amphibius* Linn	A	Throughout
Duiker	*Sylvicapra grimmia* Linn	C	Throughout
Grysbuck	*Raphicerus sharpei* Thomas	A	Throughout
Klipspringer	*Oreotragus oreotragus* Zimmermann	C	Throughout
Waterbuck	*Kobus ellipsiprymnus* Ogilby	C	Throughout E. of Masumo R.
Impala	*Aepyceros melampus* Lichtenstein	A	Throughout, rare in meander zon

Table 8. continued

Common Name	Scientific Name	Abundance	Remarks on Distribution
Roan	*Hippotragus equinus* Desmarest	R	Bumi/Umniati areas Rhodesia: 10 miles W. Kariba Zongwe R. area Zambia.
Sable	*H. niger* Harris	C	Throughout E. of Masumo R.
Bushbuck	*Tragelaphus scriptus* Pallas	C	Throughout
Kudu	*T. strepsiceros* Pallas	C.	Throughout
Eland	*Taurotragus oryx* Pallas	C	Chete to Umniati R.
Buffalo	*Syncerus caffer* Sparrman	A	Throughout E. of Masumo R.
Hare	*Lepus* sp.	C	Throughout
Porcupine	*Hystrix africaeaustralis* Peters	C	Chete to Umniati R.
Cane Rat	*Thryonomys swinderianus* Temminck	?	Kariba/Umniati areas
Bush Squirrel	*Paraxerus cepapi* A. Smith	A	Throughout
Spring Hare	*Pedetes capensis* Forster	R	Masumo R. and Binga area
Red Veld Rat	*Aethomys chrysophilus* i) de Winton	R	Throughout
Namaqua Rock Rat	*A. namaquensis* i) A. Smith	A	Kariba area
Multimammate Rat	*Praomys* ii) *natalensis* A. Smith	A	Throughout, especially settled areas
Pygmy Mouse	*Mus minutoides* A. Smith	?	Binga, Kariba
Single-striped Rat	*Lemniscomys griselda* Thomas	A	Binga area *
Spiny Mouse	*Acomys spinosissimus* iii) Peters	C	Kariba
Pouched Rat	*Saccostomus campestris* Peters	C	Binga
Greater Gerbil	*Tatera leucogaster* i) Peters	A	Throughout*

i) Ansell (1964)
ii) Davis (In press)
iii) Meester *et al* (1964)

* Very abundant during rodent "eruption", mid 1959

A = abundant
C = common
R = rare
? = status not determined

Although large mammals are numerous in the area, there are fewer species than in nearby game areas such as the Luangwa Valley and Wankie National Park. Child and Savory (1964) have remarked on species on the Rhodesian plateau which do not extend into the Zambezi Valley and there are no species so far confirmed in the Central Region which do not extend on to the plateau. Habitats in the Luangwa Valley are similar to the Kariba Basin, but there are three species found in the former and absent from the latter. These are Giraffe, Giraffa camelopardalis, Linn and Wildebeest, Connochaetes taurinus, Burchell, with relic populations in the Luangwa (Ansell, 1960a) and Puku, Kobus vardoni, Livingstone, which do not reach as far south as the Zambezi/Luangwa confluence. It is also interesting that Otters, particularly Aonyx capensis Schinz, have not been recorded along either the Central Zambezi or Luangwa rivers, although they are known from tributaries of the Luangwa (Ansell, pers. comm.) and are common above the Victoria Falls.

If, as may be expected from their presence in adjoining areas, Cheetah, Acinonyx jubatus Schreber, occur in the Central Zambezi Valley, there are 28 species of mammals, jackal-sized or bigger. This compares with 32 species in the Luangwa Valley (Ansell, pers. comm), and 35 species in the Wankie National Park.

The following remarks on distribution and density of game in the Central Zambezi Valley apply mainly to Rhodesian portions of the valley flooded by Lake Kariba, as conditions in Zambia were different.

Game was generally scarce in the densley populated meander zone below the Binga escarpment where the river wound through a flat fertile alluvial plain, up to five miles wide, before curving eastwards towards the mouth of the Masumo River. Game became more plentiful between this river and the Mwenda river and was most concentrated east of this.

Ant Bear, Grysbuck, Bushbuck and Kudu occurred along the whole length of the valley, but were relatively scarce in the meander zone. Elephant were widespread and numerous, although they were rarely found on alluvium near Binga before the beginning of 1960, but then became as common here as elsewhere. Baboon and Klipspringer had a fairly even distribution, but Hippo and Duiker were most common in the meander zone, where the latter were plentiful. Hyaena, Leopard and Bushpig were also widespread, but their secretive habits made it difficult to judge relative densities.

Impala and Buffalo became numerous east of the Mwenda river, especially between the Sibilobilo and Umniati rivers. They extended as far west as the Masumo river, which formed a fairly abrupt limit to their range. The only signs of either species in the meander zone were the spoor of two Impala, found on one occasion. The distribution of Wart Hog and Waterbuck also followed this pattern.

Eland and Lion were never noted west of Chete, although there were sporadic reports of lion, usually from some distance away from the Zambezi, from Chete to Kariba, where they occasionally wandered through the township. Rhino only occurred between the Mwenda and the Umniati rivers and, like Lion, became more numerous away from the Zambezi. Roan were limited to the area between the Umniati and Bumi rivers, Zebra spread as far as the Sibilobilo and Sable Antelope as far west as the west bank of the Sengwa.

The correlation of these distribution patterns with human settlement are discussed below and at greater length, by species, beginning on p.35.

6. THE NATIVE INHABITANTS

The majority of the native people belonged to the Tonga tribe, whose distribution in the valley was largely dependent on fertile alluvium and is shown in Fig. 11, compiled from the best available census (Scudder, 1962; Dept. reports). They had a subsistence economy based on agriculture and supplemented by hunting and gathering. The majority were casual hunters and trappers, but many villages had a few specialists, who were known to kill most species, including Buffalo and Rhino, but it is doubtful whether they hunted many Elephant.

Hunting probably had little effect on large mammal populations away from densely settled areas and was probably less significant than changes in the habitat, resulting from an expanding population retaining primitive agricultural methods. Declining conservation values were characterised by a decline in perennial grasses and scrub encroachment. When the Tonga were evacuated from the Lake Basin in 1957/58 (Nesham, 1960) perennial grasses colonised the cultivations they left, and scrub in old abandoned lands became very dense in the absence of goats which had maintained a clear browse line.

The dense settlement in the meander zone probably accounted for the paucity of game there, as there are heavy concentrations of large mammals on similar alluvium below Kariba and in the Luangwa Valley, where there is also an inverse correlation between the abundance of game and the density of human settlement. Here human settlement is not as dense as it was along the Zambezi, although this is offset to some extent by many tribesmen possessing firearms, and in the Luangwa, hunting is probably more significant over larger areas than it had been along the southern bank of the Zambezi, where there were very few firearms. Further, the trend towards greater animal density down the Central Zambezi Valley was related to diminishing human densities and consequently to progressively less disruption of the habitat. Five species did not obey the general trend. The rocky habitat of Klipspringer was useless for cultivation and offered itself reasonable protection from the regular early burning policy of the Tonga, which, as West (1958) warns, is detrimental to the veld in low rainfall areas. Further, these areas were not as heavily used by domestic stock. Hippo fed extensively from river bank cultivations, while Duiker are well known to favour intensively farmed areas allowed to go fallow, and Baboons are common in many agricultural areas in Rhodesia. It has been noted that Elephant increased in these areas in 1960, after the evacuation of the Tonga.

Although hunting probably had a limited effect on the distribution and abundance of most species, it did explain the distribution of Rhino (Roth and Child, in press). This species is easily eliminated by hunting due to the low replacement rate, resulting from long gestation and growth periods and heavy natural juvenile mortality. They were absent from the Lake area west of the Mwenda, where humans became more numerous, and along the Zambezi, where they were easily accessible to hunters from Zambia. Roth and Child attribute the lack of Rhino east of the Umniati to past Tsetse Fly Control Hunting operations.

7. TSETSE CONTROL HUNTING

Tsetse Control Hunting in the eastern half of the Umniati basin between 1946 and 1956 (Lovemore, pers. comm) almost certainly affected Rhino, but it is difficult to assess the effects on other large mammal populations. Riney (1963) has shown how the cessation of hunting can cause populations to increase rapidly, and this may even take place during the operation if the Tsetse hunting is not sufficient to arrest an increase in populations already under way for other reasons, such as may be associated with changes in the environment, or because shooting itself stimulates higher productivity (Riney, Ms.) Child and Wilson (1964b) have demonstrated that the increase may continue in a Duiker population for at least 28 months after shooting stops.

Some knowledge of the history of the populations affected by Tsetse Shooting would therefore be needed to gauge its effect.

8. BUSH CLEARING OF FISHING GROUNDS

The third factor which may have affected game distribution was the clearing of future fishing grounds. Trees submerged by the Lake were expected to take a long time to decay so that all woody vegetation and, incidentally, most other vegetation, was cleared from 250,000 acres in areas selected for fishing. This took two years, but at any given locality operations usually lasted about a week and involved heavy earth-moving machinery, gangs of axemen and fire. Plate 2 and Table 9 illustrate the effects of clearing in well developed mopane veld.

Most large mammals avoided the disturbance and Impala, Duiker and Elephant returned to clearings immediately operations had ceased. One Duiker allowed a bulldozer to pass within 40 yards of it several times, before bolting from an 'island' of surviving trees, less than 30 yards in diameter.

The regrowth of vegetation in clearings was rapid (Table 10). As noted (p.21), grasses grew more vigorously than in uncleared areas, and the proportion of mopane in the woody vegetation declined, while *Acacia* spp., *Combretum apiculatum*, jesse, *C. elaeagnoides*, *Terminalia brachystemma* and *Grewia* spp., increased. Many of these grew to six feet or more in three seasons, whereas mopane seldom grew half this height.

The following game was recorded in clearings near Binga within six months: Elephant, Duiker, Kudu, Klipspringer, Impala, Baboon, Antbear and Hippo. They mostly remained near the edges, but Elephant, Hippo and Duiker fed out in the open. Table 11 gives an indication of the species and their abundance in clearings between the Mwenda and Umniati rivers within a year. It has been suggested that some species became more numerous in clearings, but there is no evidence in support of this and it appeared that bush clearing had little effect on the distribution of game and although the biomass on Ukubula Island, which formed in a clearing, was not determined accurately, censuses on this island indicated an animal density of the same order here as on uncleared Island 17.

Although changes associated with the evacuation of the Tonga and bush clearing completely altered the ecology of the area, the potential period for observation of the effects of these changes on animals was limited by the rising waters of the new Lake. The most interesting opportunities for the study of animal behaviour and animal-environment relationships, and the most profound and lasting changes in the eco-system followed the steady rise in the level of the Lake.

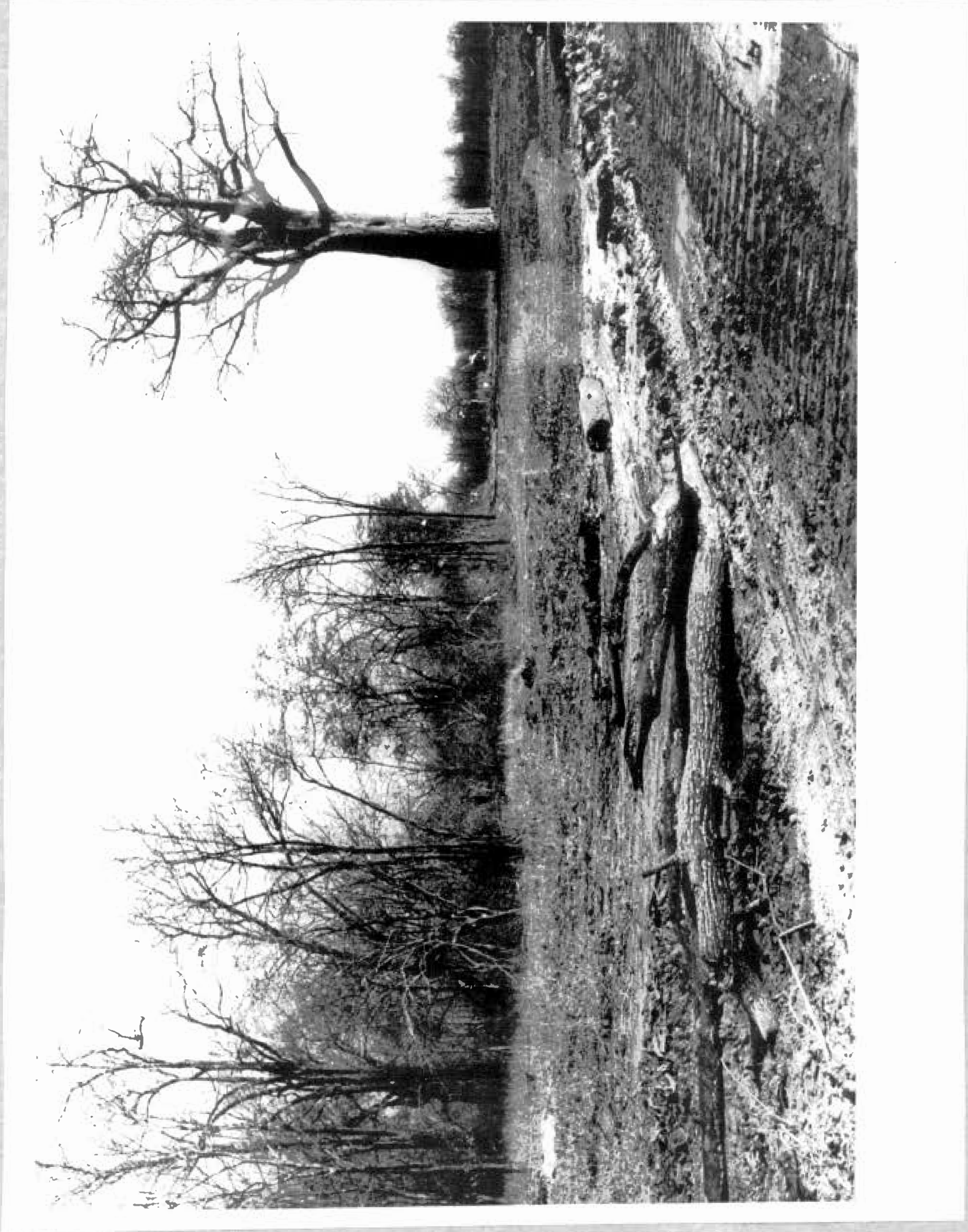


Plate 2. Shows the edge of a bush clearing in well developed mopane veld. Note the removal of all lesser vegetation.

(Photo: G. Child).

Table 9.

Effectiveness of Bush Clearing in Mopane Veld Illustrating the Radical Changes Wrought in the Habitat within about a Week.

Transect No.	No. of points on transect.	Un-cleared	Cleared	% grass + grass canopy	% woody cover	% litter
I	262	X		35.5	40.8	44.3
II	600	X		21.6	38.3	36.0
III	100		X	0	0	8.0
IV	100		X	0	0	9.0
V	100		X	1.0	1.0	11.0

Note the removal of most grass with the woody canopy.

Little natural litter survived in clearings where it consisted mainly of ash and chips from felled timber.

Table 10.

Regeneration of Vegetation in Bush Cleared Areas

Transect	No. of Points	Season	Interval since clearing	% Bare ground	% Litter	% Grass	% Grass canopy	% Woody canopy	Max.Ht. woody canopy	Mean Ht. woody canopy	Habitat
1.	100	growing	5 mths	86	12	12	29	0	-	-	Mopane veld
2.	100	dry	12 mths	97	3	3	3	3	3.0 ft	2.2 ft	Infertile alluvium with mopane.
3.	100	dry	12 mths	97	14	2	7	4	2.5	1.9	Infertile alluvium mixed species
4.	100	dry	12 mths	92	22	6	19	2	3.0	3.0	As last, but soil more fertile
5.	100	dry	12 mths	94	10	11	8	2	3.0	2.5	As No. 4, but burnt over
6.	200	dry	12 mths	98	8.5	.2	3.5	4.5	6.0	2.9	Fertile alluvium with Acacia
7.	200	dry	12 mths	99.5	1	0	0.5	0	-	-	Down-graded alluvium-old cultivation
8.	100	dry	12 mths	92	22	6	19	2	3.0	3.0	Down-graded alluvium
9.	100	dry	12 mths	94	10	11	8	2	3.0	2.5	Fertile alluvium burnt over old cultivation
10.	50	growing	12 mths	94	22	6	6	4	2.0	1.5	Fertile alluvium with Acacia
11.	100	growing	12 mths	91	3	6	4	9	7.0	4.9	Fertile alluvium with Acacia
12.	100	growing	12 mths	96	10	4	10	3	7.0	4.5	Fertile alluvium with Acacia
13.	100	growing	12 mths	88	3	8	49	2	7.0	4.5	Fertile alluvium with Acacia
14.	100	growing	2½ yrs	97	21	0	1	32	9.0	4.8	Mopane with *H. spinescens*, heavily over-populated with game
15.	100	growing	2½ yrs	98	20	1	16	15	10.0	6.6	As last, but jesse with the mopane
16.	100	growing	2½ yrs	97	46	3	15	39	10.0	4.5	As No. 14, but *T.brachystemma* with mopane.

Table 11.

Game Recorded in Clearings Within One Year.

Baboon - common along edge, one troop of 30 out in clearing two miles from trees.

Antbear - common.

Elephant - groups up to19 common.

Rhino - several along edge, two well out in clearing.

Zebra - three herds of four, five and eight.

Wart Hog - common.

Hippo - common.

Duiker - common.

Grysbuck - undetermined.

Waterbuck - common in herds of up to 19.

Impala - numerous, some herds of over 100.

Roan - one herd of six.

Sable - individuals and small groups common.

Bushbuck - undetermined.

Kudu - common.

Buffalo - three herds of over 100 and many smaller groups.

THE FILLING OF LAKE KARIBA

The dam wall at Kariba was closed on 2 December, 1958, when the level in the Zambezi was 1,283.6 feet above sea level. At first the level rose rapidly, but then slowed down as the Lake began to spread out, and it was not until May, 1963, that it reached its full capacity (Fig.12). The uneven rate at which the water level rose was an important factor in the present study. It resulted in a number of islands forming rapidly and then not submerging while the Lake level was almost static.

1. ISLAND FORMATION

Changes in terrestrial habitats were mostly along the shore where many islands formed, particularly near river mouths. Some of these islands persisted for over a year, but most disappeared sooner. Over 500 formed when high ground on a peninsula was separated from the mainland by lower ground, which flooded first. Big islands, like Island 17 (Fig. 7), formed as water backed up diverging water courses, and most of these subdivided before submerging.

2. CHANGES IN THE VEGETATION

Changes in the vegetation along the Lake shore fell into three categories :

A. Partially submerged vegetation

The importance of the fringe of partially submerged vegetation depended upon its response to flooding. Effects varied between species and individuals in the same area, so that the following is necessarily a generalisation. Forbs and grasses, excepting reeds, (*Phragmites* sp), died within about two weeks. Woody plants, however, survived longer and it was here that there was the greatest individual variation. Generally the following were the maximum periods that plants survived in water: *Acacia* spp. (excluding *A. albida*) and *Dichrostachys cinerea* under four months, *Adansonia digitata*, *Tamarindus indica*, *Colophospermum mopane*, *Triplochiton zambesiacus*, *Terminalia* spp, *Combretum* spp, *Ficus* spp, *Holmskioldia spinescens*, *Phyllogeiton discolor*, *Lonchocarpus capassa*, and *Azanza garckeana* mostly died in six to eight months, although exceptional *A. digitata*, *C. mopane* and *L. capassa* lived for 12; *Acacia albida*, *Diospyros mespiliformis*, *Kirkia acuminata* usually died within 12 months, although a few *A. albida* and *K. acuminata* lived longer, and some *Diospyros mespiliformis* and *Garcinia livingstonei* lived in water at Binga for over 14 months. It was noticeable that at Binga most *D. mespiliformis*, *Ficus* sp. and *A. garckeana* died at about the

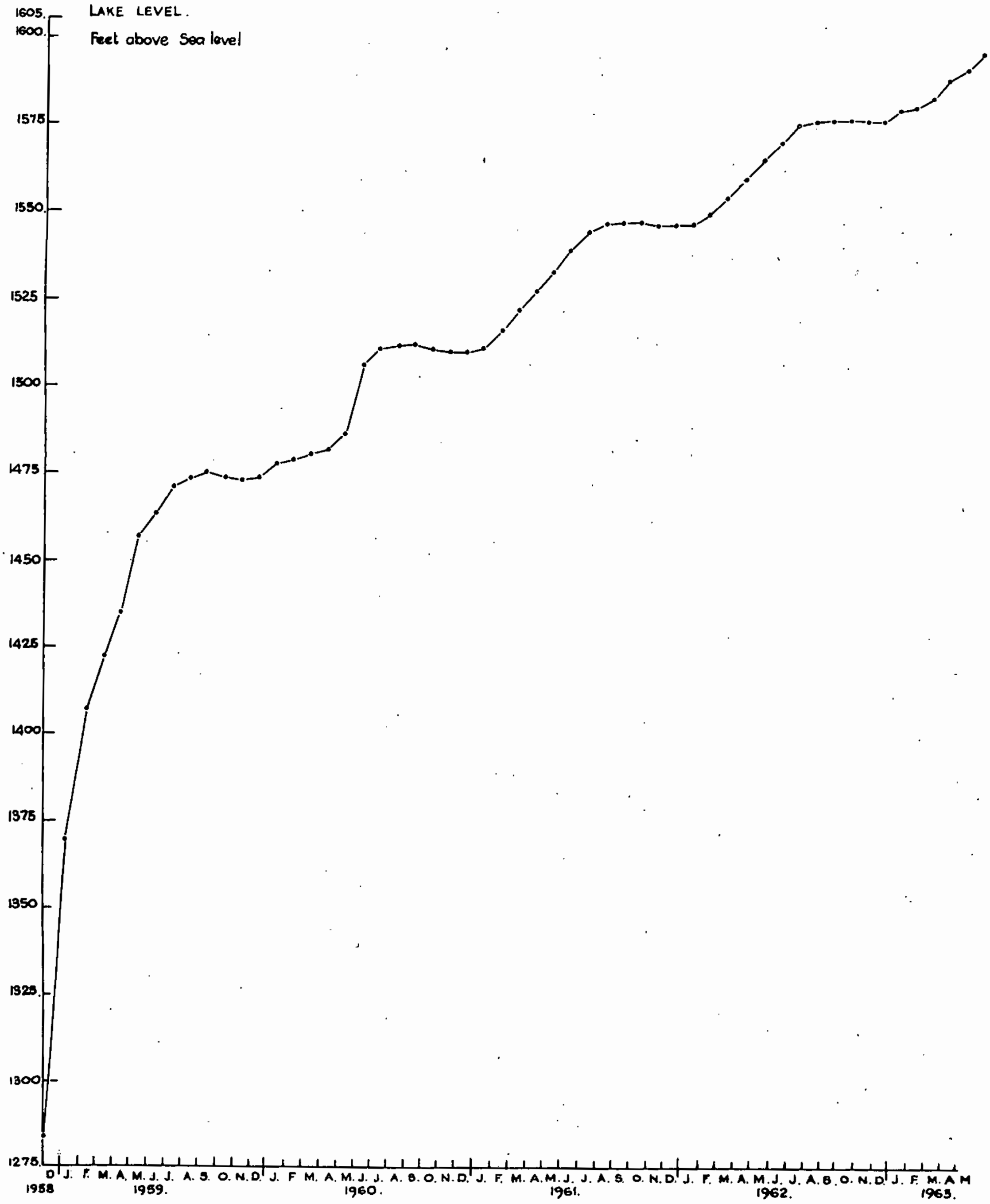


Fig. 12. Graph showing the seasonal pattern in which the Lake filled. The most rapid rise in level followed after the local rains and resulted from the seasonal floods of the Zambezi.

same time and immediately after fruiting.

Most species standing in water came into leaf and/or remained in leaf until they died. There were, however, three exceptions which shed their leaves as usual. These were A. digitata, K. acuminata and Sterculia quinqeloba. This phenomenon of deciduous trees remaining in leaf also occurred in the soak zone.

B. Soak Zone

The soak zone, as used in the present study, refers to a band 0 to 500 yards wide into which moisture permeated, causing the vegetation to flush. It merged with partially submerged vegetation and was not important during the wet season when the surrounding vegetation was green. It did not have time to develop when the Lake was rising rapidly, but from June to November it provided an unseasonable belt of green vegetation.

Four bands could be distinguished in the soak zone and probably reflect the depths of rooting systems. The surface was moist near the water's edge and grasses and forbs grew out of season, although woody scrub such as Acacia spp, and Dichrostachys cinerea showed signs of distress, much as though standing in water. In the second band, the soil was drier and favoured the woody plants more, although grasses did not do as well. In the third zone woody species and forbs were green but grasses were not, while in the fourth band only woody plants benefitted.

In the best developed soak zones near Binga in 1959, grasses and forbs flowered by the first week in October, two to three months early, and had shed their seeds by December. This green vegetation attracted birds and grazing mammals such as Hippo. Before it flushed, spoor and droppings of two herds of Hippo kept under observation, were common half a mile from the Lake, but thereafter they seldom moved more than 200 yards from the shore. The grasses were heavily grazed and trampled and in two areas spoor covered 52 and 39.7% of the points on step-point transects. Other species whose spoor was dense in the soak zone were Kudu, Sable, and Waterbuck and, on overpopulated islands it was very heavily used. On many islands it resulted in the trees remaining in leaf throughout the year.

The soak zone was best developed on fertile alluvium in 1959, and was less important in subsequent years when the Lake shore was along less fertile soils. It is therefore considered unlikely that it will give rise to extensive riparian vegetation as, in many areas, the shore is against rocky hillsides.

C. Floating Aquatic Vegetation

Large carpets of floating aquatic vegetation (Plate 3) developed in sheltered parts of the Lake west of the Umniati river. It was dominated by the fern Salvinia auriculata, a native of South and Central America, which entered the Lake in early 1959. By July there were large accumulations near Chete and in April, 1960, Schelpe (1961) estimated it covered 75 square miles. The rate of spread appeared to slow down in 1961 and 1962, however, due to increased wave action as the Lake grew and spread into bush clearings, where there wereno trees to protect the fern.

D. Effect on Animals

Jackson (1960) described the rapid build up of aquatic organisms. Insects became very abundant along the shore, especially in the soak zone and many partially submerged trees were festooned with spider web while spiders were also very conspicuous in floating vegetation.

Amphibians were locally abundant in some soak zones, but most reptiles were affected adversely as their habitat submerged. As FitzSimons (1962) notes most snakes can swim well, as can most lizards, but both groups became marooned on islands or in trees where they fell easy prey to birds. Even Crocodiles were not numerous and to contact seven along 40 miles of shore was remarkable. Low numbers were partially attributable to commercial hunting before the Lake formed, but then they became spread out along the greatly extended shore, although there was a tendency to gather near river mouths. Many of the sand banks essential to breeding were submerged and eggs were found exposed on mud banks. Thus, although Crocodiles were found feeding on carrion on the last portions of several islands to submerge, numbers are expected to remain low for some years.

Leguaans, Varanus spp., were common, especially V. niloticus, among partially submerged trees and fed extensively in shallow water. Tortoises, particularly the Leopard Tortoise, Geochelone pardalis, often became marooned on islands where many must have drowned, even though their buoyancy allowed them to swim by paddling their legs. A Tortoise was once recorded eating Salvinia.

The behaviour of birds during the formation of Lake Kariba is to be discussed more fully elsewhere, but generally they fell into two important classes. Terrestrial species disappeared or became concentrated on islands as their habitat submerged. The high numbers found on islands were due to this

Plate 3. A newly formed carpet of Salvinia.

(Photo: Rhodesian Information Service)

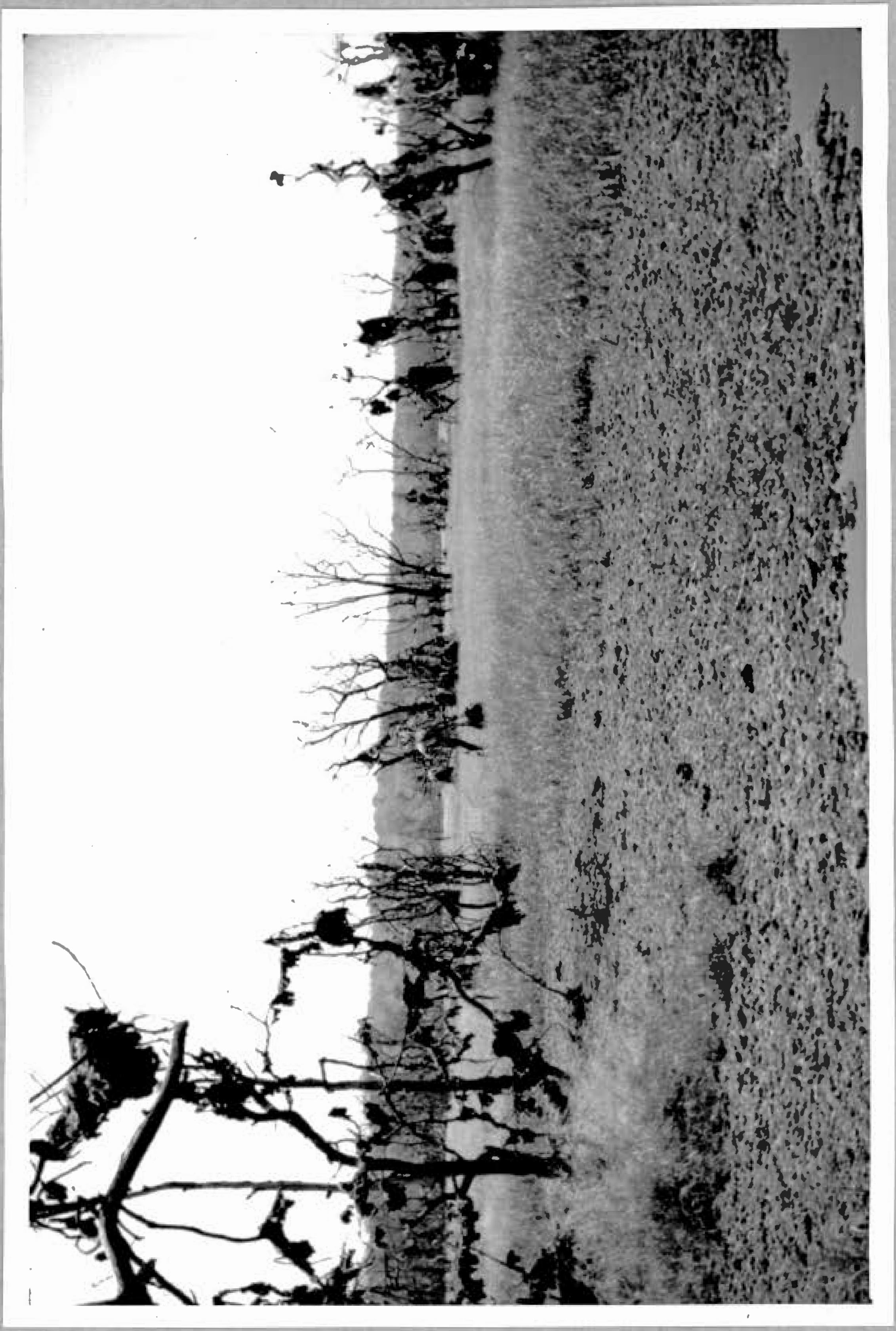


Plate 4. A well established carpet of <u>Salvinia</u> in dead, partially submerged mopane veld. Note the growth of secondary plants, including sedges and grass and dead <u>Salvinia</u> deposited in the trees by wave action.

(Photo: Mrs. Terry Donnelly)

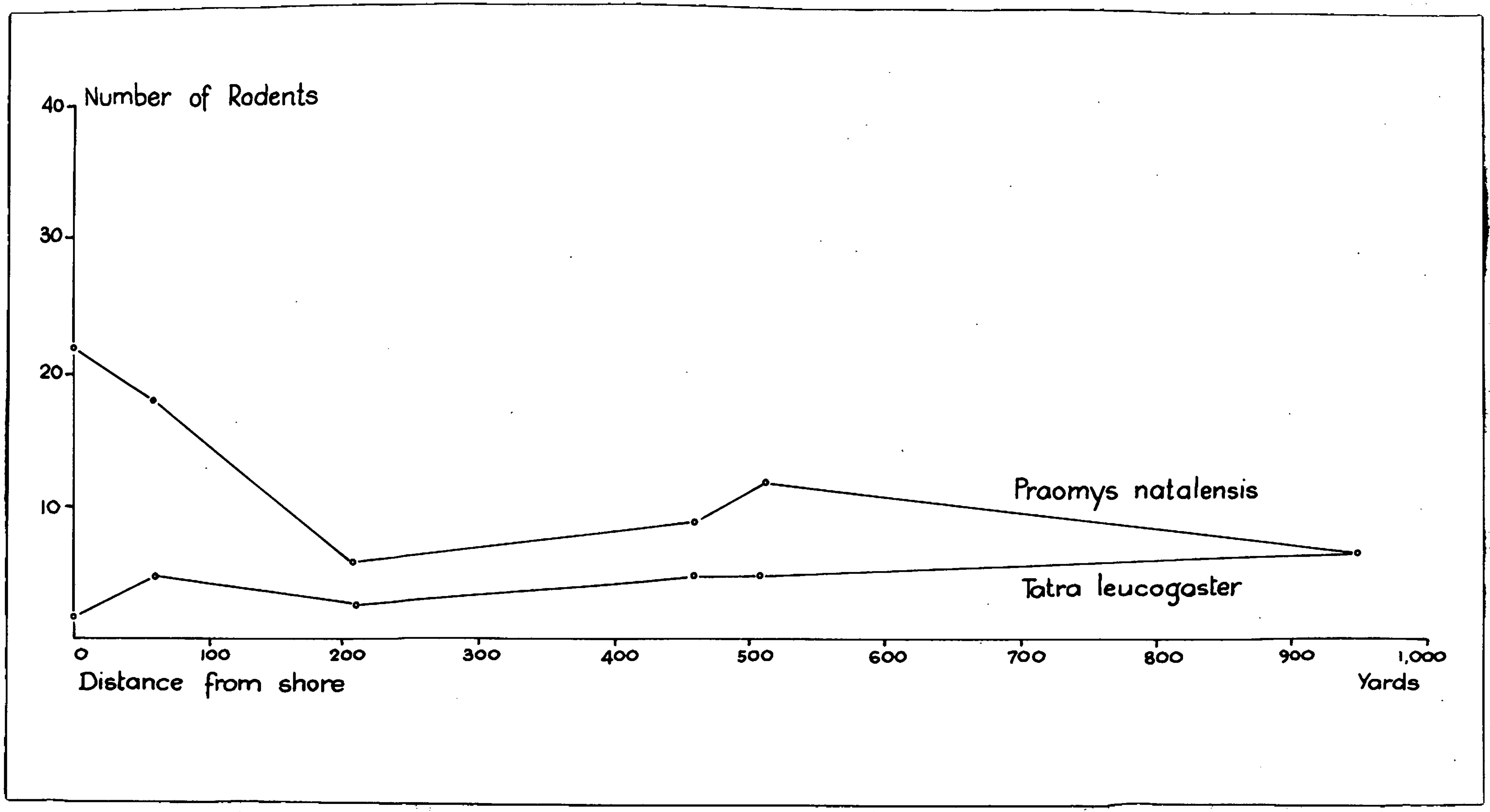
and to species which visited the islands to feed. The former, which included Swainson's Francolin, *Francolinus swainsoni*, Crested Guineafowl, *Guttera edouardi*, Helmeted Guineafowl, *Numida mitrata* and Blue Waxbill, *Uraeginthus angolensis*, eventually became limited to trees in the water as islands submerged and there they perished while species like the Long-tailed Starling, *Lamprotornis mevesii*, left islands when food was scarce. Most fruit-eating forms, such as parrots, *Poicephalus robustus* and *P. meyeri*, Lovebirds, *Agapornis lilianae*, and Layards Bulbul, *Pycnonotus barbatus* made use of partially submerged trees when in fruit, and insectivorous species, such as hornbills, *Tockus* spp., Drongos, *Dicrurus adsimilis* and bee-eaters, *Merops* spp, used dead trees as well.

The soak zone offset, to some extent, the loss of habitat for a number of species and supplied seed-eaters with food earlier in the season than normal. The early appearance of insects in these areas attracted insectivorous species while Marabou, *Leptoptilos crumeniferus*, were able to pierce the roofs of rodent burrows in damp soil. There was a false start to the breeding season among Red Bishop Birds, *Euplectes oryx*, in which the males came into nuptial plumage and built nest frames two to three months early, but these were not occupied by females.

Salvinia carpets attracted 11 species, including Long-tailed Starlings and Racquet-tailed Rollers, *Coracias spatulatus*, which normallyfeed on the ground. These species returned to flooded areas when the carpets formed. Waders and herons rested or fed on the fern and Black Crakes, *Limnocorax flavirostra*, were conspicuous on it when the soak zones, to which they had become confined, were flooded. White-winged Black-terns, *Chlidonias leucoptera*, rested on floating vegetation and fed on the spiders in carpets of *Salvinia* in much the same way as they scooped insect larvae from the water. Initially African Jacanas, *Actophilornis africanus*, suffered from the loss of aquatic vegetation, but numbers soon increased in areas with fern where, judging from the number of juveniles seen, they must have bred successfully.

Most birds normally associated with open water became common on the Lake. Waders were plentiful along shallow water and re-exposed mud-banks, after the Lake level dropped a few feet. They were especially plentiful near the soak zones during the dry season and here, ducks and geese became very numerous at certain times of the year, especially in cleared areas. Fishing species such as Darters, *Anhinga anhinga*, Reed Cormorants, *Phalacrocorax africanus*, Fish Eagles, *Haliaeetus vocifer* and some of the kingfishers, Family *ALCEDINIDAE*, were

Fig. 13. The distribution of dominant rodents in relation to the lake shore during the height of the 1959 population eruption.



less restricted by the depth of the water and were consequently widespread. Exceptions to these generalisations were the Pratincol, Glareola pratincola, and the Water Dikkop, Burhinus vermiculatus, which became limited in distribution after 1959.

Generally terrestrial species had a reduction in habitat, compensated to some extent by the soak zone and carpets of floating aquatic plants, while those species normally associated with water became numerous along the shore. Both groups, however, lost many nests which submerged while occupied, or were swamped by Salvinia deposited in them by wave action, or were destroyed as banks eroded away through the increased wave action.

There were similarities between the behaviour of birds and mammals, as representatives of both groups became marooned on islands, while others visited islands to which they were attracted by improved feeding conditions or experienced an increase in potential habitat. Most mammals could swim to some extent, but many drowned or became marooned on islands or in partially submerged trees, where they starved or fell easy prey to birds. Other species benefitted from the soak zone and some swam to islands to feed, but then left when the food supply diminished.

Most rodents and other small mammals perished. Birds of prey frequently took up stations on small islands and several were seen preying on mammals marooned in trees, where the commonest species were Bush Squirrels, Night Apes and Pouched Mice. There was an eruption of rodents at Binga in the first half of 1959, but it is doubtful whether the Kariba project was responsible. The commonest species were Prayomys natalensis A. Smith, and Tatera leucogaster Peters, which represented 60.6% and 37.8% of the rodents trapped between June and August, 1959. Although the Tonga eat many rodents, the absence of the people was of little importance, as rodents were plentiful 15 miles south of Binga in densely settled areas. The spreading of the Lake displaced only P. natalensis for a short distance. Figure 13, based on catches in water traps at different distances from the shore, suggests they may have been compressed in a band 50 to 100 yards wide along the shore, which supports Yeager and Anderson (1944), Stickel (1948), McCarley (1959) and Ruffer (1961), who found that rodents remain in their home ranges during a flood. T. leucogaster, on the other hand, was more plentiful away from the water's edge where the sandier habitat along the foot of the Binga Escarpment was apparently more suitable. Fluctuations in rodent density over 100 yards from the shore were attributable to local habitat differences. The behaviour of these two populations suggested a normal eruption.

Numbers were reported as high in 1958, higher in 1959, but in 1960 rodents were scarce and only one Pouched Mouse was caught in August under similar conditions to those in which 18 P. natalensis and T. leucogaster were caught in six water traps, exactly a year before. These two species were abundant down river from Kariba in 1959 and the Tonga could recall similar eruptions from previous years. Mowbray (pers. comm) reports high numbers in the Sabi Valley in 1954, 1956 and 1959 and Malherbe (1963) and Davis (1946, 1959, 1960) indicate similar outbursts of these or related species in other parts of Central or South Africa.

Bush clearing, however, did appear to hasten the crash in rodent numbers. P. natalensis numbers declined during the last week in July (Table 12), when many dead rodents were found, even where scavengers were numerous. There were few signs of disease or heavy parasite infestation among 228 rodents autopsied during July and most had some subcutaneous fat and fat around the kidney, although 64 to 71% had not yet acquired adult size as determined from flesh measurements. The drop in T. leucogaster numbers took place a little later (Table 12) and here too, the 142 specimens dissected showed no cause for the sudden mortality.

The presence or absence of rodent pellets was recorded in plots of one yard radius at every tenth point along nine step-point transects, run in September, in similar cleared and uncleared veld within a distance of half a mile (Figure 14 (a)) and showed a fairly even distribution. Pellets were divided into fresh and old droppings, on colour and texture, and the incidence of fresh pellets is shown in (b), indicating greater losses in the clearing during the die off. Old rodent pellets were probably not over two to three months old, judging from pellets kept under observation. The covering of woody canopy, and grass and forb canopy along the lines is given in (c) and (d) respectively, and shows the correlation between fresh rodent pellets and woody canopy. It was also significant that the die off of P. natalensis coincided with the general leaf fall in the area sampled, suggesting shade may be important for the survival of high numbers of this species, as Bodenheimer (1957) has demonstrated for other burrowing forms in marginal areas. This would be particularly important at the beginning of the hot season in an animal whose burrows seldom went deeper than 13 inches.

Large mammals were less subject to predation than small species and some moved to and from islands, but there were many which perished in spite of Game Rescue operations. There were numerous islands which submerged before they were cleared, most of

Table 12.

The Decline in Rodent Numbers in mid-1959

Month	No. trap nights	No. *T. leucogaster* caught	Average per night per trap	No. *P. natalensis* caught	Average per night per trap
July	39	43	1.1	95	2.4
August	33	23	1.0	18	0.6
September	20	2	0.1	0	0.0
TOTAL	89	73	-	113	-

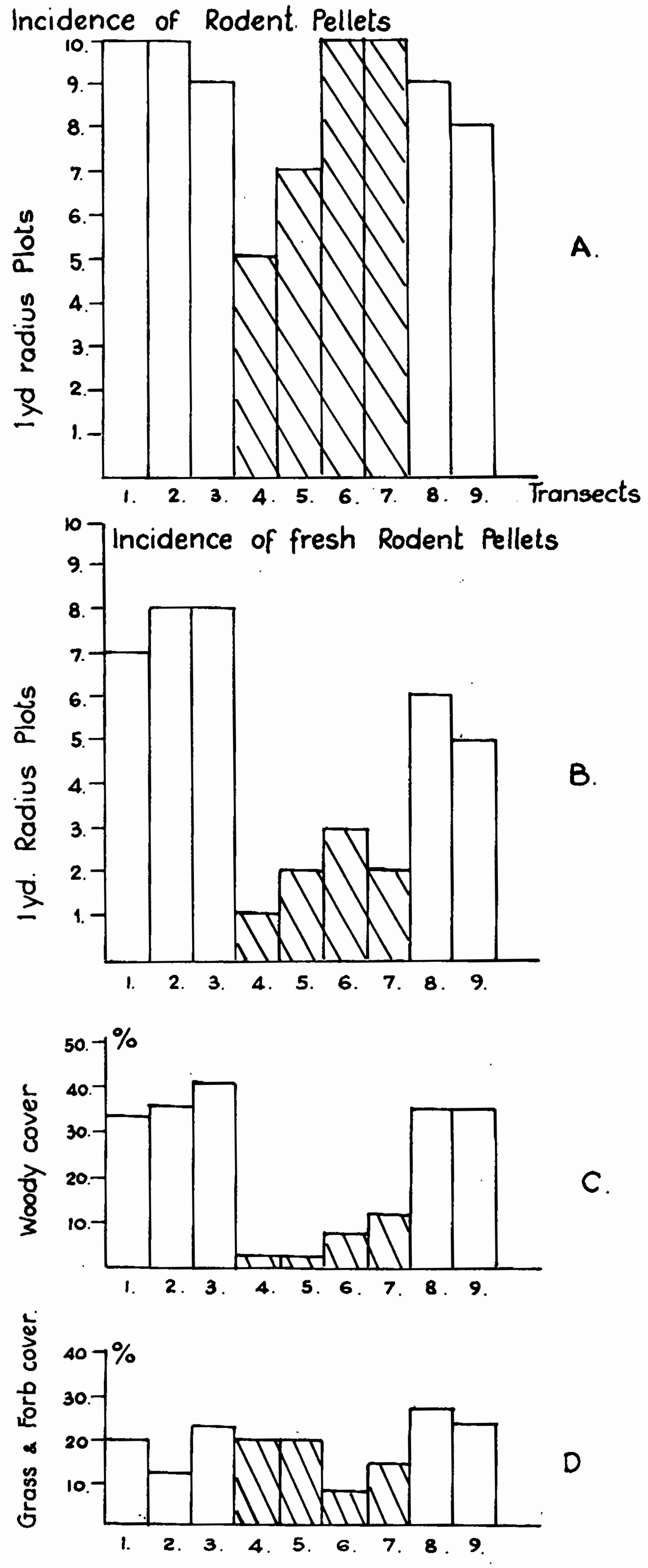


Fig. 14. The distribution of rodent pellets and fresh rodent pellets in relation to vegetation during the decline in rodent numbers following the 1959 population eruption.
Open histograms = uncleared transects
Shaded histograms = transects in a bush clearing.

which were surrounded by Salvinia through which small boats could not pass. There were also islands where animals died of starvation before the whole population could be removed.

THE BEHAVIOUR OF LARGE MAMMALS DURING LAKE FORMATION

The rest of this paper deals with the effects of Lake formation on large mammals and the responses of the various species to the marked changes induced in the habitat. In most cases, it is convenient to consider, first their reactions to flooding, and secondly their response to being marooned on islands under differing environmental conditions.

The readiness with which different species entered the water and their swimming ability are compared with present knowledge of their movement patterns, as the extent to which each species was localised in its movements appeared to be the main reason some species became trapped on small islands, others only on larger islands and some hardly at all. Islands sometimes formed quickly, but this was never a sudden process and was preceded by a concentration of animals on the peninsula giving rise to an island. Free movements within an animal's home range at this stage would have reduced its chance of being marooned, unless the greater part of its range was in the area giving rise to an island, as the shore would have constantly deflected movements until the animal eventually reached the isthmus connecting the incipient island to the mainland. The greater concentration of animals in this portion of the home range would have enhanced the effect. This is borne out by the fact that animals which are known to be very localised became trapped on small islands, those with intermediate home ranges in larger areas, while others which move considerable distances were only marooned on very big islands, or when the spreading of the Lake eventually submerged their whole home range.

The area from which the population on an island was derived was calculated from 1:25,000, 25 foot interval contour maps, taking into account the pattern of flooding in the region. These areas represented the maximum from which animals would have been moved without having been trapped on previous islands, allowing that such islands formed from large enough areas.

The response of animals to flooding showed how gradual inundation of an area would affect a particular species. Apart from animals which may actually be washed away, this behaviour would probably be similar during any severe floods, such as affect parts of Africa almost every year.

The behaviour of animals and animal populations marooned on over-populated islands enabled some interpretation of their basic habitat requirements in the Kariba Basin. Also of particular interest were the responses of browsing and grazing animals to critical shortages of habitat resources on islands which submerged slowly.

It is convenient to describe each species individually in the systematic order proposed by Ellerman et al (1953), beginning with a brief elaboration of their distribution in the study area, followed by their reaction to flooding and concluding with the response to conditions on islands of those which became marooned.

1. BABOON

Chacma Baboons, Papio ursinus Kerr, were common all along the Central Zambezi Valley where large numbers became marooned during the formation of Lake Kariba. Many drowned or starved as islands submerged and they became confined to partially submerged trees. The number of Baboons trapped greatly exceeded the totals shown in Table 1, based on Rescue Reports, as their agility in escaping through the canopies of partially submerged trees when disturbed by motor boats, made estimating numbers very difficult, especially as troops often split up in different directions.

While data was being collected for this paper, priority was placed on determining which sex and age classes were represented in a group or troop. This information was more important for determining changing trends in population structure than the totals of animals present.

A. Response to flooding

Baboons apparently became marooned on islands because troops occupied fairly restricted ranges. Near the Nyamune River, several groups became isolated on islands of less than 10 acres, which formed slowly over several months in an area, which did not exceed 700 acres. These small groups probably represented the splitting up of a larger troop. On the east bank of the Bumi River two large troops, totalling over 80 individuals, were trapped from an area of about 7.5 square miles, while on the west bank of the Bumi a troop of over 50 became marooned in an area which had not exceeded 3.8 square miles.

Six of the groups in the Nyamune area were on islands within easy reach of the mainland, as Baboons can swim well, took to the water readily when disturbed and, in any case, could have covered a fair proportion of the distance to the mainland through the canopies of partially submerged trees.

At least four troops of Baboons of over 20 individuals took to the water voluntarily and swam to fruiting trees. One tree was within 10 yards of land, but to reach another the Baboons must have swum at least 30 yards and Haslam reported a third troop which he estimated had swum 50 yards. Rescue Reports mention the return of a fourth troop to trees from which it had been driven the previous day.

There were 49 observations of the behaviour of eight troops on islands, towards the approach of humans. Generally they ran across an island and into the shallows where they climbed trees before it became necessary to swim. This caused troops to break up as smaller animals had to climb trees sooner than adults. This fragmentation of the troop was purely temporary and is not to be confused with the break down in troop structure described below.

If the Baboons in the trees were pursued, they showed little hesitation before jumping into the water, if other trees were out of reach. This included all age classes, from small adult-coloured juveniles upwards, and all escaped individually, although Junor (1960) indicates dark infants were carried by their mothers, even when the latter were swimming. This pattern of flight was to be expected from observations of troops under normal conditions; the main difference being that small animals fell back more quickly.

It is not surprising that Baboons took to the water readily from islands or partially submerged trees, as Hall (1963) mentions that in the Cape of Good Hope Nature Reserve, a troop crossed a shallow vlei, where several became drenched during a squabble. He also notes that frequently, when feeding along the coast at the edge of the waves, these Baboons walked through rock pools.

Baboons swam well. Junor (1960) describes how the smallest specimens swam under water like Monkeys, while the lumbar regions of older animals were seldom submerged, although they held their heads beneath the surface when approached. There was a complete intergradation from small animals which swam under water to large animals which swam on the surface, and the submerging of the head was apparently an attempt at concealment derived from the way juveniles swam. The greatest distance a Baboon swam under water was 20 yards, although the maximum distance swam, according to Junor was one and a half miles. This was exceptional, as they seldom escaped towards open water and usually climbed a tree within 50 yards. An average swimmer had little difficulty in overtaking Baboons in poor physical condition.

Thus, Baboons took to water readily, could swim well when necessary, and could move considerable distances through partially submerged vegetation. They moved off small on-shore islands and from trees in the water along the mainland shore, so that small home ranges appeared to be the main reason they became trapped. Although the actual sizes of the home ranges could not be determined, there were at least five troops which originated from a total area smaller than the smaller of two ranges in the Cape described by Hall, where the troops occupied 13 and five and a half square miles respectively. With the exception of an island on the west bank of the Bumi River, where there was an island of trees in a large bush clearing, islands were in continuous similar habitat with that on the mainland and in all cases the islands formed slowly over several months. Near the Bumi River isthmuses persisted for three to seven months, while the incipient islands remained about the same size. By this time over-population was marked and had their ranges reached to the mainland, it is probable that they would have left the islands. Further, if they foraged three miles each day and did not always return to the same sleeping places (in this case trees), as Hall found in the Cape, there would have been even less likelihood of their being trapped, as they would have tended to move off the peninsulas.

It is to be expected that Baboons would remain within their home ranges during abnormal floods. If the whole range were affected, they would seek refuge on islands or in partially submerged trees. When these too disappeared, most of the population would be eliminated, as it is unlikely that many would swim to safety across open water. The ability to climb trees obviously makes them less susceptible to floods of short duration than other purely terrestrial species, but if the floods persisted the tendency to take to trees might be a disadvantage. Instead of giving ground before the rising water, they would become marooned, even where no islands formed.

B. Behaviour on Islands

Baboons became too numerous for the food supply on a number of islands where they also showed signs of being short of cover before the islands submerged. Hall (1960) does not mention Baboons using cover to avoid danger, but the following observations demonstrate that it is important in some circumstances. Fothergill watched two Baboons being chased by a Leopard. They did not attempt to climb trees, but went to ground between two rocks when his presence distracted the Leopard. This was not simply a case of the Leopard being too close to allow them to slow down and climb a tree, as they had ample opportunity of doing so when

Fothergill intervened. Baboons also went to ground in holes in the presence of humans. This was observed on 22 occasions and always involved lone adult Baboons in poor condition. This suggested that when weakened by starvation they attempted to avoid danger by hiding, but it is possible that the same behaviour is used by small groups when pressed by a predator, as Fothergill did not consider the two animals, mentioned above, to be in poor condition.

There were two reports of their sharing a hole with another species. On one occasion it was a Porcupine, while on the second there was a Wart Hog and an Antbear in the hole. On Island 17, most usable holes were occupied by Wart Hog or Hyaena and there were 14 examples of Baboons hiding in depressions quite inadequate for the purpose. A Baboon usually lay on its side with its hands near its face and remained motionless watching the observer approach, and at least three were caught before they bolted.

Baboons began dying of starvation on Island 17 early in June, 1960. By then the island had been heavily trampled by the concentration of other game. There were no fruiting trees and a search for possible insect foods under likely rocks was unsuccessful. They were often seen scratching for roots and bulbs in damp soil in the soak zone, but an investigation of numerous scats showed they were feeding mainly on leaves and bark, especially those of mopane. The droppings were large and soft with a greenish appearance, due to many poorly digested fragments of mopane which indicated little selection when feeding, as their digestive systems were unable to cope with the mopane which is bitter to human taste and was taken very sparingly by browsing species on the island.

Most of one troop fed extensively for about a week on the internal fibrous material of a fallen baobab. They chewed the tissue for juices and spat out the pulp, rather as Robertson - Bullock (1960), and Napier Bax and Sheldrick (1963) have described for Elephant during periods of food scarcity.

Carrion was plentiful on the island and there was some evidence of Baboons eating flesh, although not to the extent which might have been expected among starving omniverous feeders. Heavy Baboon spoor round a Wart Hog and an Impala carcass suggested they may have been responsible for removing the viscera. The cries of small Duiker, with the damp umbilical cord still attached, attracted attention on 23 June. It was being attacked by two adult Baboons, one of which had bitten it about the head and left fore limb. Autopsy revealed a tooth had punctured between the left frontal and parietal bones, but the attempt at killing was very clumsy compared with the techniques of most predators.

On another island Fothergill came upon Baboons feeding on a Bushbuck, whose carcass was still warm, and which had presumably been killed by the Baboons. The abdomen had been ripped open and part of the viscera was missing. In yet another instance where Baboons were starving, Fothergill found them eating maggots around a rotting Elephant carcass.

Hall (1961) and (1963), Shortridge (1934) and Fitzsimons, (1919) show that Baboons take a wide variety of plant and invertebrate foods, as well as occasional lizards etc., but it is unlikely that they were serious predators of game in the study area. They may have killed a number of newly born animals, but even when starving made little use of abundant carrion, and seldom attacked full grown animals. This is in accordance with Ansell (1960a) and Poles (1956), both of whom conclude that Baboons seldom prey on game, and tends to contradict Dart (1963) who describes predation on wild and domestic ungulates in South and East Africa and recounts heavy predation on small stock in one farming area. Attacks were directed at adult as well as young animals and Dart considers that Baboons need a constant supply of protein.

When islands submerged Baboons lived almost exclusively on browse and often denuded one side of a tree or trees to a remarkable extent, leaving the other sides almost untouched, and feeding was usually limited to a few trees, although others of the same species were within easy reach.

There were at least 79 Baboons on Island 17 in June 1960, and during five weeks of observation, not a single animal was classified as in better than poor condition and most were suffering from acute malnutrition. By the end of June, they were dying and a total of eight carcases were found. Islands 202, 203 and 205 were also predominantly mopane veld, but there was less deterioration of habitat, and a troop of over 50 Baboons were in much better condition and were more alert in April, 1961. On the other hand, eight Baboons were in very poor condition on Island 108, a mopane veld island reduced to a diameter of five yards by June 1961. These animals had disappeared by mid-July. The relative physical condition of these three samples reflects the status of the habitat which was very poor on Islands 17 and 108, and much better on Islands 202, 203 and 205, where in addition it was more varied.

Under such stress the structure of Baboon populations changed. There was a reduction in breeding activity and a disorganisation of normal troop structure. Hall (<u>op. cit</u>) has pointed out that the gregarious habit and complex intra-troop behaviour is characteristic of Baboons, except possibly under very severe conditions such as appertained on islands at Kariba. He worked on Island 100 in July, 1961, and observed four major points which are substantiated by work elsewhere on the Lake: (a) Baboons, with two exceptions, foraged in small groups, often of six or less animals, which Hall felt represented a splitting up of one or more larger troops, (b) no oestrus females were observed, (c) only two carried infants were seen and (d) there was a general breakdown in the social responsiveness between members of a group.

Most troops on the mainland were extremely vocal, but on islands Baboons were seldom heard to utter any sound at all and the alarm bark was never recorded, not even on Island 17 where the Rescue Unit camped near the Baboons for three and a half weeks. Not a single oestrus female or dark coloured infrant was seen in five troops on islands, totalling over 200 individuals. This interruption of the female cycle in Baboons is paralleled by the cessation of menstruation in women restricted under severe conditions in Japanese Concentration camps in Java between 1942 and 1946 (Dr. G. Broekhuysen, pers. comm.) The only animal which was carried was a small fawn-coloured juvenile on Island 203 and even this was abandoned by its mother the second time the troop was flushed and had to take to shallow water. This and its size, indicated it was almost at the stage of becoming independent.

Hall (op. cit), Ansell (1960a) and Zuckerman (1931) describe Baboons as breeding throughout the year, and while working on Island 17, two troops, contacted by the author on the mainland, each contained at least one oestrus female and several dark infants. A large troop of over 60 in the Luangwa Valley, where the habitat is similar to the Kariba Basin, had at least five oestrus females and seven infants in July, 1963. According to Hall the presence of oestrus females and infants at any time of the year is normal, and their absence on islands was, therefore, unusual and apparently resulted from three separate factors: the inhibition of the normal female cycle, pregnancy failure and a heavy juvenile mortality. There was no direct evidence of pregnancy failures, but it cannot be discounted as, with a gestation period of six to seven months (Asdell, 1946; Kenneth and Ritchie, 1953), many females could have been mated before conditions deteriorated. This was particularly true on Island 17, where an area of 7.5 square miles was reduced to 120 acres in four months.

The reduction of breeding activity among females, coupled with the obvious heavy die off among juveniles, led to a marked change in the age composition of troops, which could be expected during a natural catastrophe, similar to that induced by the formation of Lake Kariba.

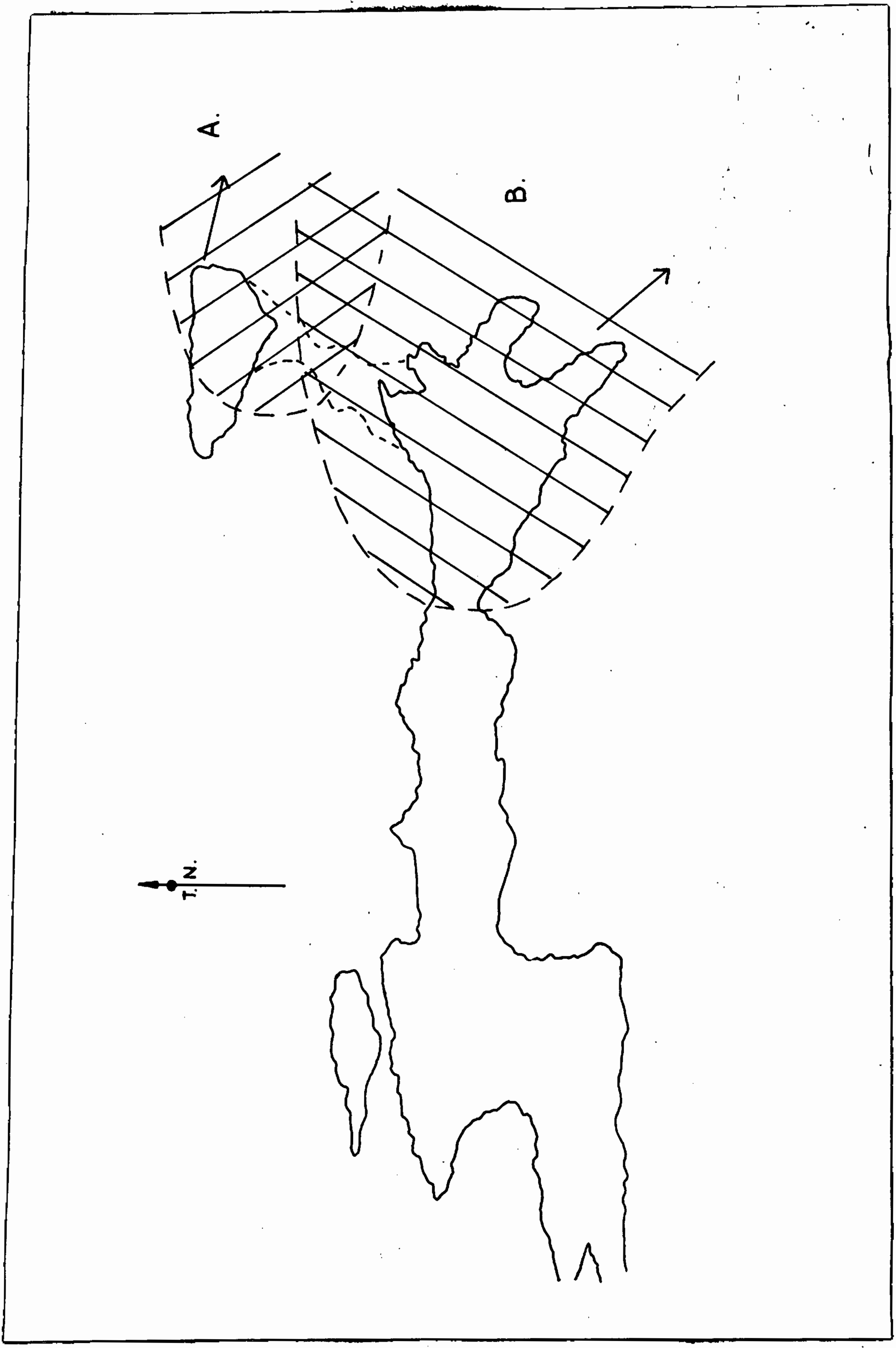


Fig. 15. Shows the areas occupied by the two troops of Baboons marooned on Island 17 and the direction in which they normally escaped. Adults which broke away from these troops to forage individually or in small troops extended over the rest of the island.

The breakdown in troop structure found on Island 100 by Hall, was also apparent on Island 17, where there were at least 79 Baboons, which had evidently belonged to two troops, occupying roughly the areas marked as A and B in Figure 15. The best counts of these two troops were 35 (two counts) for A and 28 (one count) for B, but by then the troops had begun to disintegrate and five juveniles had been caught. When flushed they usually escaped into partially submerged trees in the direction of the arrows, suggesting they had been compressed on to the island from different directions and had ended up in poor habitat. Further, conditions deteriorated rapidly during June. A few solitary animals and groups of two or three were noted on other parts of the island during the first week of the month. They were all adults of either sex and the number increased during the month until 28 were counted on the 20th. This count excluded seven carcasses and several other adults which were destroyed or expired in partially submerged trees.

Nineteen animals were removed from the island and included the five smallest juveniles (one female with a hind foot of 122 mm, and four males with feet ranging from 147 to 161 mm), which were with the troop when caught; five large sub-adults or young adults (two females with hind feet of 144 and 147 mm, and three males with hind feet between 162 and 169 mm) also removed from the troop, and 12 solitary adults. In the last group, six females had hind feet between 191 and 212 mm, while in three males they ranged from 196 to 223 mm in the largest male found on the island.

When the island was left on 5th. July, 1960, the two troops still retained their respective areas, but were much smaller and consisted of uniform-sized animals. It was difficult to decide whether these were old sub-adults or small adults, but both sexes were represented. In February, 1961, 19 of these animals remained on Netting Point, the only unsubmerged portion of the island, and they still retained a tight troop formation. There were 12 left in April, by which time they were limited to partially submerged trees, but even then remained as a compact group. The eight Baboons on Island 108 were all about the same size as the last survivors on Island 17 and probably represented the remnant of a troop. They included at least one male and three females and, like those on Island 17, flushed as a group.

It would thus appear that the severe conditions on islands affected Baboon troops in the following order: females ceased coming into season and there were very few infants or other small animals; then as conditions deteriorated further, adults became dissociated from the troop and lived and fed individually or in small groups. These were the weakest animals on the island and their carcasses were the only ones found, although some juveniles probably died earlier. The last portion of the population to survive in three troops consisted of animals just reaching physical maturity, and at least one group remained gregarious for 11 months after the adults began breaking away. These animals had completed the period of maximum growth, assuming Baboons follow a normal growth curve, but probably had not yet bred which is a severe strain on the individual, judging from the cessation of breeding among older animals.

2. SPOTTED HYAENA

Hyaena, Crocuta crocuta Erxleben, were widespread (Table 8), but remained inconspicuous and were known from only two islands. There were five Hyaena on Island 17, judging from spoor after two had been removed.

Two sub-adults, with half grown permanent canines, took to the water from Island 17 after three men had walked around the island once on the day the Rescue Unit landed there. When picked up in a boat, they were swimming strongly, dog fashion, and had covered a distance of at least 1.25 miles. The other three Hyaena were never seen, as they spent the day in burrows, but they remained on the island for three weeks before disappearing. They visited several large Ant Bear holes most nights and apparently used several for lying up in during the day.

Carrion was plentiful on the island and in most cases the Hyaena limited themselves to removing the viscera, although on one occasion they took the skin of a skinned Impala while the carcass lying alongside it, on the side from which they approached, was ignored.

3. LEOPARD

Leopard, Panthera pardus Linn, occurred throughout the Central Zambezi Valley, but being more or less solitary, nocturnal and silent, like Hyaena, they remained inconspicuous and even on islands on which they were known to occur, were seldom seen.

They were found on a number of small islands, but Rescue Reports are not specific as to their exact location, so that it has not been possible to calculate the areas from which these formed. In several instances, however, they did not exceed a few square miles, but Leopards took to the water voluntarily and swam considerable distances. The longest recorded swim was of a Leopard which left Island 21 on 7th. June, 1961, after most of the game on the island had been removed the previous day. The Leopard was found soon after sunrise in an isolated tree about 1,000 yards from the island and still some 2,000 yards from the mainland.

A. Behaviour on Islands

Leopards were very successful predators on a number of islands, but disappeared from the islands when prey became scarce. Shortridge (1934) and Roberts (1951) suggest Leopard feed mainly on medium-sized antelope, of the size of Impala or Duiker, although smaller prey may be taken. Mitchell *et al* (*In press*) analysed 96 Leopard kills, which included 21 mammal species ranging from Hares to Wildebeest and Lichtenstein's Hartebeest, *Alcelaphus lichtensteini*, Peters, but included mostly Reedbuck, *Redunca arundinum* Boddaert, Puku, Duiker and Impala. The largest kill recorded on islands at Kariba was a full grown Sable in very poor condition, but the main prey in this area appeared to be Wart Hog, and the smaller antelope, including Impala, Bushbuck, Duiker and Grysbuck. Mitchell *et al* have one record of a Leopard eating fish to which may be added three reports from the Zambezi Valley, in each case fish which had been stolen from fishing camps.

When Island 21 was first located, it supported at least 35 Impala, numerous Wart Hog and smaller numbers of Grysbuck, Bushbuck and Kudu, in addition to four Rhino. When it was cleared 13 months later, there were only 11 Impala, in spite of the intervening calving season, and there were no recent signs of Wart Hog. The island was not seriously over-populated so that the reduction in animals was attributed to the activities of the Leopard.

The Leopard left the island the day after the Impala and two Kudu were removed. It is possible that the disturbance associated with their rescue stimulated it to do so, but this seemed unlikely as the Leopard remained on the islands five weeks before, while extensive areas of scrub were cleared in preparation for the capture of the four Rhino. Further, there were reports of similar behaviour on other islands. A Leopard disappeared from one after killing 10 of the 27 Impala on it, while another only left an island well stocked with small game when it had reduced their number to one Bushbuck and two Baboons. A third report described a Leopard moving from one island to another after game had been rescued from the first.

This behaviour of Leopards suggests that, under normal conditions, they would emigrate from an area when food became scarce. Leopards are usually regarded as fairly localised, which, if true, shows a basic difference in their movement patterns from that of localised ungulates, at least some of which starve rather than leave an established range (p.62).

The confined nature of the islands probably simplified hunting and on Island 21, where the Wart Hog were eliminated, there was a noticeable shortage of burrows for cover. This situation resembled the experimental conditions described by Gause (1934, quoted in Allee et al 1961), in which predatory unicellular organisms completely eliminated their prey before dying out themselves. This probably rarely happens under normal conditions where the Leopard could be expected to move out of the area or shift its attention to a different species, before the whole population was eliminated.

4. LION

Lion, Panthera leo Linn, were recorded on only four islands and were not a conspicuous species in the Central Zambezi Valley, where they were seldom heard at night. The patchy distribution mentioned on p.24 suggested they move about a fair amount and, although nowhere common, may be more numerous in areas of broken country.

A. Response to Flooding

Lions cross water quite freely and like most cats are good swimmers. Carr (1962) describes how two tame Lions frequently crossed the Luangwa River, and Lion are well known to move on and off islands in the Upper Zambezi River system, where they are reputed to prey mainly on Sitatunga, Tragelaphus spekei Sclater, and Bushbuck. Shortridge (1934) notes that, "like tigers and leopards, lion enter the water readily and frequently cross rivers. In the Northern Kaokaveld they habitually swim across the Cunene - which has an average width of 80 to 90 yards - and appear to choose places where the river is rapid and comparatively shallow .... At Andara, in the Western Caprivi, where the Okavonga splits into several channels, lion have often been known to swim to islands in mid-stream in order to attack herds of cattle which are kept there". The most remarkable report of the swimming powers of Lion comes from Mrs. Joy Adamson (pers. comm), who describes their swimming to islands beyond the coral reef off the East African coast.

A total of 19 Lions were recorded on islands. Two on Sampakaruma Island, first reported early in 1959, may have been marooned when the island formed. One was shot by a poacher late in 1960 or early 1961, but the fate of the second was never established, although Rescue Reports indicate it disappeared from the island.

There were no Lion on Island 100 during the 1961 rescue season, but, by April, 1962, a pride of six had swum to the island, which was then over one-and-a-quarter miles from the mainland. By April, the island had split into four, but still held fair populations of game, including at least 30 Buffalo, four Zebra, three Sable, a number of Impala, Kudu and other smaller animals (Haslam, pers. comm). Spoor showed where the Lions crossed between islands on several occasions, substantiating the following report from Haslam. The Rescue Unit landed and camped on the islands in the position shown in Fig. 16. During the first night, the Lions moved past the camp from the eastern tip of A, and the following morning were found on D. They were driven from here to C with some difficulty, but by the afternoon were back on D, before returning to A during the night. Two Lionesses were rescued in 1962, but the remainder stayed until the end of January 1963, when a Game Scout saw them swim to the mainland, a distance of at least six-and-a-half miles. This undisturbed behaviour was similar to that described for Leopards when prey became limited on islands.

The behaviour of this pride is described in some detail as it was similar to that of Lion away from Lake Kariba, which cross to islands inhabited by suitable prey. It is interesting that in the Central Zambezi Valley they swam at least one-and-a-quarter miles to game concentrated by Lake Kariba, as there were no natural islands in the region capable of supporting a large game population, those in the Zambezi having been heavily cultivated.

The 11 Lion on Ukubula Island included four cubs from two litters, which Haslam estimated to be about two and six months old respectively, and a male believed to have swum $1\frac{1}{2}$ miles to the island after having been disturbed from part of Ibuyuamonga Island (Dr. H. Roth, pers. comm). Ukubula Island was well stocked with game, those listed in Table 13 being a conservative estimate based on the first survey of the island. An adult male and female and one of the larger cubs were shot, but two days later the Lion were still on the island. That night they were fired at unsuccesfully but then disappeared and must have swum to the mainland, a distance of at least one-and-a-quarter miles, as no drowned carcases were found in an area where they could hardly have been missed.

Mitchell et al (In press) found that Buffalo were the most important prey of Lion in the Kafue National Park, and it is significant that three islands on which 19 Lion were found, were the only ones where more than three Buffalo were known to have been marooned, although one of those on Ukubula Island probably swam there following its disturbance from another island where there were no Buffalo. Buffalo signs were widespread on Sampakaruma Island, although the population was never estimated, but on both

Table 11.

Rough [illegible] animals marooned on Umbali Island.

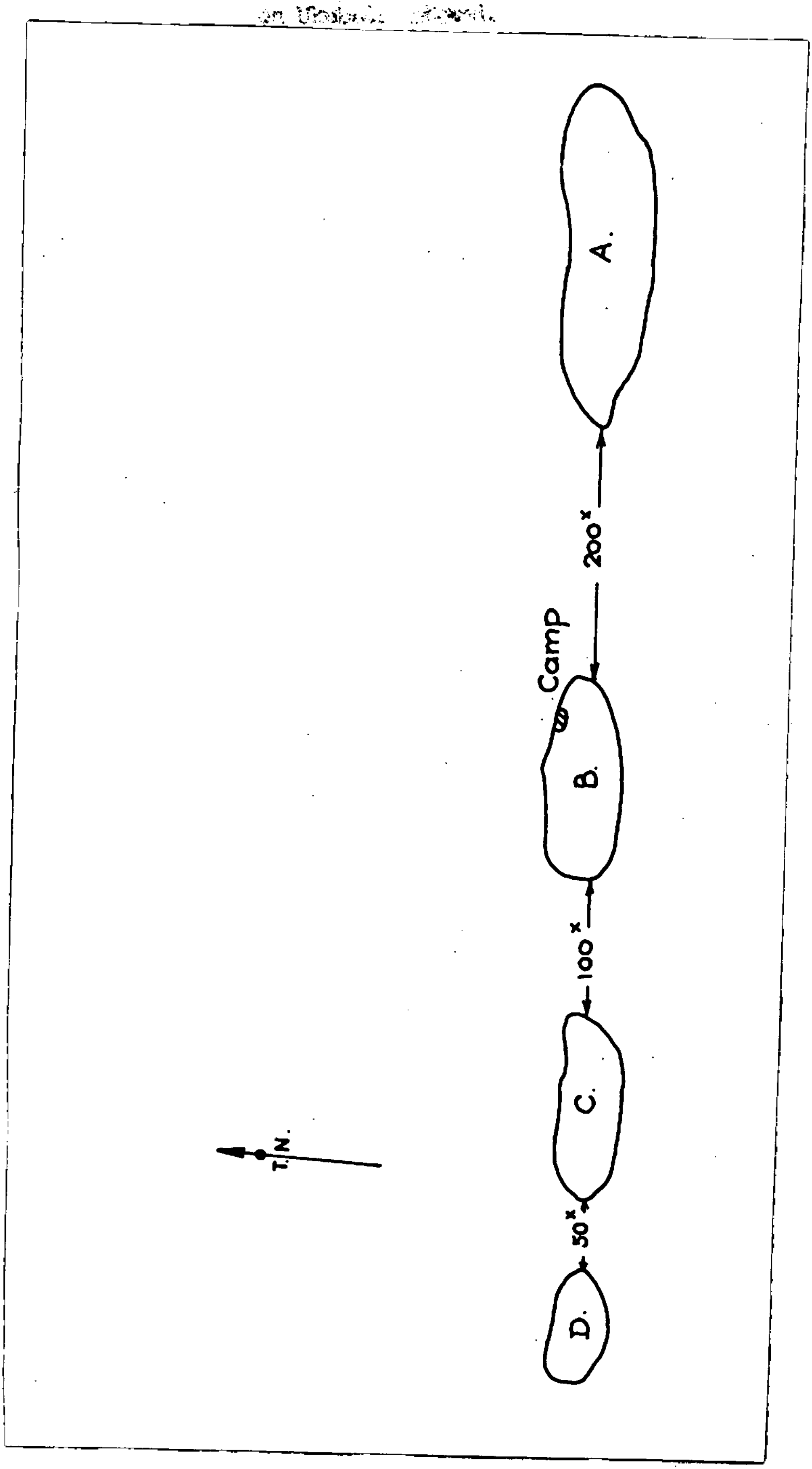


Fig. 16. Shows the approximate distances Lion had to swim when crossing between sub-divisions of Island 100.

the other islands there were large herds of about 30 and 200 respectively. The Buffalo became over-populated on these two islands and lost condition so that, with other species on the island, they must have been relatively easy prey for the Lion.

Lion are strong swimmers, which apparently roam over large areas so that it is unlikely that many would become trapped by floods, as they are quite capable of swimming a swollen river. They evidently benefitted temporarily from the concentration of game on three islands at Kariba, where their behaviour on Island 100 showed a natural tendency for Lion to swim to islands with suitable prey.

5. ANTBEAR

The widespread distribution of Antbears, Orycteropus afer Pallas, noted in Table 8, was based on the occurrence of their holes, as this nocturnal species is rarely seen out by day.

A. Response to Flooding

Antbears sought cover in holes when danger threatened, which made them difficult to drive into the water, although once in the water they could swim reasonably well, as Junor (1960) has noted. Antbears spend the days down holes, which are larger than those made when feeding, suggesting they have fairly localised habits, although little is known of their movements or how many sleeping holes there are within an individual's home range. It is, therefore, difficult to estimate the effects of flooding on an Antbear population. The use of holes for shelter during the day and their behaviour on large islands suggests many would drown. This is supported by observations made by Mr. R. Smithers (pers. comm) during flooding in the Okavonga region of Bechuanaland. Here the land is very flat and large areas flood to a depth of a few inches and Antbears, driven from their burrows, become marooned on the mound of earth thrown up at the entrance, where they are easily killed by Bushmen. On the other hand, Antbears never became trapped on islands which originated from small areas at Kariba, although their holes, including sleeping burrows, were common on such islands. The smallest areas in which Antbears were known to have been marooned were approximately 1,000 and 2,000 acres respectively. The latter was on alluvium and only one animal was recorded, but there were two or three Antbears on the former in mopane veld, where termitaria were more common.

B. Behaviour on Islands

Antbear burrows were important refuges for a number of species such as Genets, Civets, Wild Cats, Hyaena, Baboons, Wart Hog and Grysbuck. Some of these may have disputed possession of the holes with the Antbears, as Rescue Reports describe at least two with badly mutilated tails, in one case with the tail severed completely. These wounds were atrributed to Bush Pig, as they were the only species capable of having inflicted them. A dead Antbear on Island 17 may have been killed by Hyaena.

There were two islands where Antbear could not dig and where they were found wandering about during the day. The first was a flat alluvial island with the water table within 18 inches of the highest point. Numerous burrows had been started and abandoned when they reached moist soil. An Antbear splashed ashore at 16.35 hours, after the observer had been on the island about an hour and a half, during which time it must have been hiding in the shallows. Conditions on this island were rather similar to those in the Okavonga described by Smithers.

The soil was rocky on the second island, which had formed from the crest of a ridge. An Antbear was seen at 13.00 hours, while another was found asleep in a shallow horizontal burrow tunnelled three feet into the base of a termite mound. The animal was lying on its side in a semi curled-up position, with the snout near the chest and covered by the fore limbs. It did not wake up with four people less than six feet away, until deliberately disturbed, whereupon it bolted out of the burrow, instead of attempting to dig away from the danger, as was their custom.

The islands' soils were clearly unsuited to burrowing and droppings found contained a high proportion of earth to insect remains, compared with those from other islands. There were several active termite mounds, but except for the one mentioned, none had been fed from to any marked extent, although most bore signs of superficial Antbear activity. Two had fresh castings where the Antbears had succeeded in piercing a small hole into one of the outer chambers of the nest. Excepting for one mound on a steep rocky area, all were old with well weathered surfaces and, judging from the scratches on them, were too hard for the animals to dig open. Shortages of Antbear food were reported from two other islands, on one of which three Antbears were very thin and weak.

These food shortages were caused by the unusual conditions at Kariba as Antbears were forced into unsuitable habitat. It is unlikely, however, that such specialised feeders would experience much inter-specific competition or suffer from the type of food shortages facing most game mammals, as a result of failure of the vegetation through drought.

6. ELEPHANT

Elephant, Loxodonta africana Blumenbach, were among the most conspicuous mammals in the Central Zambezi Valley. A number were cut off when large islands were formed, but could hardly be classified as marooned as Elephant swam to and from islands. This was confirmed on 17 islands, but probably happened very much more frequently. One island was about a mile from the mainland and here, the number of Elephant fluctuated irregularly between zero and 14 over a period of nine months, during which time the Rescue Unit visited the island on eight occasions. Elephant now swim to an from Ukubula Island (Dr. H. Roth, pers. comm), a distance of one and a half miles.

How the Elephant found their way to the first of these islands through the homogenous, partially submerged mopane veld, presented an interesting problem. It was also difficult to understand why they took the trouble to swim to it. Some islands visited by Elephant had well developed soak zones, which may have attracted them, especially when grass was green out of season, but in this case, the vegetation was similar to that along the mainland and had actually been more heavily used by the Elephant. Nicholson (1954), Buss (1961) and Napier Bax and Sheldrick (1963) all found that Elephant eat mostly grass when it is available, although they also take woody plants and yet there was very little grass on this island, where the Elephant had eaten browse from species which were readily available on the mainland.

A possible explanation is that Elephant have conventional movement patterns, which in this case included the area in which the island formed, but this still does not answer the question as to how they knew of the island's presence in such flat country, or how they located it. It is hardly conceivable that they simply swam about in search of islands.

It is not surprising that Elephant could swim to and from islands, especially those near shore, as they often swim to islands in the Zambezi below Kariba and above the Victoria Falls, and it is well known that Elephant take to water readily and can swim well (see for example, Carrington, 1958). It is, therefore, interesting that Elephant were reluctant to leave at least six islands when humans were present, although they did so later when undisturbed. This entailed a swim of over a mile for some, but the maximum distance recorded was that covered by a female which had to be caught in the water to prevent her drowning. According to the men responsible for her capture, she was at least two miles from land, but probably had swum much further.

Only three elephant remained on islands for any length of time after the habitat had deteriorated. An adult bull was found on Island 7 on 3rd. June, 1960, having swum to the island since the Rescue Unit's previous visit some four weeks before. This Elephant could easily be chased into shallow water, where it once attempted to hide by lying down, so that only its trunk was above the surface, but all efforts, spread over five weeks, to drive it into deep water failed. Shots were fired near it, it was pelted with stones and a dead tree on the side of the island was soaked with petrol and set alight, but with no success, although the island was less than two acres and consisted of two islets separated by a narrow strait. The Elephant had starved to death after removing all edible browse on the island and in the shallows by the time the Rescue Unit returned to the area in September.

The second island where Elephant remained after food became scarce was Island 101. A herd of about a dozen was first reported there in October, 1960, but left some time in December or January, while a female stayed behind on the island. In February it was noticed she had a small calf, but she and the calf did not disappear from the island until the latter half of March. A careful search for carcasses indicated that both had reached the mainland almost a mile away. This demonstrated the remarkable swimming ability of a young Elephant calf, which could not have been more than three to four months old. By the time the cow left the island, most of the browse had been eaten.

This cow had apparently waited to calve and then allowed the calf to grow before leaving the island. The reluctance of the bull to leave Island 7 was probably due to fear resulting from efforts made to drive it into the water. As already mentioned, Elephant were reluctant to go into deep water in the presence of humans, apparently appreciating how vulnerable they are when swimming. Similar behaviour was noted for Rhino (p.53) and Buffalo (p.106).

Elephant are strong swimmers and can probably avoid most natural floods as, although little is known of their movements, it is obvious that they wander over considerable distances.

7. BLACK RHINOCEROS

The rescuing of Black Rhinoceros, Diceros bicornis Linn, from island in the Lake was a priority for the Rhodesian Rescue Unit and, as they had to be drugged and handled individually, their capture was better documented than that of any other species. This enabled Roth and Child (in press) to supplement personal observations with Rescue Reports and so describe in some detail the distribution of the whole population from the area affected by the Lake. They also deal with some of the characteristics of the population's structure and dynamics and some of the behaviour of Rhino on islands so that it is now necessary only to summarise their findings and to mention some of the behaviour they did not cover.

The distribution of Rhino was limited to areas on the south bank where human settlement had been sparse and where there had been no previous Tsetse Control Hunting Operations (p. 25). Roth and Child attribute this to the sensitivity of the Rhino populations to hunting. A total of 62 were recorded between the Umniati and Mwenda Rivers and probably represented the bulk of the population resident in this area as, although Rhino frequently wallow, they avoid deep water and were therefore readily trapped on islands. The only reference found in the literature to their swimming is the description by Hawthorn and Lock (1960) of one which had to swim at Kariba. Here, there were several additional records of Rhino swimming up to 20 or 25 yards, which was approaching the limit of their endurance, as Black Rhino are poor swimmers and, unlike the Asiatic species, do not like deep water. Mr. N. Dean (pers. comm), senior warden in Hluhluwe Game Reserve, Zululand, which has a dense Black Rhino population, is of the opinion that this species will not cross a rapidly flowing stream if it is over 15 inches deep. He also found they preferred wallows with more mud than water, although they continued to use them after rain with water up to 18 inches deep. This is in contrast to the three Asiatic forms. Barbour and Allen (1932) note that the Javan Rhino, Rhinoceros sondaicus Desmarest, is partial to entering streams, and Hubback (1939) records the same for the Sumatran species, Didermocerus sumatraensis Fischer, which frequently goes into clear streams up to three feet deep, while Ripley (1952) found the Indian Rhino, Rhinoceros unicornis Linn, to be an accomplished swimmer with, among others, a record of one which swam the Brahmaputra River.

The fact that some Black Rhino went into deep water at Kariba was therefore unusual. Rescue Reports describe spoor leading from one island to another through water up to three feet deep, and a family party was observed feeding in about this depth of water on Island 17, but charged back on to the island as soon as they were disturbed. The male of this group hid in the water on three occasions after the female and calf had been rescued. During pauses while attempting to drug it, it waded 50 to 100 yards into the shallows and stood motionless in thickets with only its head above the surface, but bolted back on to the island as soon as men gathered on the shore. It also crossed 150 yards of water up to three feet deep at least five times, but, as when hiding, never did so while being chased. This was the animal Hawthron and Lock described swimming about 25 yards and was the only one reported to have done so before being darted with drugs, although a number entered the water afterwards and some drowned when they collapsed in the shallows under the influence of the drug.

Rhino are weak swimmers which experience difficulty in holding their heads above the surface. Like Elephant, they appear to realise how vulnerable they are in the water, which accounts for the fact that they could seldom be driven into the shallows and explains the behaviour of the male on Island 17, which charged back on to the island as soon as men threatened to block it off from land.

Localised habits also contributed to their being marooned on islands. Six marked individuals were contacted after release, and all were within four miles of the release point. An adult male seen at the north eastern corner of the Umniati West bush clearing, had been noted in this area on several occasions by Mr. Stokes, the Ranger in charge of the area. It was then 3.5 miles from where it had been released six months before, which probably represented its maximum movements in 11 months, as it became marooned for a second time when Island 100 formed between this locality and the release point, in March 1961.

In this general area, two marked Rhino were seen after "a couple of months" within "a few miles" of the release point. One of these animals was later contacted one and a half miles from the release point a year after release, but the other died in the area in the meantime, (Dr. H. Roth, pers. comm).

An adult female was retaken on Ukubula Island, which formed nine months after its release. The break through giving rise to this island was four miles from the release point. An adult male from this island has remained within "about five miles" for several months since its release (Warden P. Coetsee, pers. comm) and another, liberated on the east bank of the Sengwa River, was contacted five months after release when it had moved less than three miles into the nearest suitable habitat.

On 16th. April, 1961, an adult Rhino was disturbed by a boat and ran about a mile into a bush clearing, but then slowed down and circled round, so that it headed back in the direction whence it came. When lost from sight, it was almost back in the same clump of trees from which it had been disturbed.

Small home ranges seem to be normal for Black Rhino, which frequently defecate in the same place, as Dean (op. cit), basing his conclusions on recognisable individuals in Hluhluwe, notes that "For the greater part (black) Rhino have very definite home ranges in which they appear to spend the greater part of their lives. I do not consider the home range to be in excess of six square miles and often as little as four square miles. An important factor controlling the size of the home range here is probably the availability of water. In most parts of the reserve even in dry years, no great distance need be travelled to find it. I have only one record of a cow and calf leaving their normal home range for another area, eight miles away, crossing a river (presumably with little water) to do so where they have since remained permanently."

There were two male Rhino in the Nagupande Tsetse Area and these remained in a small area of about 12 square miles for 12 months after selective, but intensive hunting (approximately one hunter per 3.5 square miles) began in the area. They then moved 13 miles and left the area, breaking through the game fence surrounding it, (Mr. J. Kerr, pers. comm). A male with a peculiar kink in its tail was observed in July, 1963, and was reported to have remained within half a mile of the confluence of a small tributary and the Luangwa River, during the dry season, for at least two years, although during the rains it may have been forced a mile or so from the Luangwa by the inundation of the flood plain. This animal was seen by the author within one mile of the same locality 14 months later, in September, 1964.

This evidence indicates Rhino are generally fairly localised although the availability of open water probably determines the size of the home range as Dean has suggested. Ritchie (1963) indicates they wander five to 15 miles from water to feed in parts of Kenya, as well defined Rhino paths lead out this distance from water holes. Stockley (1950) and Ripley (1958) have gone as far as to describe them as territorial, on account of their defecating on middens and then scattering their dung with their feet. Although Rhino do occasionally fight, the active defence of territories needs substantiating in view of the small amount of aggressive behaviour found by Roth and Child, when Rhino populations become compressed on to islands at Kariba. Further, Ripley (1952) has suggested the great Indian Rhino are also territorial as they too have middens, but Gee (1953) disagrees, as several animals may use the same dung heaps and this author suggests they may play a role in establishing social hierarchies within a group.

Black Rhino are probably susceptible to abnormal floods where these affect the greater part of their home range, even if the water were only a foot or so deep. A female and calf drowned in this much water within a few days of an island submerging, indicating it is essential for Rhino to lie down, as they often do, when sleeping.

A. Behaviour on Islands

Black Rhino are generally accepted as browsers of a variety of trees, bushes and shrubs, although they seldom eat much grass. They experienced shortages of food as islands diminished in size, which may have led to the deaths of two very small calves and an adult, but Roth and Child have argued that this had little effect on the structure of the population, although most marooned Rhino were thin.

The plants eaten by three Rhino on Island 17, based on observations of undisturbed feeding and the obvious signs of browsing, included *Combretum apiculatum*, *Diospyros quiloensis*, *Holmskioldia spinescens*, *Dichrostachys cinerea*, and traces of mopane were found in a few droppings. These were similar to the plants taken by other browsers, especially Impala, the most numerous species on the island, and suggest considerable competition for food. This may have caused the three Rhino to feed in the shallows, where Impala never went, and was substantiated by the following incident. One of the Rhino had broken down a branch of *Combretum apiculatum* and was defending it from Grysbuck, an Impala and a Bushbuck. In this, it was not very successful, as usually, when lunging after one of them, the other two were able to nip in and feed.

The breaking down of small trees or branches up to four and a half inches in diameter was more prevalent on this island than in any other area investigated on the Lake. It was done with the chin and meant Rhino could obtain food from above the clear browse line left by Impala (p.86). This behaviour in response to food shortages is common in Hluhluwe according to Dean, who describes areas of two or three acres in which most of the *Acacia karroo* is damaged.

Rhino populations withstood considerable compression into the small areas on islands, without the various smaller groups losing their identity (Roth and Child, *op. cit.*) and without inter-specific competition for food resulting in a heavy mortality. Obviously there is a level at which food supplies will limit further growth of a Rhino population, but as a limiting factor it may be less significant than hunting, or the availability of water to this localised species, in extensive areas of otherwise suitable habitat. With the possible exception of the Somaliland race, *D. bicornis somaliensis* (Stockley, *op. cit*), Black Rhino are generally agreed to be dependent on regular access to open water.

Roth and Child have explained the ease with which the species can be eliminated by hunting, as the replacement rate to the breeding herd is slow (8% - 9% per annum) and the maintenance of the population relies largely on the survival and longevity of sexually active adults. This means that a population could only fluctuate slowly and sporadic food shortages would not affect numbers to the same extent as they may in rapidly breeding species, which can become numerous between successive periods of food scarcity, even if the intervals are fairly short. Further, on Island 17, Rhino evaded the critical lack of food by obtaining food from a higher level than any other browsers, and the ability to eat twigs meant that they used food unsuited to most species except

Elephant. This, and the fact that Rhino density is usually low in poorly watered areas, suggests that open water is the main limiting factor to this species, which lives in small groups in restricted home ranges.

8. BURCHELL'S ZEBRA

Zebra, Equus burchelli Gray, were only recorded between the Mwenda and Umniati Rivers within Rhodesian portions of the Kariba Basin. This indicates the influence of human settlement on their distribution in the Zambezi Valley, where they are scarce compared with the southern lowveld. Here numbers are high, even on down graded ranges, and they are one of the chief species culled commercially. In one area of just under 400 square miles, 14,307 have been shot in the 11 years ending in 1963 (Dept. Report). This population has withstood an average annual crop of 1,301 head, but Zebra may be more sensitive to habitat deterioration, or hunting, in the Zambezi Valley, where the fatty nature of their flesh would have been prized by the Tonga.

61 head were recorded on three islands during the present study and constituted 90% of those found on islands in Rhodesian waters before 30th. June, 1961.

A. Response to Flooding

Zebra were very reluctant to enter water when trapped on large islands. They were chased about a good deal on Island 17, both during their capture and the netting of other species which preceded it. Two tangled in the nets and 31 were run down in chases lasting three to six hours of June 13, 14 and 17, but it was not until the third day that any entered water over a few inches deep. On that day 19 crossed back and forth to netting point (Fig. 10) several times, through water two feet deep, while 12 of their number were caught. Five of the seven left on the island that evening had disappeared by next morning and the other two took to deep water after a short chase.

The behaviour on Island 201 was similar. Two were caught on land after three hours before one took to the water and again the four which remained on the island disappeared during the night. On Island 151 all 17 were run down without going into the water, although the prolonged chase resulted in 10 dying of exhaustion.

On these three islands, Zebra were reluctant to go into the water, even when pressed by beaters, but the islands were 25 to 120 acres. On a fourth small island, however, three took to water as the Rescue Unit approached and drowned after swimming 300 to 400 yards (Rescue Reports). These distances must represent the limit of their swimming ability, as the two from Island 17 were exhausted within 200 yards and the one from Island 201 was tiring after 150 yards. The first two had been weakened by starvation, but the last was in fair condition, so that Zebra are obviously weak swimmers. They are also slow, and the only other large mammals which showed less ability were Rhino.

Klingel (1964) gives the daily movements of Zebra in East Africa from the sleeping area to food and water as about 10 km. (c 6 miles) and the smallest area in which Zebra became marooned was 3.8 square miles. This suggests they would avoid most natural floods, although water would be an effective barrier, and this is borne out by Mr. D. F. Vesey-FitzGerald's (pers. comm) observations that they were cut off by rivers when Lake Tanganyika reached an abnormally high level in 1963/64, where they were the only species drowned.

B. Behaviour on Islands.

Zebra are normally predominantly grazers, judging from most accounts and field observations, including 10 stomach analyses. The only area where they are known to make extensive use of plants other than grass is in the Cape of Good Hope Nature Reserve, where grasses are relatively scarce numerically in the Cape sclerophil vegetation. Here at least two species of Cyperacea were eaten in fair amounts in early 1959, in addition to small amounts of six species of grass, including Pentameris macrantha and Ehrharta sp. Most remarkable in this area, to which Zebra have been introduced, was the extensive use made of the younger shoots and bristly flowers of Metalasia cephalotes, a stiffly-branched woody Compositae about 60 cm. high. Two Zebra were once seen feeding on nothing but the apical shoots of this species for over half an hour, and judging from the plants this was common behaviour.

It was amazing that Zebra withstood the food shortages on Islands 151, and 17, both of which were in mopane veld and had been heavily trampled. Zebra frequently returned to the few over-grazed tufts of perennial grass on Island 17, but ate mainly litter derived from trampled annual grasses and fallen leaves. The last did not exceed 10% of the contents of any of the five stomachs examined and were probably taken fortuitously as they were relatively much more common on the ground.

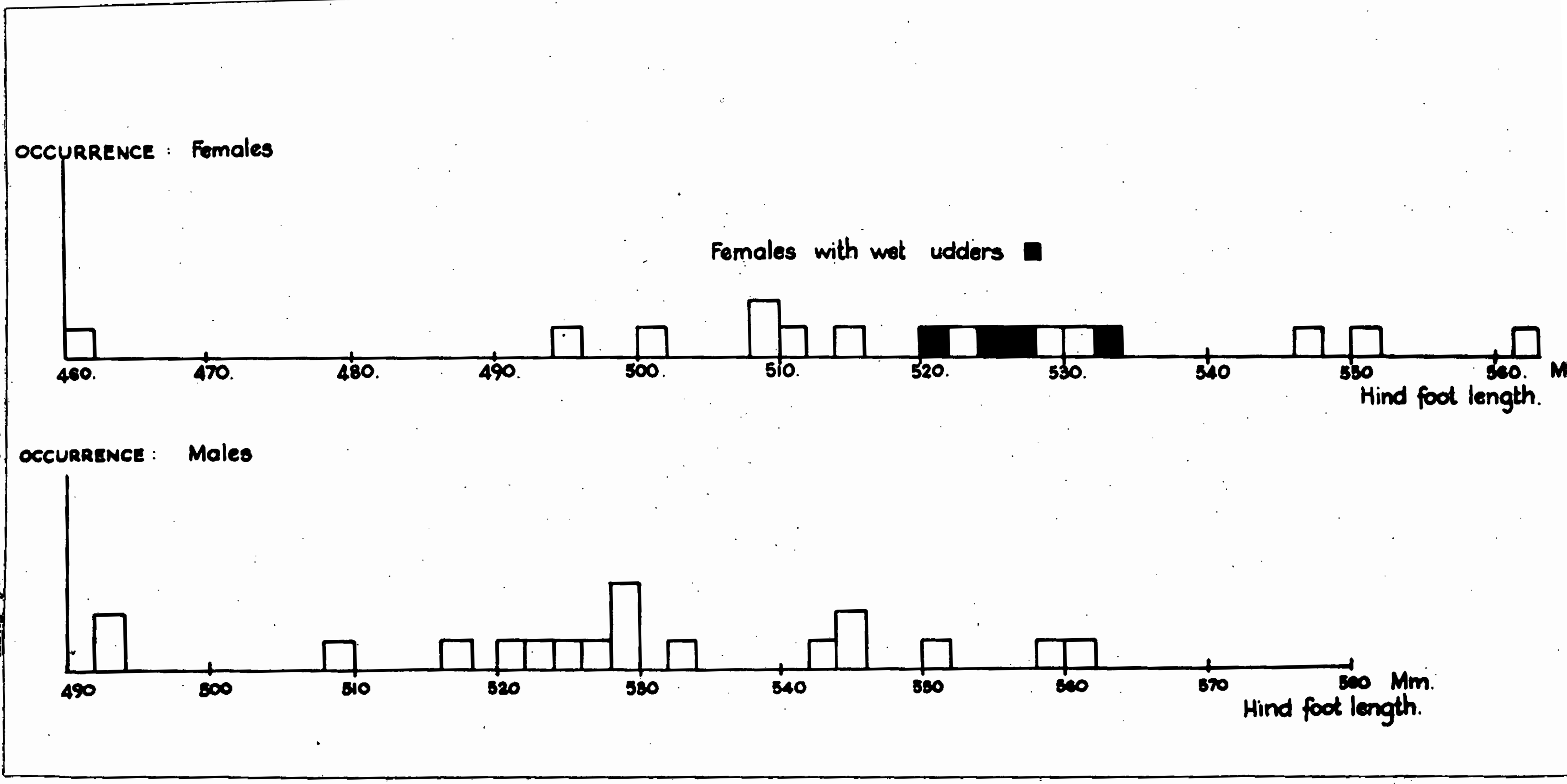
On Island 201, on the other hand, there was ample green perennial and annual grass in April 1961, and this reflected in the better condition of the Zebra. Both adults caught were fat and even the juvenile was in better shape than the 24 Zebra conditioned on Island 17, all of which were very thin.

Being marooned seemed to have little effect on the sex and age class structure of the 41 Zebra on Island 17. A young nursing foal was the first to starve, but was followed within a week by two adults. The 36 Zebra handled consisted of equal numbers of males and females and included three additional foals which were still nursing, and the five which disappeared from the island without being sexed were all full grown. Zebra have an extended foaling season in Rhodesia and Klingel (op. cit) suggests females mature at between one and two years in East Africa, so that growth is obviously rapid. If the present sample, taken in June, is broken down according to hind foot lengths (Fig. 17) it gives four (9.8 : 100 head of population) small foals and a total of seven (17.1 : 100 head) immature animals. These compare with 3.7 and 9.6 "young of the year" and 5.6 and 21.7 total immature per 100 headof sample obtained by Dasmann and Mossman (1962b) in samples of 514 and 83 taken between May and September and in April from the Henderson's Ranches and the Fort Tuli area, respectively, in the southwest of Rhodesia. Talbot and Stewart (1964) obtained 18.2% juveniles under about 15 months old in a sample of 1,604 from the Serengeti - Mara region of East Africa.

Although these ratios vary constantly, depending on current habitat conditions and stocking rates, they support the contention that there was no appreciable change in population structure in the Zebra marooned on Island 17. It is to be expected, however, that prolonged stress would lead initially to a heavy juvenile mortality, so that it is not surprising that no shift in the sex ratio was detected. Dasmann and Mossman obtained 109 males : 100 females in 88 Zebra culled on the Henderson's Ranches, and Wildlife Utilization Services, operating in the south of Rhodesia, obtained 93 : 100 in an annual crop of 1,163 adults, where no attempt was made to shoot either sex.

In spite of three deaths due to starvation on Island 17, Zebra survived remarkably well while their range was reduced from between 7.5 and 15 square miles to less than 120 acres, considering the heavy competition from other ungulates. They subsisted mainly on litter, but had free access to water which may account for their obvious success on depleted range in marginal cattle ranching areas in the south of Rhodesia, where water is provided for domestic stock. They are, however, very susceptible to fences. Wilson (Ms.) and Child (unpublished) have noted this in relation to game fences, while Mr. P. Johnstone (pers. comm.) has found numbers lower in areas cut up into paddocks than in undeveloped areas under a similar management regime. In addition, Silberbauer (1964), recorded no Zebra in the Central Kalahari from where they have apparently disappeared as the result of a "disease control" cattle fence.

Fig. 17. The hind foot lengths of Zebra rescued from Island 17.



9. BUSH PIG

Bush Pig, Potamochoerus porcus Linn, occurred throughout the study area, but their secretive habits made any estimates of relative densities along the Central Zambezi Valley most unreliable. They still occur in intensively farmed areas around the City of Salisbury, so that it is unlikely that any but the densest Tonga settlement would have eliminated them.

They became marooned on islands but were very adept at avoiding capture and many must have drowned, although they were very hardy and few died after being caught.

A. Response to Flooding

Bush Pig on islands went into the water with little hesitation, usually as the Rescue Unit approached. They were less afraid of water than any species, except Waterbuck and, in spite of a tendency to hide in thickets, were usually among the first animals to leave an island. This behaviour was noted for 38 specimens, although Bush Pig remained on part of Island 17 for 10 days while game was caught elsewhere on the island.

They were strong swimmers and Junor (1960) recorded a marked male which swam over a mile, while a female swam an estimated 1,300 yards and was still swimming strongly when picked up. This is not surprising as Fitzsimons (1919) remarks that they are "expert swimmers", and Bigourdan (1948) that they are excellent swimmers, crossing large rivers without hesitation and in this way appear periodically on lagoon islands in West Africa.

There were five islands with Bush Pig within easy swimming distance of the mainland and it seems that, when more is known of their movements, they will be found to have localised habits. Junor (pers. comm.) suggests that the marked male he recaught was swimming towards the island from which it had been removed and another male stayed on an island, where food was critical, within half a mile of the mainland. Finally, Bush Pig returned to islands with limited food even though they were nearer to alternative and better habitat.

B. Behaviour on Islands

Bush Pig are found in a variety of habitat types, but in the Nagupande Area, where the vegetation is similar to that in the Kariba Basin, most of the 109 shot on control were in areas with riparian or jesse thickets. The habitat on most islands was, therefore, quite suitable although, in a number of cases, they lacked normal food and cover through overcrowding by other species.

There were 17 to 21 Bush Pig on Island 17, but four was the maximum recorded on other islands and intraspecific competition was generally light. They overcame the shortage of cover by hiding in the water where they made frequent use of termite mounds, which showed above the surface and were often surrounded by scrub. There was also a report of one which hid in deep water and remained afloat by resting its head on a branch.

They normally feed on roots or other vegetable products such as fruits, but several authors note that they will take carrion when it is available. They experienced considerable competition for roots from Wart Hog on Island 17, where there were no fruiting trees, but were able to use the readily available carrion which Wart Hog did not. Although criteria for assessing the physical condition of Bush Pig have not been developed, with one exception, those seen or caught on islands were not thin. The exception had extensive fresh scar tissue on the hind quarters, apparently caused by a Leopard.

No deaths were recorded from starvation, even on Island 17 where there was a high proportion of immature animals. Roberts (1951) suggests they may farrow twice a year, but most young seem to be born during the rains (November to March). There may be as many as 10 foetuses in a litter (Roberts, op. cit.) but Ansell (1960a) gives three or four as usual and, in the Nagupande, five unborn litters varied from two to four (mean 3.2). On Island 17, there were two sounders and several individual adult and sub-adult animals. The sounders each had two sub-adults, judged as yearlings, and one had three and the other four sucklings between four and six months old. The high number of immature animals in these two sounders and the presence of other yearlings indicated that there was little stress on the sample, as Mohr (1960) describes juvenile mortality as very sensitive to food supply in the closely related Sus scrofa Linn, and this also applied to Wart Hog at Kariba.

Their elusiveness made it difficult to judge the effects of flooding on Bush Pig populations, but their behaviour and survival on islands underlined their versatility, which is probably largely responsible for their having remained widespread in developed farmland within 10 miles of Salisbury (Child and Savory, 1964).

10. WART HOG

Wart Hog, Phacochoerus aethiopicus Pallas, were plentiful in the Kariba Basin east of the Masumo River, particularly near the Bumi River, and were the second most numerous species marooned on islands, contributing 12.9% of the mammals rescued by the end of June, 1961. Their absence from the meander zone was attributed to the poor perennial grass cover induced by Tonga agriculture, as they are fairly resistant to hunting.

They were virtually eliminated by anti-tsetse control shooting operations in parts of Zululand (Mr. I. Player, *pers. comm.*) but have withstood similar operations in two areas in Rhodesia and Zambia. In a third, a hunting intensity of one man per 3.5 square miles resulted initially in a rapid decline in numbers, but then for the next 18 months hunting successes remained fairly uniform and it is debatable whether this intensity of hunting would have achieved their elimination. Bigourdan (1948) stresses their high "intelligence" and adaptability when persecuted. Among other things, they become less diurnal which explains contradictions in literature between authors such as Shortridge (1934), Stevenson Hamilton (1947), Ansell (1960a) and Mohr (1960), who found them most active during the day, and Fitzsimons (1919) who describes them as nocturnal.

A. Response to Flooding

Wart Hog were readily trapped on islands, in spite of the ease with which many were driven into the water and their considerable swimming ability, mainly because of localised habits. Bigourdan found a number of groups resident in small areas throughout the year, but does not indicate the size of the home range in either Senegal or the Sudan, where he worked. Riney (*pers. comm.*) reports a known male, with an unmistakable tail reduced to a stump about an inch long, which was regularly observed in the one clearing in the Gwai Forest Reserve in Western Rhodesia for five years. It was usually in the same part of the clearing and the greatest distance it was seen up and down a river was under a quarter of a mile. The animal did not apparently cross the clearing, so that this was the edge of its home range, which may have extended back to the top of a ridge about one half mile away. Mr. J. Kerr (*pers. comm*) has eight sightings, spread over 10 months, of a recognisable family party on one side of a particular one mile stretch of road near the Nagupande area.

The smallest areas which gave rise to islands on which Wart Hog became trapped were of the order of 600 acres, while a total of 72 were marooned on Island 17, which arose from 7.5 square miles, giving an average density of about 10 Wart Hog per square mile. A similar, although less exact figure applied to Ukubula Island. The low number of recapture records during rescue operations of marked animals resulted from the ease with which Wart Hog lost ear tags. At least four such animals were handled and others may have been overlooked. One tagged animal was retaken on Island 17 within half a mile of where it was released seven to eight months before the island formed. Another was on an island between the one from which it had been rescued and the release point, and Junor (*pers. comm*) is of the opinion that it was returning to its former home range. Finally, there was an adult male released and re-caught with the same Grysbuck after 10 months.

The size of an island governed the ease with which Wart Hog could be driven into the water (Table 2). Although they wallowed in the shallows around large islands, they were difficult to drive into the water and often flushed past unconcealed humans, rather than enter water in which they had to swim. Adults showed a little less hesitation before doing so than either sucklings or yearlings, but all that did enter, did so over recently submerged land between two islands. The vegetation was similar to that in the shallows elsewhere and, according to Silhelm (1933), they have poor eyesight and in most cases could not have seen the other island, so that their behaviour towards water is further evidence of localised habits in an area with which they were familiar.

They were strong swimmers, one animal being caught over a mile from the island from which it had been flushed, another over half a mile, and swimming distances between 100 and 200 yards were common. They were strong, not especially fast swimmers and often when approached in the water charged a boat in a most determined fashion and in a few cases actually went out of their way to attack. One female adult which had avoided capture on the Rescue Unit's first visit to an island, when all burrows were blocked, took to the water immediately the Unit returned, after an interval of over a month and hid behind a large mopane tree in deep water, where in order to remain afloat she rested her head on a branch. Two others hid beneath thick carpets of Salvinia, with only the tip of the snout and the eyes above water, and did not flush until approached to within five yards.

With the exception of their swimming, the behaviour towards flooding at Kariba was very similar to that described by Bigourdan (1948) during seasonal inundations of the Senegal River Valley. Here a proportion of the population becomes marooned on small islands for four or five months every year, while others, whose ranges do not include temporary islands, give ground before the flood, and Bigourdan suggests they may disperse 100 km. from the river as Wart Hog are found during the rains, in country quite unsuitable for them in the dry season. Movements of such magnitude require verification, including observations on marked individuals as Wart Hog can do without water for long periods lasting up to six consecutive months, although, as this author has noted, the availability of water probably controls absolute numbers. They are resident in parts of Bechuanaland and the south east of Rhodesia where there is no water for over 40 miles in the dry season, and in the Nagupande Area, did not concentrate on certain water holes as others dried up at the end of the 1962 dry season, although there was a rapid decline in the physical condition of specimens from waterless areas.

Bigourdan's work suggests they are well able to live in areas subjected to regular seasonal flooding, but high losses were recorded during the unusually severe floods in Zululand in July, 1963 (Natal Parks Board Records). In this case, cold weather preceded the rain and drove Wart Hog into their burrows where many drowned. Player (pers. comm) estimated that in parts of the Umfolozi Game Reserve some 75% of the population perished within a few days from the combined effects of cold and drowning.

B. Behaviour on Islands

The essential components of Wart Hog habitat appear to include adequate suitable perennial grasses and good cover, which in Rhodesia is often derived from the burrows in which the adults of this markedly diurnal species sleep. These burrows are also very important during the farrowing season. Geigy (1955) gives temperatures around 30°C and a relative humidity of about 90% in one he excavated, and Sowls and Phelps (Ms.) have shown that sucklings have limited control over their body temperatures and in the laboratory require artificial warmth, at least until they are over two months old, although by the time they are four months old they can survive overnight at 40°F (4.4°C). This was substantiated by practical experience when raising young Wart Hog in the Nagupande Area, where they continued to favour warmth until well over four months of age.

Several authors have stressed the importance to this species of Antbear holes or other burrows and Ansell (1959) suggests a positive relationship between the distribution of the two species in Zambia, although Bigourdan indicates ravines and dense thorn thickets are suitable alternatives. There is, however, little doubt that Antbear holes are important for high numbers of Wart Hog in the Central Zambezi Valley. There are few natural dens and Wart Hog probably never make their own holes, although they will modify those of other species. Captives used both the fore feet and the rhinorium when thus engaged. The former were used with the animal down on one "wrist", which enabled the other foreleg to be extended forward and then swept back with sufficient force to move a stone, six inches in diameter, some 10 to 12 feet. This form of digging is apparently reserved mainly for hard objects, as the snout is used in soil and, according to Mr. V. Wilson (Pers. comm) it can be used, with the animal lying on its back, for raising the roof of a burrow.

There were five Antbears on Island 17, which apparently provided enough holes in the 7.5 square miles from which the island originated, for the 72 Wart Hog which became marooned there. As the island diminished, however, Wart Hog became short of cover. Normally they made frequent use of holes toavoid being caught, but on this and other islands, there were 32 records of their attempting to shelter in holes which were already overcrowded, or were too shallow to accommodate the whole animal. There were also six records of Wart Hog sharing a hole with another species as follows : two Antbears, a Baboon and an Antbear, a Grysbuck, a Civet Cat, and twice with a Porcupine, and as noted, three Wart Hog hid in the shallows.

The use Wart Hog make of dense cover and their aptitude for remaining hidden in small patches of scrub are not generally recognised, but are probably important for their survival in areas where they are hunted extensively. In 11 instances, different individuals remained hidden in thickets eight to 10 yards across, and even when they were surrounded by men throwing stones and sticks at them, remained motionless and would have been overlooked had their presence not already been established. This behaviour was continued on overbrowsed islands, but was naturally ineffective.

No serious fight for possession of a burrow was noted, even when cover was critical, or when Wart Hogs occasionally forced their hindquarters into an over crowded hole. Three adults in holes on Island 17 did, however, adopt an aggressive attitude when approached by a yearling which, in each case, moved on immediately. On this island there were three or four yearlings with scars on their hindquarters, attributable to lunges from adults, which occasionally jabbed at them when they hampered their escape during a drive. The lack of fighting may have been due to their poor condition and lack of energy, as Fitzsimons (op. cit) records Wart Hog fighting for suitable burrows.

The importance of burrows suggests populations may have been restricted, even before islands formed, when individuals became compressed on to incipient islands or along the mainland. Weak animals crawled into holes to die, further aggravating the shortage, as on Island 17 it was exceptional for an animal to shelter in a hole containing a carcass. On Ukubula Island, carcasses were found on the surface only after most holes contained a dead animal, according to Rescue Reports. This behaviour suggests a useful adaptation against the spread of disease in a species which favours bodily contact to the extent that individuals will huddle together in the sun or a wallow.

Adults can survive without holes, but observations on Island 21 demonstrated their importance for avoiding predation. On this island a Leopard eliminated a population, described as "considerable" in Rescue Reports, within 10 to 11 months. Bigourdan is of the opinion that adults are immune to Leopards and are safe from Lion while in a burrow, but the former is obviously not the case and there are records of Lion digging Wart Hog out of holes in the Wankie National Park.

Ewer (1958) suggests Warg Hog are chiefly grazers of the aerial portions of grass and only root as an emergency, as their jaw musculature is unsuited for obtaining food in this way, and although Mohr (1960) does not quote Ewer, she is in general agreement. The leaves and stems undoubtedly provide most of their food in Zululand, where Ewer observed their feeding, and after many years in the field in this well grassed area, Mr. I. Player (pers. comm) could only recall two occasions when he had seen them rooting. In most of their range, however, they root extensively, at least seasonally. Fitzsimons (1919) records it in parts of South Africa, Shortridge (1934) in South West Africa, Ansell (1960,a) and Mitchell (1963) in Zambia, Lamprey (1963) and Geigy (1958) in East Africa and Bigourdan (1948) in the Sudan and Senegal. This also applies in all areas in Rhodesia and Bechuanaland so far investigated. In addition to grass and sedges, they take fruits, and Bigourdan, who notes their obvious liking for vegetation in damp places, also lists eggs, rodents, snakes, lizards, crickets and carrion. The occasional use of carrion also remarked on by Steinhardt (1924), quoted by Shortridge (1934), and Mr. P. Johnstone (pers. comm) and the wide range of cooked and uncooked foods, including most meat, with the exception of raw Wart Hog flesh, taken by captive animals is important to later discussion.

Thirty two stomachs from the Nagupande area in October 1962 contained grass to the almost complete exclusion of other matter. Stomachs from most areas contained over 90% roots, particularly those of Loudetia superba, but also small amounts from dicotyledonous plants, and there were extensive signs of rooting with patches up to 18 yards in diameter completely ploughed up. Stomachs from areas where grass had flushed following fire contained varying proportions of leaves, depending on the extent of the flush. A tame free-ranging Wart Hog ate both roots and the leaves and stems of grasses and sedges between February and July, but had the exclusive use of green vegetation around a spring. There was ample green grass, both annual and perennial, which had remained green later than usual in the soak zone extending over most of Island 201 in April 1961. Wart Hog had rooted extensively, however, and the stomach of an adult male casualty in very good condition contained only the swollen roots and very basal portions of grass stems.

A summation of these observations suggests Wart Hog feed on the portions of grass, and to a lesser extent, sedges, which seasonally have the highest food value, and that rooting is not an emergency mechanism as Ewer (1958) and Morh (1960) suggest. On Island 201 grass roots were very swollen at the end of an optimum growing season, while plants were growing rapidly around the spring and in burnt areas in the Nagupande and would, therefore, have had food reserves mobilized in the serial portions of the plant. It is also possible that the explanation for the survival of Wart Hog without free water for months at a time may rest in their use of these roots, as in areas with a very dry season, perennial grasses generally have a well developed rooting system.

Feeding observations and five stomachs from Islands 17 and 144 showed that even when critically short of food, Wart Hog took little besides perennial grass. Whole areas up to 50 yards across on Island 17 had been rooted. Their physical condition on seven islands showed a close correlation with the status of the grass, especially perennial species (Table 14) and 32 of 40 (80%) animals over a year old and classed as good or fair, came from islands where perennial grasses were arbitrarily assigned as common. The only exceptions were from Islands 102 to 112 where, although plentiful, the grasses had been heavily overgrazed. It is, therefore, remarkable that Petrides and Swank (<u>in press</u>) found Wart Hog numbers increased in parts of East Africa, while perennial grasses deteriorated towards more bare ground and scrub encroachment.

It is also interesting that Wart Hog made little, if any, use of the abundant carrion available on Island 17, as they are known to eat meat, even when well fed incaptivity. This suggests that in the Kariba Basin Wart Hog are not as omniverous as Mohr (1960) and Bigourdan (1948) imply, as the Wart Hog on this island were starving.

The decline in physical condition culminated in losses on several islands, including Island 17 and Ukubula Island, which led to shifts in population structure. Observations on Island 17 covered relatively early losses, while jaws from Ukubula Island included the animals which survived the longest and died on the surface after most holes contained a carcass. Before discussing changes in population structure, it is opportune to outline briefly the life history of the species as far as it is known.

In most areas, there is a peak farrowing season, whose timing varies locally, but in Senegal and to a lesser extent in the Sudan, where the seasons are not clearly defined, Bigourdan

Table 14.

Physical Condition of Wart Hog on Islands

LOCATION	CONDITION													VEGETATION					
	Adults & Yearlings						Young under 1 Year							State of Grasses					
	Good		Fair		Poor		Good		Fair		Poor			Annual Spp.			Perennial spp.		
	M	F	M	F	M	F	M	F	M	F	M	F		Occurrence	Condition	Use	Occurrence	Condition	Use
Island 17			3	3	18	29					1	2	Mopane and scrub	Common	Dry	Heavily trampled	Rare	Green	Heavily grazed
Island 151			2		5	3					1		Mopane	Common	Dry	Heavily trampled	Absent		
Island 144			9	2									Mopane and bush clearings	Common	Dry	Moderate	Common	Dry	Moderate
Islands 202 - 206	3		8	5	1				3	1			Terminalia and thicket etc.	Common	Green	Light	Common	Green	Light
Island 5												2	Mopane	Common	Dry	Heavily used	Absent		
Island 101				1									Thicket	Common	Dry	Light	Common	Dry rank	Light
Islands 105 - 113			1	4	4	3			1		3	2	Alluvial hillocks	Rare	Dry	Light	Common	Dry rank	Heavy

M = Male, F= Female.

(1948) recorded births in most months, but suspected a peak in the Sudan during the rains (June to October). Child et al (Ms) describe a definite peak in the Nagupande Area around the end of October, with births from September to mid-December, between 1962 and 1964.

Bigourdan (1948) reports that litters varied from one to eight, with an average of 3½, while Child et al (op.cit) found it to be over 3.7 (range 1 - 8) in a sample of 21 late term pregnancies during the first season of hunting in the Nagupande, but note that the average declined in subsequent seasons, probably as a result of the hunting.

Child et al (1965) agree with Bigourdan (1948) and Roth (1965) that early growth is very rapid, but that it is readily influenced by the plane of nutrition. Growth is prolonged and continues in males, at least, until they are over 36 months old. Females mature in their second year and farrow for the first time on their second birthday in the Nagupande, where males mature a year later (Child et al, Ms). It is possible, however, that like other pigs (Mohr, op cit) improved habitat conditions may hasten maturity in Wart Hog, as Roth (op. cit) describes a female which was raised on a greatly supplemented diet and which, at seven to eight months, would have been indistinguishable from free ranging adults, except for her smaller tusks. Similar early maturity is known in domestic stock and deer raised under optimum conditions.

Bigourdan (1948) found they were practically weaned at two months, when the sucklings left the burrow in which farrowing took place. The last lactating females were found in the Nagupande four to five months after peak farrowing and three to four months after the last recorded pregnancy. In this area, sucklings left the burrows within days of birth and over 30 were captured with the umbilical cord attatched and, in a few cases, still wet, and yet, according to Bigourdan, the cord is shed after about a week. Whether or not these small young accompany their mothers for long periods or not requires further investigation, as unaccompanied non-pregnant, lactating females are fairly common during the farrowing season.

Simpson (1964) describes rutting behaviour in May in the Wankie National Park and Child et al (Ms) found it to be about the same time in the Nagupande Area, which approximates to the gestation period of 171 to 175 days, given by Brawn (1936) and the observed peak in farrowing in this area.

Adult males and females do not associate together for long periods, according to Bigourdan (1948) who describes several pregnant females running together, before splitting up to farrow, as well as unstable bachelor groups of two to six animals. His overall sex ratio was very constant, however, with equal numbers of males and females, which is similar to the ratio obtained for the

Collared Peccary, Pecari tajacu (Linneaus), by Sowls (1961). There were 491 sexed Wart Hog skulls collected during the initial six weeks of hunting in October and November, 1962, in the Nagupande Tsetse Area. Of these, 242 were males and 249 (97 : 100) were females, including 12 male and 18 female sucklings, 64 male and 54 female yearlings and four mature females which could not be aged further, in addition to the adults listed in Table 17, which indicates a remarkably constant sex ratio in all age classes. Further evidence for a constant sex ratio comes from Table 15, where the sex ratio does not differ significantly from parity ($Chi^2 = 0,82$) and remained constant at different levels of sampling, as Wart Hog were cleared from east to west on Island 17.

These data suggest that the breeding pair is the basic sociological unit in the population, particularly as Child et al (Ms) obtained a complementary number of immature males over two years old to the number of mature unbred females. Further detailed research is needed, especially into male/female relationships, as it is possible that an alteration of the ratio may produce effects important to the management of the species.

Child et al (Ms) calculated a total reproductive potential of over 268 sucklings per 100 sexually mature females, but Bigourdan (1948) argues that one young per year per female is adequate to maintain a stable population with an average adult life expectancy of three to four years, so that the value of multiple births must relate to expanding populations, the significance of which is discussed on p.122.

Another feature of Wart Hog behaviour which will be discussed later in the paper, is the habit of some females adopting the young from others which have died. This is mentioned by Shortridge (1934) and Mohr (1960), who also found it in Sus scrofa, and is apparently fairly common in some of the Zululand Game Reserves. Mr. G. Stewart (pers. comm.) has several records of females accompanied by more young than the maximum litter size recorded in this area, and this is particularly true for parts of the reserves in which there is widescale culling of the expanding Wart Hog population.

The absence of records of pregnant or lactating females on islands at Kariba was due to the seasonal nature of births, coupled with the short gestation and lactating periods, and the small sample of female casualties available for autopsy. It is to be expected however, that the low plane of nutrition would have reduced the average litter surviving to full term, as this is established in the Domestic Pig (Hammond, 1960), where the number of developing conceptions is variable due to the resorbtion of surplus embryos, and Child et al (op. cit) have found this tendency in Wart

Table 15.

The Sex Ratio at Different Levels of Sampling on Island 17.

% of Total population	Sample	Male	Female	% Level of population	No. in sample	Male	Female
25	16	7	9	25	16	7	9
25	16	5	11	50	32	12	20
25	17	9	8	75	49	21	28
25	17	8	9	100	66	29	37

Hogs. Runts are also common in unborn litters and Mohr (1960) describes variations in the reproductive rate of <u>S. scrofa</u> from 150% to as low as 60% of the original population, depending on the availability of food in a given year. At least one hoglet was, however, born on Ukubula Island during the final collapse of the entire population.

It is possible to deduce a heavy mortality among juveniles especially sucklings (o to 12 months), marooned on islands. Bigourdan (1948) describes heavy losses in Wart Hog two to six months old, and Mohr (1960) has found the same in other suids. Roth (1955) suggests that the weaning period is very critical for Wart Hog, as captives reared on a uniform diet showed a downward deflection of their growth curves at this age. Bigourdan's figures indicate a marked decline in the suckling to adult female ratio during the first half year from 350:100 to 200, or less:100. Similar heavy losses are evident in most populations, but are less marked than those found on islands at Kariba.

The 491 Wart Hog collected from the first six weeks of hunting in the Nagupande yielded 118 juveniles 11 to 12 months old and 123 females 35 months old or older, and therefore capable of having bred the previous season. It was policy to eliminate all Wart Hog, but hunters would have tended to have selected the largest targets so that there may have been a bias towards shooting more adults from mixed groups. If so, the ratio of 95.9 sucklings, which survived the whole of the previous year, per 100 adult females, would have tended to be low.

The ratio of three, seven to eight month old sucklings with 25 (12:100) adult females obtained on Island 17, was, however, very much lower, in spite of the sucklings being younger. Conditions became critical later in the year on Ukubula Island, but here too the suckling ratio was very low. Eighty four jaws were available from the 93 carcasses found on the island and included three juveniles approaching 12 months, and 68 specimens in their third year or older, so that if half of the latter were females, there were about nine sucklings:100 adult females.

Suckling losses were heavy on most other islands (Table 16), even where food was relatively plentiful and the adults in reasonable condition, which stresses the sensitivity of this age group to the availability of food, as well as cover, and those handled were all very thin. There are no published figures of the proportion of yearlings to be expected in a population, apart from general statements to the effect that females are often accompanied by one or two yearlings, in addition to the current season's young. This

Table 16.

The Composition of Wart Hog Populations from Islands

Location	Sucklings		Yearlings		Adults		All classes		Total
	M	F	M	F	M	F	M	F	
Island 17	1	2	4	9	23	25	28	36	64
Islands 201-204	3	1	2		11	5	16	6	22
Island 144					9	2	9	2	11
Island 151	1		2		5	3	8	3	11
Islands 109-110			1	1	2	3	3	4	7
Island 113	3	2			1	1	4	3	7
Island 111	1				1	1	2	1	3
Island 7	2	2					2	2	4
Island 5		2			1	1	1	3	4
Island 101						1			1
Total	11	9	9	10	53	42	73	60	134

M = Male
F = Female

infers a ratio of 100 to 200 yearlings: 100 adult females. The sample of skulls from the Nagupande contained 94 (44 males and 50 females) 23 to 24 month old individuals, which represented 76.4 yearlings: 100 females, which survived the previous year.

These figures may not be truly representative, but serve as a guide, and underline the low numbers of yearlings, 13 with 25 (52:100) adult females, on Island 17. Thirteen yearlings survived with the last portion of the population on Ukubula Island, indicating a survival rate to the age of 24 months of c39:100 adult females during the final collapse of the population (assuming approximately even numbers of males and females among adults), which is significantly lower ($Chi^2 = 6.62$, $P > 0.02$) than that found in the Nagupande.

On both these islands a differential mortality favoured Wart Hog over 30 months old, primarily at the expense of the sucklings, but to a lesser extent also the yearlings. There may also have been heavier losses among three-year-olds on Ukubula Island than among individuals of four years and older. Child et al (1965) found that 23 to 24 month old males had the third molar up to 26 mm long, while in females it was 24 mm. In males 35 to 36 months old it reached 41 mm, while in females, where the division was less clearly marked, it was about 39 mm. As few of the carcasses on Ukubula Island could be sexed, the sample is broken down, for the purposes of Table 17, using 25 mm and 40 mm M_3 lengths, as the division between two-year-olds and three-year-olds, and three-year-olds and older animals respectively. If two specimens with 40 mm teeth are classed as three-year, the difference in the proportion of three-year-olds on the island and in the Nagupande is significant at the 5% level ($Chi^2 = 3.902$), but if these specimens were older the difference is significant at the 1% level ($Chi^2 = 6.921$). The comparison is, however, based on single samples and there was no indication that three-year-olds were weaker than older animals on Island 17, so that the possibility that there is a differential mortality among adult Wart Hog during the decline of a population, requires further investigation.

There was no evidence to indicate a differential loss from either sex on any islands, while the close adherence of a sex ratio approaching unity suggests there was none. The slight differences in Table 16 are not statistically significant ($Chi^2 = 0,547$). Further, Table 15, in addition to showing the distribution of the two sexes over Island 17, also gives a remarkably constant sex ratio for samples caught during a period of four weeks, when the population was on the brink of collapse. Many of the animals were so weak that they could hardly walk so that had there been a marked difference between the two sexes, it would have shown as more of one or the other in later samples.

Table 17.

The Age Structure in a Sample of Wart Hog Two-years-old and Older Compared with that of the Last Survivors on Ukubula Island.

Age in Years	UKUBULA ISLAND			NAGUPANDE		
	No.	% Total	No : 100 4 years and over	Number total (M,F)	% Total	No : 100 4 years and over
2	13	16.0	26	94(44,50)	27.7	59
3	18	22.2	36	87(42,45)	25.7	55
4+	50	62.7	100	158(80,78)	46.6	100
Total	81	-	-	339(166,173)	-	-

M = Male

F = Female

Mortality in Wart Hog followed the classical pattern, with successively older juveniles being eliminated during a food crisis. In this respect they were more akin to the solitary antelope and Zebra than to the highly gregarious forms such as Baboons, Impala and Buffalo, although they were often under similar stresses through over-population, as they became concentrated in greater numbers than the more or less solitary species.

Thus Wart Hog, which associate together in small groups, typically have multiple births and feed chiefly on perennial grasses, were marooned on islands because of their restricted home ranges and in spite of their considerable swimming ability. They were the second most numerous species handled by the Rhodesian Rescue Unit and experienced limitations of habitat on several islands. These led to a decline in physical condition and a classical pattern of mortality between different age classes, with affected primarily the sucklings, and least, animals over 30 months old.

11. DUIKER

Duiker, Sylvicapra grimmia Linn, was among the few species which were more common in densely settled parts of the Kariba Basin. They were numerous on alluvium along the foot of the Binga escarpment where the people had been absent for about two years. Seven were once contacted along a traverse of 250 yards in dense bush, and 14 were marooned on an island derived from about 2,000 acres, giving a density of one Duiker to 140 acres.

They are well known to favour intensively farmed areas allowed to go fallow, apparently because of the large amount of low browse which becomes available with the encroachment of scrub and forbs. A sample of 64 Duiker collected in October 1963, along the Mzola vlei in the Cewali Tsetse Area, had eaten nothing but browse. The plants varied with local availability, but Duiker taken from areas where forbs were numerous had eaten little else and, in all the stomachs identifiable, fragments were of browse, obtainable within a foot of the ground.

The number and proximity of many of the Duiker to old villages at Binga, suggested that the population was expanding rapidly. This may have been due to their release from a considerable hunting pressure or to rapid environmental changes resulting from the evacuation of the Tonga (p.24). The Mzola sample demonstrated the high productivity of the species (Child and Wilson, 1964,b) which, under ideal conditions, could theoretically quadruple itself in about two years.

Duiker were relatively scarce in areas in which most rescue work took place and constituted only 4.6% of the animals removed from islands by the end of June 1961.

A. Response to Flooding

They took to water readily and, for their size, were strong swimmers, although they frequently attempted to hide in the shallows. On 35 observed, 31 (89%) showed little hesitation in going into the water when flushed, and the four exceptions were on Island 17 and did not need to go into the water.

They could swim about as fast as a man and Junor (1960) noted they swam up to 1,320 yards. The longest distances recorded by the present author were : 1, over 300 yards; one, 200 to 300 yards; three, 150 to 200 yards; four, 100 to 150 yards and four 50 to 100 yards. None of these animals showed signs of tiring when caught and, even those which covered more than 150 yards, could have swum much further.

Localised habits probably accounted for Duiker becoming marooned on islands. Dixon (1964) tells of a marked calf that remained for several months within 200 yards of where it had been marked, and two tagged adults, with moderately worn permanent teeth, were re-caught at Kariba on the nearest land to where they had been released. In six weeks, this pair had remained within a mile, and three others were on the nearest available land after 21 months. Two were within two and the third within three miles of the release point, but in all cases most of the intervening distance had been inundated, so that voluntary movement was less than half a mile.

The 14 Duiker on the island near Binga were limited to three acres and when 11 of them were flushed, they bounded away and then slowed down or stopped before slowly working their way back past the observer to the same small area of bush from which they had been disturbed. Similar behaviour was observed in the Nagupande Tsetse Area during the game drive described on p.82. Numerous Duiker were flushed and after bounding away 200 to 400 yards would turn and double back through the beaters, who in many instances were less than 10 yards apart. Only two animals flushed along the edge of the beat attempted to out-flank the drive.

An adult ram bedded under the same bush for several days on Island 17, until the rising water forced it to an adjacent one. This was repeated three times over a period of two weeks and each time it had to use less and less suitable shelter, as the water advanced towards a clearing. It could have avoided this by moving 100 to 150 yards into more suitable habitat. On the same island a family group, consisting of a male, a female and an almost full-grown female calf, recognisable by their remarkable colour variation, were usually together in an area of about four acres, although the island was 120 acres, supported only seven Duiker, and food shortages could have been expected to induce less localised animals to wander further.

Gradual flooding would probably lead to the elimination of Duiker, in spite of their swimming ability, as they would remain on any small elevations which formed temporary islands. This was noted on five islets under 50 yards in diameter, near Binga, where a total of seven Duiker became marooned and apparently perished within 100 yards of land, as no signs of their having crossed to the mainland could be found in damp soil along the shore.

B. Behaviour on Islands

Duiker were generally marooned in small numbers; the island on which 14 were trapped near Binga being a striking exception, so that there was little intra-specific competition, although they obviously suffered to some extent from over-crowding by other species. They were short of food on Island 17 due mainly to Impala, but were among the least affected species. Extended periods of observation of undisturbed feeding showed they ate mainly *Holmskioldia spinescens*, *Combretum apiculatum*, including dry leaves and, to a lesser extent, *Pterocarpus brenanii*, the last of which was less heavily used by other species. Riney (*pers. comm*) found that Duiker subsist around villages in parts of South Africa, where there is no vegetation available for several months of the year, by eating human excreta, and they may, therefore, have used the poorly digested defecations of other species, such as Baboons, on Island 17.

On this and other islands, they were short of cover, as they frequently shelter in thickets or long grass, and seven were seen hiding in water nine to 12 inches deep. Here they lay down in dense vegetation, but never attempted to hide in deeper water.

With the exception of a Duiker caught in March, all 26 handled were in poor condition. They are, however, very hardy and can withstand considerable depletion of fat reserves. The 64 Duiker collected on the Mzola Vlei were taken soon after the vegetation began to flush at the end of the dry season, and all were classed as poor, as none had more than a trace of back fat, 62 had no kidney fat and the bone marrow was poor throughout the sample. In spite of this, the population was apparently still increasing. This hardiness was found in Duiker marooned on islands, where not a single natural death was attributed to starvation.

A calf was born on Island 17 during the third week in June 1960, indicating Duiker continued to breed under adverse conditions but, although the sample was small, the low number of physically immature animals found, suggested a high mortality among Duiker under six months of age. This is supported by Rescue Reports, which give seven juvenile Duiker in a total of 144; including 57 males and 80 females. As Duiker grow rapidly (Riney and Child 1960), and males develop horns from about two months of age (Riney and Child, 1964), animals classed as juveniles in Rescue Reports may have included only those up to four to six months old, nevertheless the number is very low, as Duiker reproduce rapidly. Riney and Child (1960) found calving in all months between October 1958 and March 1960, in the Cewali Tsetse Area, with minor peaks in January and June, and Ansell (1963) and Child and Wilson (1964b) show that, in captivity and the wild respectively, females reach sexual maturity at eight to 10 months. In addition, the last authors give evidence of females calving twice a year.

12. <u>SHARPE'S GRYSBUCK</u>

Grysbuck, <u>Raphiceros sharpei</u> Thomas, the smallest antelope found on islands, occurred throughout the Kariba Basin in small numbers and made up 7.8% of the mammals rescued before 30 June, 1961. This wide distribution and the small islands on which they became marooned, suggested a number may have been overlooked during rescue operations, as in the Nagupande Tsetse Area they favoured habitat along water courses or the edges of thickets.

A. <u>Response to Flooding</u>

Little is known of the seasonal movements of Grysbuck, although the habit of frequently defecating on middens suggests they are very localised. Three marked Grysbuck were re-taken on the nearest available land to the release point. Two were within one mile after six to eight months, by which time most of the intervening area had been flooded, while the third was released and recaptured by Fothergill within 100 yards, after an interval of two months.

Additional evidence for their localised habits comes from the history of several islands on which they became trapped. A pair was found on two adjacent islands in a bay and within 70 to 150 yards of the mainland. They crossed back and forth between the two islands several times, in spite of its necessitating a swim of 10 yards, but seven men were unable to drive them into the water in any other direction, although the total area of the island was less than half an acre.

A Grysbuck became marooned on an island which formed on the inside of a bend in the Ruzimuhuru River. The island was made up of part of the bank of the river and was nowhere over 150 yards from the mainland, while the shortest distance was less than 50 yards. This animal was cut off by the partial flooding of two to two-and-a-half acres of similar habitat, which spread beyond the affected area, so that choice of cover would not have influenced its movements, at a time when the Lake was filling slowly and island formation was gradual. Another 19 were on small islands within 50 to 1,000 yards of the mainland in areas derived from five to 15 acres.

Grysbuck took to the water readily, but almost always over land which had recently connected two islands. Of 28 observed, 26 (93%) were caught in the water, the two exceptions being animals caught on a large island. This secretive species seldom rushed headlong into the water, but picked its way delicately through the shallows, well ahead of the drive. They swam well for their size, but could easily be overtaken by a man. There were four which swam over 100 yards, one over 300 yards, while Junor (1960) gives the maximum observed distance as 400 yards, but estimated another must have swum at least a mile.

This swimming ability meant a few, which became marooned on small onshore islands, may have been able to reach the mainland, when these islands submerged, although generally their localised habits and preference for habitat along water courses would make them very susceptible to abnormal flooding.

B. Behaviour on Islands

Grysbuck experienced severe competition for food from other species because of their low reach and lacked adequate cover on over-populated islands, although they were often the only species marooned on the smallest islands.

Cover is obviously important to this largely nocturnal species, which often flushes at under 20 to 40 yards during the day. This distance increased to 50 to 60 yards on over-populated islands, where they were frequently observed crouching in unsuitable vegetation. Three were seen to go to ground in Antbear holes, which was not unusual according to personnel on the Rescue Unit, and has been recorded elsewhere (Shortridge, 1934), although it is unlikely that they would share a burrow with a Wart Hog under normal conditions.

It is generally agreed that Grysbuck are predominantly browsers, which, in certain seasons, take young grass to the virtual exclusion of leaves. This applied to two stomachs from Kariba examined between April and July, which contained *Terminalia randii*, *T. stulmanii* and small forbs, and to 17 from the Cewali, Nagupande and Chipinda Tsetse Areas, all taken towards the end of the dry season. They were, however, obviously short of food on Islands 17 and 107, due to clear browse left by Impala and Bushbuck, and on Island 17 one was seen actively competing for food with a Rhino, an Impala and a Bushbuck (p.55) at about 16.00 hours.

These food shortages reflected in their physical condition. Seven caught on islands with plenty of food in March and April included five adults in fair and two in good condition, while 19 from over-browsed islands in June or later included 17 in poor and two in fair condition. Normal seasonal fluctuations in the availability of food could hardly have produced such a rapid deterioration in condition, which resulted mainly from competition with other species.

It is difficult to assess the effects of unsuitable habitat or food scarcity on the population structure of Grysbuck, as very little is known of their breeding biology or rate of maturity. Stevenson-Hamilton (1947) and Asdell (1946) suggest most calves are born from early to mid summer, which might have accounted for the only small calf and lactating female, handled on islands, being taken in late September. A definite calving season seems unlikely, however, as Ansell (1960,a) records births in the Central Zambezi Valley in October, December and July, to which may be added the September calf, another in February and one in May (neither of which was over two months old) , and a well formed fully haired foetus collected on 28 April. It is, therefore, likely that Sharpe's Grysbuck will be found to breed throughout the year, as in the congeneric Cape Grysbuck, R. melanotus (Shortridge, 1934) and Steenbuck R. campestris Thunberg (Dasmann and Mossman, 1962,d). Only two calves were captured with 18 adult females (11:100) which suggests an abnormally low ratio on islands, either due to juvenile mortality or reproductive failure, and that there had been a shift in population structure in favour of full grown individuals. There was no evidence, however, to suggest a change in sex ratio, as of 222 sexed Grysbuck recorded in Rescue Reports, 113 were males and 109 were females, and in many instances one or more pairs were captured at the same locality.

13. KLIPSPRINGER

Klipspringer, Oreotragus oreotragus Zimmermann, were widespread and common in the Central Zambezi Valley, especially along the final rocky descent which gave rise to the greater part of the ultimate Lake shore. Smaller numbers occurred on isolated hills and outcrops on the valley floor and it was mainly these which became marooned. Only 20 Klipspringer were rescued in Rhodesian waters before 30 June, 1961, as they tended to become marooned in areas where game was generally scarce and where it was not economic to employ the whole Rescue Unit, as would have been necessary to effect their capture.

The nature of their habitat rendered it least liable to change as a result of Tonga farming practices. This and their ability to withstand hunting, as shown by their being one of the few species to survive Tsetse Control Hunting in Zululand (Mr. I. Player, pers comm), would account for their continued success along the fringes of dense human settlement.

A. Response to Flooding

The occurrence of small numbers of Klipspringer in isolated pockets of suitable habitat and the behaviour of defecating on middens, is indicative of localised habits. They were also reluctant to enter water, with the result that they were easily trapped on islands. In three cases, it was very difficult to chase them into the water, while in seven cases all attempts failed. Conversely, Shortridge (1934) once saw a group cross a shallow, fast flowing river without fear, and he felt they would have swum if necessary. The behaviour at Kariba could not be attributed to the general tendency to escape uphill, as they were frequently chased to the water's edge and two, caught by the author on a narrow flat peninsula, attempted to break past three men as they approached to within five yards, rather than go into the water.

They were slower swimmers than any other antelope and used the same leaping gait in the water, as is used when bounding over rocks. They could cover considerable distances with this ungainly method, however, as Junor (1960) recorded a marked individual which swam half a mile and saw another swim 300 yards, while the present author caught one after it had swum 120 yards.

Klipspringer sometimes occur along rivers, but this is frequently near kopjes, so that it is unlikely that unusually high floods would seriously affect them.

B. Behaviour on Islands

Klipspringer became marooned on isolated hills and outcrops, but, as the tops of these features provided the most favoured habitat (Wilson and Child, 1965), unlike other species they were never forced into entirely unsuitable habitat. Further, the steep nature of most of these hills meant a relatively slow reduction in area, as the Lake level continued to rise, and little competition from other species. This was borne out by the fact that all five Klipspringer handled were in fair condition.

The sample of Klipspringer caught was very small, but circumstantial evidence indicated their being among the last species to be affected by isolation on islands.

14. COMMON WATERBUCK

Waterbuck, Kobus elipsiprimnus Ogilby, occurred throughout the Kariba Basin east of Binga, but seldom became marooned on islands as they moved to and from islands more freely than any other species, with the exception of Elephant. This meant they seldom had to be caught and could be made to swim to the mainland, so that the sample handled by the Rescue Unit was biased in favour of small calves, adult males and heavily pregnant females.

A. Response to Flooding

Waterbuck took to the water very readily and were strong swimmers. One appeared on an island which was nowhere less than a mile from land, but Junor (1960) recorded them swimming up to one-and-a-half miles. The swimming ability was developed at an early age, as a small calf, with eight inches of umbilical cord, swam over 200 yards before being caught with difficulty. A half-grown calf was assisted when it showed signs of tiring after 600 yards, but adult rams were handicapped by the weight of their horns and two very gravid females had to be caught after 120 and 200 yards.

They were fast, manoeuverable swimmers compared with other antelope and were only a little less difficult to catch in the water than Bushbuck. Junor indicates they usually swim in a line, but this applied mainly to family groups, which tended to arrange themselves in order of descending age behind the female, as groups of males seldom did this. In the water, the white band around the hindquarters had the apparent function of maintaining contact between individuals in a family group and one small calf actually rested its head on the rump of the animal ahead of it, in the way Junor has already described.

Waterbuck swam to at least nine islands, but probably visited many others, apparently attracted by vegetation which flushed out of season, as they were very active in the soak zone on the mainland. They left islands when food became scarce and three of four animals with permanent dentition were in fair condition, the exception being a heavily lactating female.

As with Elephant, it is difficult to understand how they located some of these islands, separated as they were from the mainland, by homogeneous partially submerged vegetation through which the island could not be seen.

There was one case of a family group, consisting of an adult male and female and a well grown calf, hiding in the shallows, (Dr. H. Roth, pers. comm), but generally this species was not greatly affected by Lake formation. It is probable that they could avoid any gradual flooding, although some were washed away in the violent floods in Zululand in July 1963 (Mr. I. Player, pers. comm).

15. IMPALA

Impala, Aepyceros melampus Lichtenstein, was the most common large mammal on the floor of the Central Zambezi Valley, east of the Masumo River, where 1,316, or 39.1% of the large mammals rescued, were caught by the Rhodesian Unit prior to the end of June 1961.

They were mainly associated with well developed mopane veld, even where this bordered densely settled areas. The highest concentrations found on islands were between the Sibilobilo and Umniati Rivers, where large areas of flat homogeneous veld were very susceptible to island formation. There were 298 Impala on Island 17 at the beginning of June 1960. Island 144 held 143 in May 1961, and other useful information for this study came from a survey of Ukubula Island in December, 1962, and smaller groups caught on Islands 14, 15, 21, 28, 201, and 203.

A. Response to Flooding

Impala are dry land antelope which are unknown to enter water more than a few inches deep under normal conditions, and can be contained in a required management area by a narrow river (Riney and Kettlietz, 1964). It is, therefore, not surprising that they were usually reluctant to enter water after they had become marooned on islands. The capture of 389 was witnessed, of which only 22 (5.1%) were caught in the water, although most could have taken to the water as they were chased about islands during netting operations, or while being run down on foot. There are, however, two reports of herds of 20 to 30 which took to water easily, and eight of the nine Impala on Island 203 went into the water when the first men were put ashore. These exceptions are discussed below in relation to the home range of Impala and do not detract from the generalisation that Impala were extremely reluctant to enter water.

Junor (1960) deduced the movements of one Impala which swam two miles and saw another swim a mile, but these distances are remarkable as they were slow, weak swimmers compared with other ungulates of a similar size, such as Bushbuck, Bush Pig and Wart Hog. They were easily overtaken by a man and could not swim as fast as Duiker, which were less than half their size. During the present study, an adult ram crossed between two islands 500 yards apart, two Impala had difficulty completing 200 yards and five of 11 were exhausted within 100 yards. None of these was critically thin, so that it is obvious that Impala are poor swimmers.

Nevertheless, the main reason for large numbers being marooned on islands was their localised habits. They were never trapped on islands which began as less than four to five acres and in four cases, where such islands were about to form, all the freshest spoor led on to the mainland. The smallest islands on which they were marooned were originally 10 to 15 acres.

The Natal Parks Board Staff have marked a fair number of calves in the Hluhluwe Game Reserve. Most contacts of these animals, over a period of two years, have been within two miles of where they were marked, although a few individuals have been sighted over 20 miles away. These exceptions can be explained in terms of dispersing individuals, discussed below.

Dasmann and Mossman (1962,c) have suggested that the size of the home range in the southern lowveld of Rhodesia is governed by the availability of drinking water, andmay extend 15 miles from water during the dry season. Lamprey (1963), on the other hand, found Impala could subsist for long periods by drinking dew, and Impala have been collected 40 miles from water in the Guluene River area in the south east of Rhodesia, at the end of the dry season, when dew is rare or absent, and in this case had not fallen for at least 10 days, showing that, in some circumstances, Impala may do without water for considerable periods. Data relating to the movements of 161 marked Impala, which became marooned for a second time, are summarised in Table 18, based on Rescue Reports. These reports seldom define the release and recapture points accurately so that many recaptures have had to be omitted, while others exaggerate movements, as particular care has been taken to over-estimate distances where there is any doubt.

Most of the animals caught within one year were handled at least once while the author was on the Rescue Unit. A second factor leading to over-estimates of movement was that it was seldom possible to determine from which portion of an island animals were caught and, of course, whether they had used portions of the island which were currently submerged. Thus the animals' free movements covered an area somewhere between the distance they were moved by the rising water and the maximum distance they could have moved away from the release point and still have been marooned on the island, or portion of island, on which they were recaptured. This distance approximates to the greatest "diameter", or distance across the island from the point on the island nearest the release point, although in several cases Impala did not use the whole distance.

Table 18 shows the localised nature of this species, several of whom did not move over 1.5 miles on a year round basis, although incipient islands became overcrowded, especially during the dry season when the Lake level was almost static (Figure 12). The maximum recorded distance that they moved freely was 1.25 miles.

Table 18.

Observations on Movements of Marked Impala

Sex	Age at release.	Number caught	Date released (A)	Date re-captured Island formed (B)	Interval A – B months	Locality	Distance animals moved by water. miles	Max. "diam" of Island or part of Island. miles.	Max. distanc moved. miles
M	Adult	1	IX 1959	II 1960	5	W. Umniati River		0.25	.2
F	Adult	4	VIII 1959	II 1960	6	E. Bumi River	0.1	0.4	0.5
M	Adult	1	IX 1959	II 1960	6	W. Bumi River	?	0.25	1.5
M	Adult	1	VIII 1959	III 1960	6	Sibilobile River	?	0.25	3.0
M	Adult	19	V 1961	II 1962	10	W. Bumi River	1.25	2.5	3.75 (1)
F	Adult	17	V 1961	II 1962	10	W. Bumi River	1.25	2.5	3.75 (1)
M	Calf	2	V 1961	II 1962	10	W. Bumi River	1.25	2.5	3.75 (1)
F	Calf	3	V 1961	II 1962	10	W. Bumi River	1.25	2.5	3.75 (1)
F	Adult	3	III 1959	II 1960	11	E. Bumi River	0.75	1.5	2.25
M	Adult	1	III 1959	II 1960	11	E. Bumi River	0.75	1.5	
M	Adult	14	V 1961	IV 1962	11	W. Bumi River	0.1	1.1	1.25
F	Adult	37	V 1961	IV 1962	11	W. Bumi River	0.1	1.1	1.25
M	Calf	13	V 1961	IV 1962	11	W. Bumi River	0.1	1.1	1.25
F	Calf	4	V 1961	IV 1962	11	W. Bumi River	0.1	1.1	1.25
F	Adult	5	V 1961	IV 1962	11	W. Bumi River	– (2)	– (2)	2.5
M	Adult	1	V 1961	IV 1962	11	W. Bumi River	– (2)	– (2)	2.5
F	Adult	4	V 1961	IV 1962	11	W. Bumi River	1.75	1.25	3.0
M	Adult	1	V 1961	IV 1962	11	W. Bumi River	1.75	1.25	3.0
M.	Calf	1	V 1961	IV 1962	11	W. Bumi River	1.75	1.25	3.0
F	Adult	1	VIII 1960	V 1961	11	W. Umniati River	?	?	3.0
M	Adult	1	II 1959	II 1960	12	E. Bumi River	0.75	1.25	2.25
F	Adult	2	IV 1960	IV 1961	12	W. Bumi River	1.0	3.5	4.5
F	Adult	4	VI 1960	II 1962	19	E. Bumi River	0.75	1.5	2.25
M	Adult	1	VIII 1959	IV 1961	20	W. Bumi River	?	?	4.0
F	Adult	1	VIII 1959	IV 1961	20	W. Bumi River	?	0.5	3.0
F	Adult	3	IV 1960	II 1962	22	E. Bumi River	0.75	1.75	2.5
F	Adult	7	VI 1959	IV 1961	23	W. Bumi River	?	1.75	3.0
F	Calf	1	VI 1959	IV 1961	23	W. Bumi River	?	1.75	3.0
F	Adult	1	IV 1959	IV 1961	24	W. Umniati River	1.25	3.5	4.75
M	Adult	1	IV 1959	IV 1961	24	W. Umniati River	1.25	3.5	4.75
M	Calf	1	IV 1959	IV 1961	24	W. Umniati River	1.25	3.5	4.75
F	Adult	3	V 1959	III 1962	34	E. Bumi River	1.0	2.0	5.0
M	Adult	1	V 1959	III 1962	34	E. Bumi River	1.0	2.0	5.0
F	Adult	1	IV 1959	IV 1962	35	W. Bumi River	4.75	1.25	6.5
		161							

(1) A large proportion of these animals were recaught within two miles of the release point, having been moved 1.25 miles by the rising water.

(2) These animals moved a minimum of 1.25 miles. They were the only exceptions to the general rule and were not recaught on the nearest land to the release point. Therefore the distance they were moved by the rising water could not be determined.

M = Male
F = Female

These animals are signified in Table 18 and were the only ones which were not recaught on the nearest unsubmerged land to the release point.

The sample includes 74 of 129 (57%) Impala released between 28 and 30 May, 1961, in the area where Ibuyuamonga and Kuyagetera Islands formed 11 months later. These included all major sex and age classes. This area was especially interesting as 68 (92%) of the recaptures had not moved over 1.25 miles, although Impala were already common in the area and similar continuous bush cleared habitat extended in all directions. Six were caught on an adjacent portion of Ukubula Island and had moved 1.25 to 1.5 miles. Island 100 was the only one not connected to the mainland by similar habitat, as the break through forming the island was along the edge of a bush clearing in open scrub savannah, which is not good Impala habitat.

Even greater localisation was evident on islands where Impala remained in areas which did not cover the whole island. Attempts to drive Impala from four such areas were unsuccessful, until animals became exhausted. Impala often broke and doubled back, but this usually took place anywhere during a drive and could often be attributed to a disturbance ahead of the drive, unless they were being encouraged to leave their home range. On Island 17 a number of Impala were readily headed into the game nets from area A. (Fig. 18). The next day, however, a herd of 27 could not be driven out of area C, which was about 21 acres, and on seven occasions doubled back past beaters in B. By this time, they were so exhausted that they were caught on foot, but even then only five left what was taken as the edge of their range, as the herd had been seen almost daily for three weeks on this portion of the island. There was nothing to cause the Impala to double back at this particular point. The vegetation was similar over this part of the island, any scent from the nets or people behind them would have been carried away by a cross wind from open water, and neither the men nor the nets could be seen through the trees with 10 x 50 binoculars. To test the hypothesis that B represented the edge of the herd's home range, two men were placed conspicuously up wind of the Impala in area C during the fourth and fifth drives. The Impala ignored them and many passed within 15 to 25 yards of them.

Six rams behaved in a similar way on the eastern part of Island 15 and, after doubling back in the same area five times, took to the water from the point. This point and the neck separating it from Island 14 was the best Impala habitat on a big island on which Impala had been liberated. It was flat and open, with an intrusion of palatable browse plants in otherwise pure mopane.

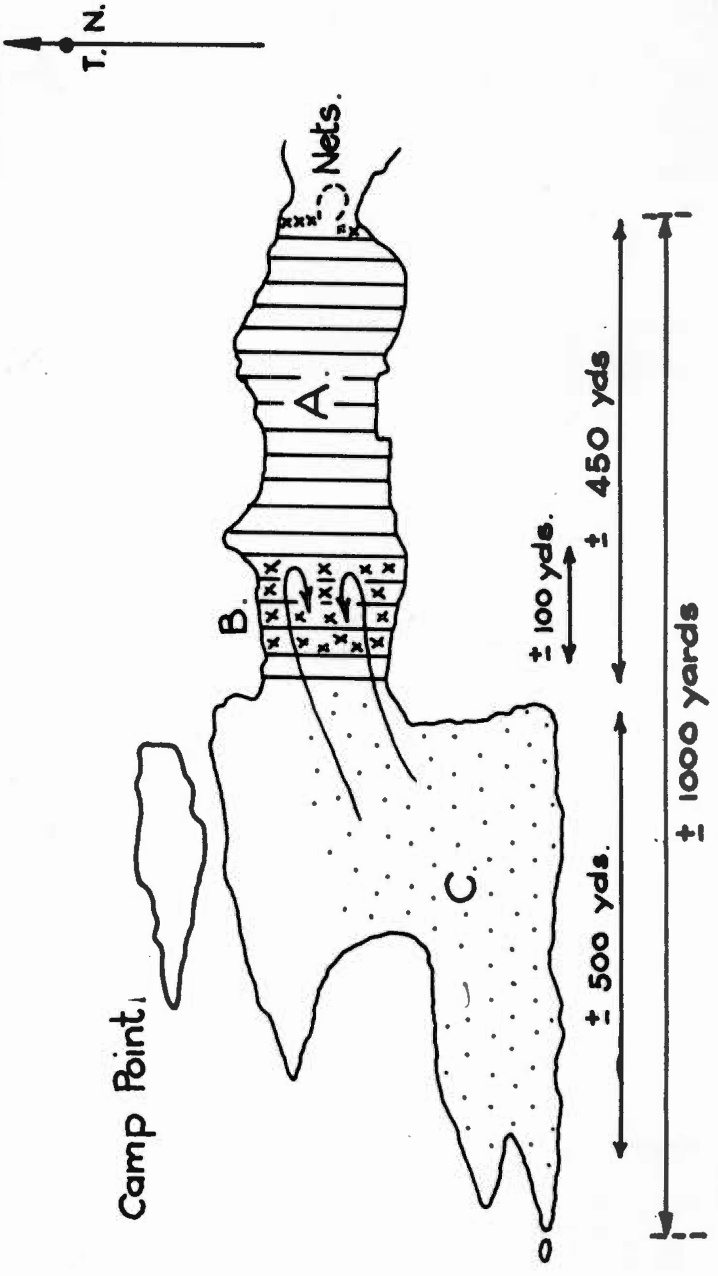


Fig. 18. The movements of a localised herd of Impala on Island 17 when efforts were made to drive it from its home range.

A (shaded) - Area from which Impala were caught the previous day,
B (marked with x) - The edge of the herd's home range,
C (stippled) - The assumed home range of the herd.

A large herd was regularly seen in the area where Island 144 later formed. Three counts in April gave 108, 111 and 118 (mean 112), but there were other individuals and small groups, particularly yearling and adult males, loosely associated with the herd, which probably accounted for the additional animals found on the island in May. The herd always hung around the edge of the clearing near the western tip of the island, and the distribution of spoor showed that they neither went far out into the clearing nor deep into the woodland, thus demonstrating, in almost classical style, the "boundary effect" described by Lamprey (1963), which was also clearly discernible in the behaviour of Impala along the edges of bush cleared water courses in the Chipinda Pools Tsetse Area. The arrows in Figure 19 represent the approximate path taken on 12 unsuccessful drives to net these animals.

In view of the above observations, five attempts were made to move a herd of 74 females and calves from a narrow peninsula on Ukubula Island, using a Landrover and 20 beaters. The animals were driven about 400 yards on seven occasions, but then, as expected, doubled back. On the third day, this applied to the females and calves only, as five rams, which had joined them since the previous drives, did not turn back with the rest of the herd at the usual place. A drive in the Nagupande Tsetse Area produced similar results. The area which was driven by a line of 235 beaters was roughly triangular with a base two miles long and the other two sides five to six miles long. The drive took place from the base, between a line of log fires at 20 yard intervals on one side and a game fence on the other. Three adult rams doubled past the beaters while they were 20 yards apart, after the animals had been driven about half a mile, but a herd of about 30 females and juveniles was driven a mile and a half to two miles. Two escaped through the fires and nine attempted to go through the fence, but only one succeeded, before the remainder broke back past the beaters, who were then less than 10 yards apart.

This reluctance to leave an established range is similar to that described by Hahn and Taylor (1950) for White-tailed Deer, which starved rather than do so, and Riney (1950) was unsuccessful in organising a drive to shift a family of Mule Deer <u>Odocoileus heminonus</u> (Rafinesque), from their home range. Impala on islands were limited to small areas. On Islands 144 and 15, they remained within the unsubmerged portions of their original range, but whether this applied on the other two islands could not be determined.

These observations demonstrated how easily Impala became marooned on islands over a few acres in area, and offered an explanation as to why some took to water more readily than the majority,

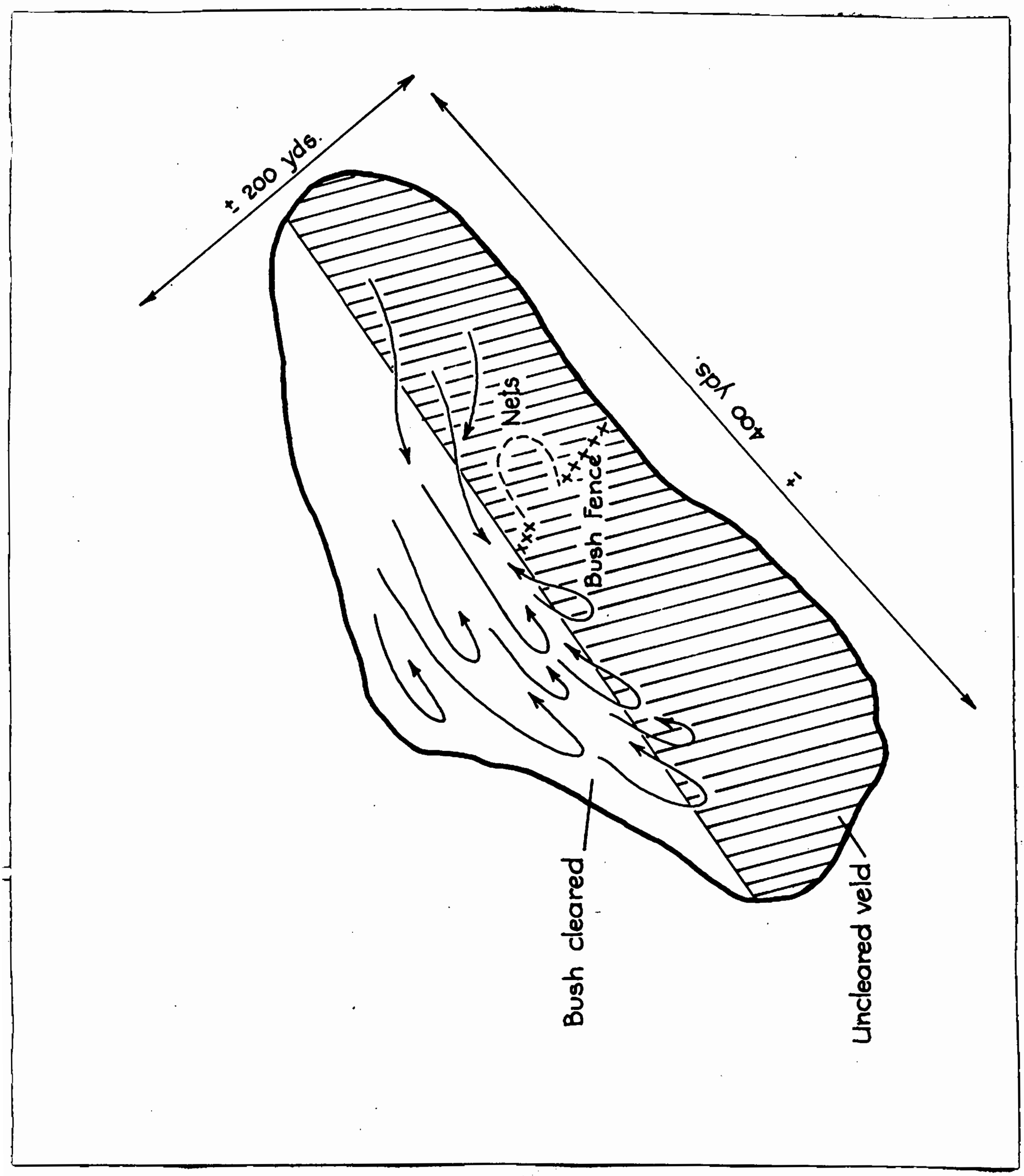


Fig. 19. The movements of Impala on Island 144 when attempts were made to drive them from their home range.

which were very reluctant to do so. The Impala on Island 203 had been in the area when Islands 203 and 202 were united, and when they took to the water, they did so in the direction of Island 202, which had been part of their range until a week before. Of the remaining 15 Impala seen to enter water, 11 did so over the most recently submerged land bridges connecting two islands, and this was also the case with the two herds which were reported to have taken to the water unexpectedly. Such behaviour would imply a memory of the area in which they lived and is further evidence for the possession of restricted home ranges as, in flat country, the partially submerged vegetation around an island was similar in all directions.

The limited home ranges occupied by Impala in the Central Zambezi Valley, and their poor swimming ability, suggest that Impala would be particularly susceptible to abnormal flooding. It is therefore not surprising that fair numbers were known to have drowned during drastic floods in the Zululand Game Reserves in July 1963 (Natal Parks Board Records). The sexual segregation of adults into different parts of the habitat, which Anderson (<u>in press</u>) had demonstrated, would make the female herds more susceptible than the males, as he found males remained on high ground for most of the year, while females concentrated along the river in a small area in Hluhluwe Game Reserve.

The flood plain of the Luangwa River is not well documented during the rains when the river overflows its banks for distances of up to about three miles. The depth of this flooding varies and numerous islands form in the slowly moving water. Mr. J. Feely (<u>pers. comm</u>) has found Impala marooned on termite mounds during an exceptionally high flood, while Mr. M. Ronaldson (<u>pers. comm</u>)reports a large herd was surrounded by water for some time during the 1963/64 rainy season. An albino female had remained in the same small area, about a mile and a half across, near where the second observations were made (Mr. V. Wilson, <u>pers. comm</u>) for three to four years, indicating a close parallel between observations here and at Kariba.

B. <u>Behaviour on Islands</u>

The restriction of Impala to areas smaller than their normal ranges led to a rapid deterioration of the habitat, which was reflected by a fall off in the condition of the animals (Table 19) and eventually to shifts in the structure of the populations. Impala was the most numerous species on Island 17, and Ukubula Island, where observations of undisturbed feeding behaviour showed they were responsible for the clearly defined browse line about 60 inches above the ground (Figure 20). The main plants taken on Island 17 were <u>Holmskioldia spinescens</u>, <u>Combretum apiculatum</u>, <u>Terminalia brachystemma</u>

Table 19.

Physical Condition of Impala Marooned on Eight Islands

Location	Date	Sample	Physical Condition															Status of Habitat
			Male & Female			Males									Females			
			Calves			Yearlings			Adults			Total			Yearlings & Adults			
			G.	F.	P.	G.	F.	P	G.	F.	P.	G.	F.	P	G.	F.	P.	
Island 17	June/July 1960	197			20						25			70		1	106	Good Impala habitat - severely over-populated.
Islands 14/15	Sept/Oct. 1960	9									8			8			1	Limited suitable habitat, over-populated
Island 202	April 1961	5					1	1		3			4	1				Good habitat, abundant food.
Island 204	April 1961	9									1			1			8	Good habitat, food limited.
Island 144	June 1961	75			9			10			21			31		10	25	Good habitat, over-populated.
Island 21	June 1961	11						3						3		1	7	Limited suitable habitat.
Island 28	June 1961	3			1												2	Limited suitable habitat.
Ukubula Island	December 1962	141			7			23			34			57		1	76	Good habitat, severely over-populated.
	Total	450			37		1	37		3	89		4	171		13	225	

G = Good condition
F = Fair condition
P = Poor condition

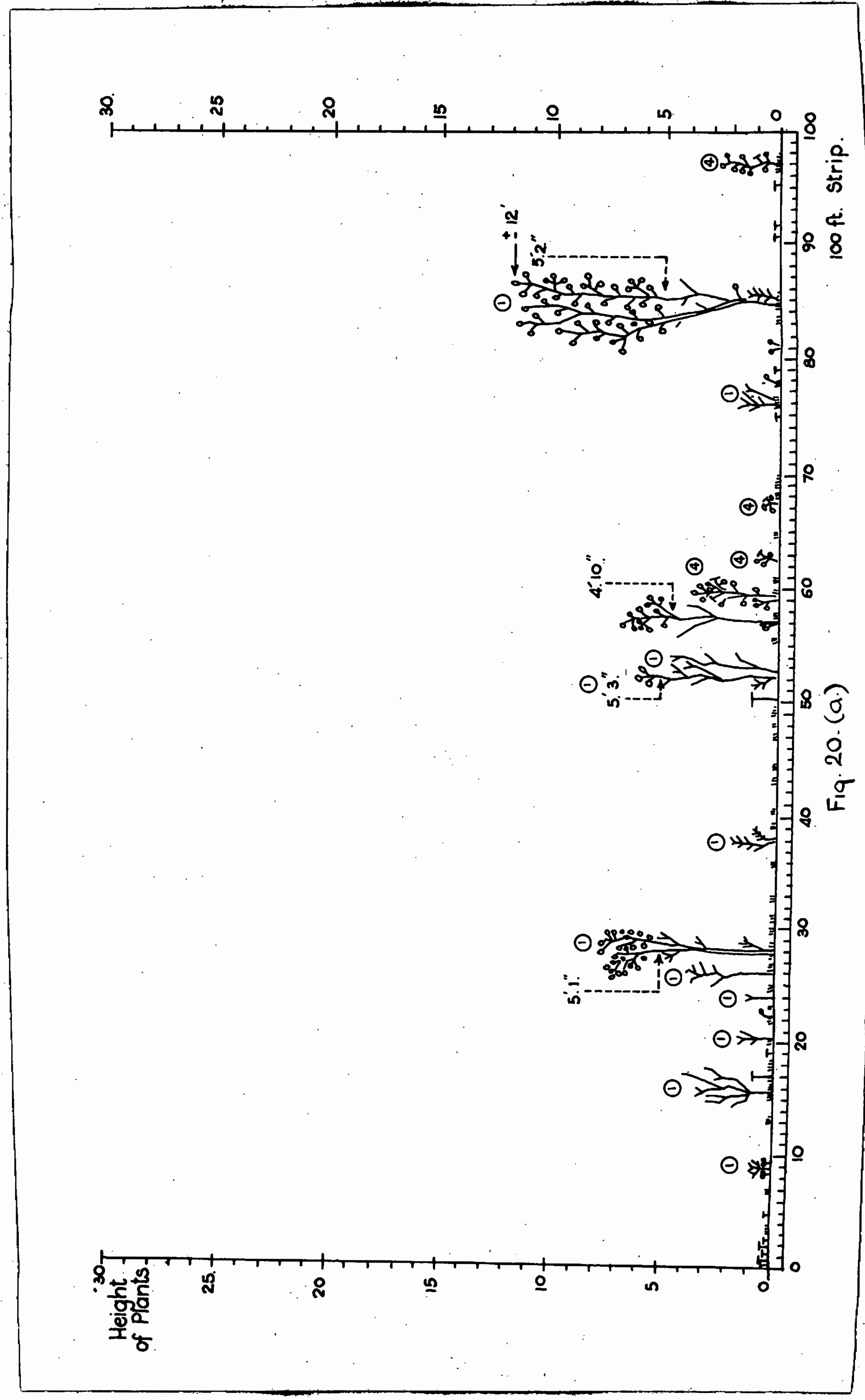


Fig. 20. (a.)

Fig. 20. Strip transects showing the clearly defined browse line around five feet left by Impala on Island 17, (a) and (b); and on Ukubula Island, (c) and (d).
1. *Combretum apiculatum*; 2 *Holmskioldia spinescens*; 3 *Terminalia brachystemma*; 4 *Colophospermum mopane*; 5 thorn; 6 *C.elaeagnoides*; 7 *Baphia massaiensis*; 8 *Pterocarpus brenanii*.

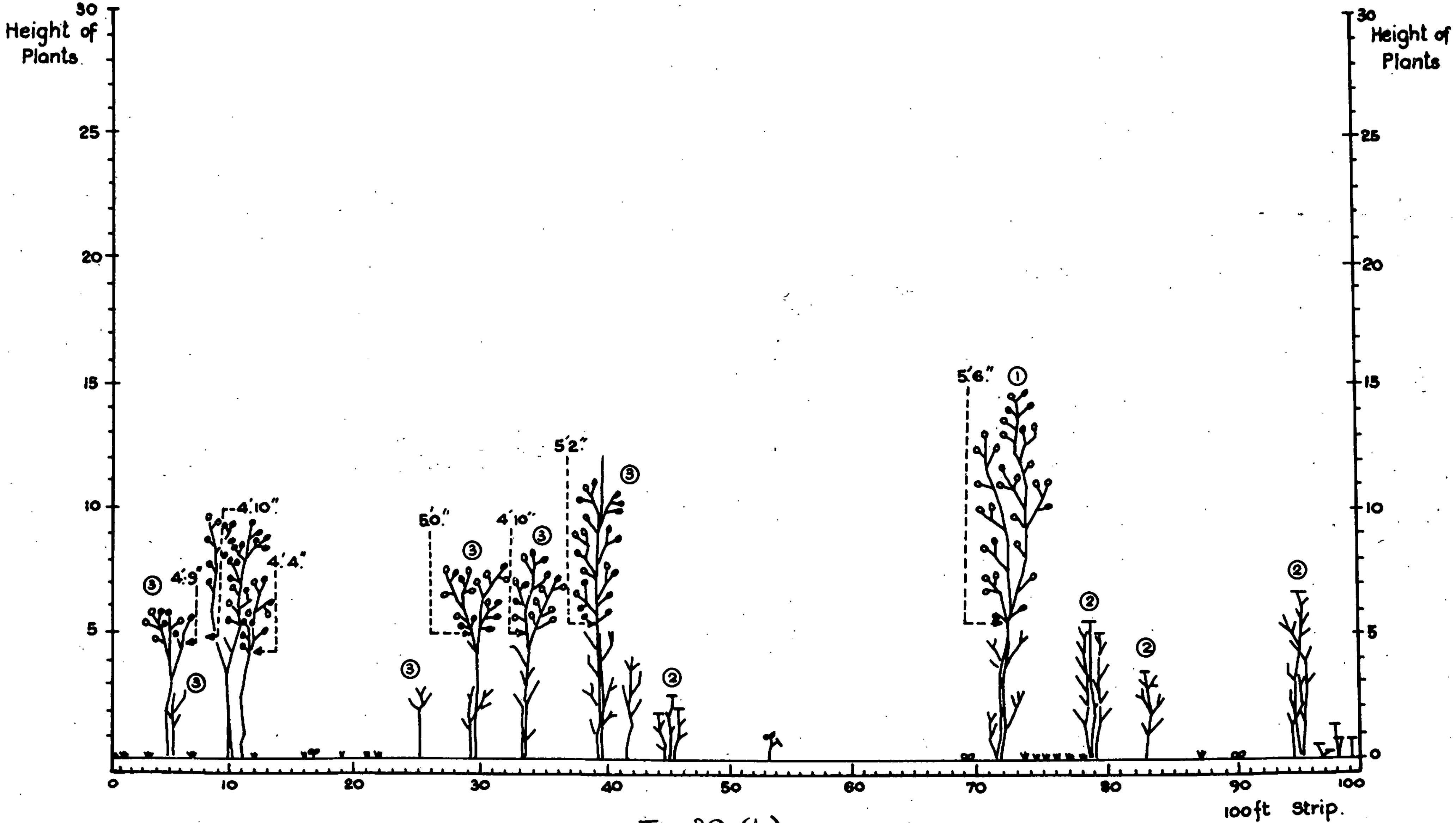

Height of Plants
30
25
20
15
10
5
0
4'9"
4'10"
4'4"
5'0"
4'10"
5'2"
5'6"
③
③
③
③
③
③
②
②
②
②
②
①
0
10
20
30
40
50
60
70
80
90
100
100ft strip.

Fig. 20. (b).

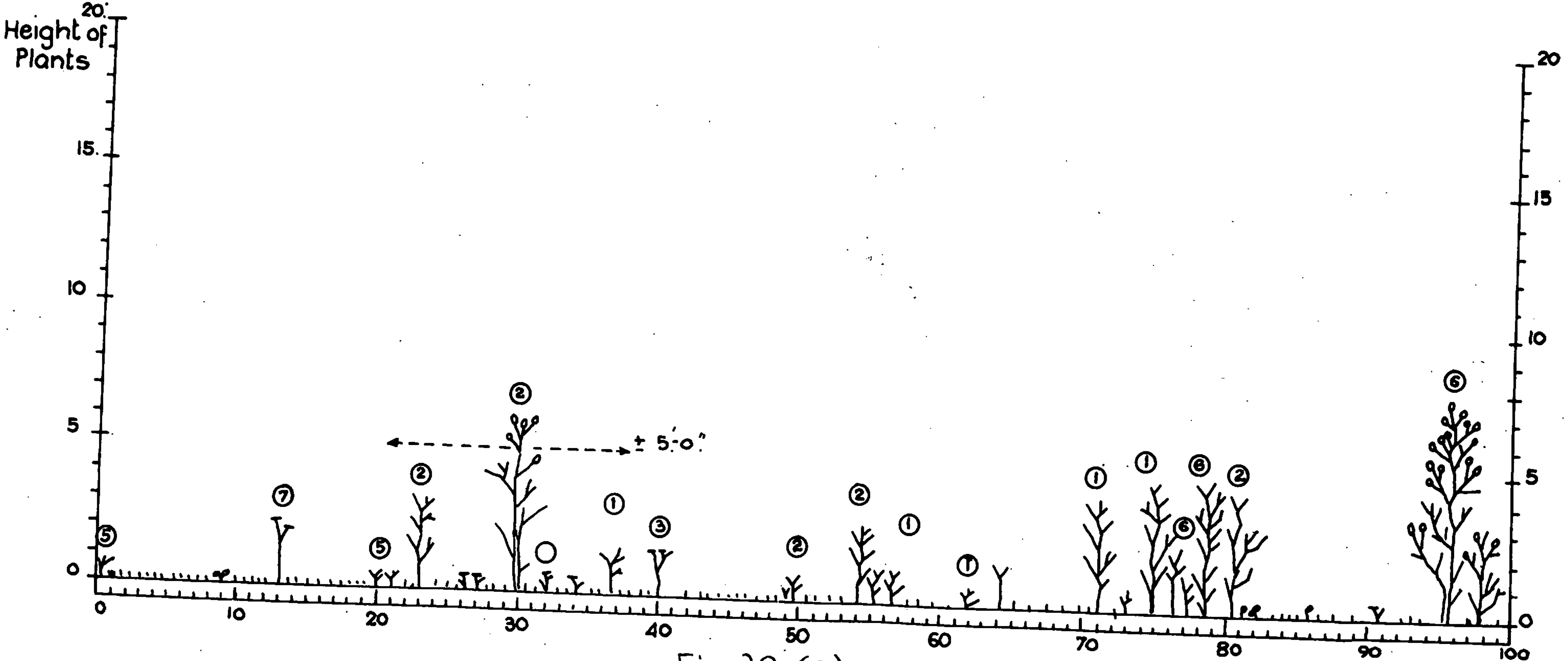

Height of Plants
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
⑤
⑦
⑤
②
②
± 5'0"
①
③
②
②
①
①
①
①
⑥
⑥
②
⑥

Fig. 20 (c)

Erythroxylum zambesiacum, Diospyros quiloensis and traces of mopane, Colophospermum mopane were found in all 62 stomachs investigated. No grass and very little jesse, C. elaeagnoides, was taken by Impala on this island, although on Ukubula Island jesse had been very heavily browsed.

The order of preference for common plants in the Island 17 area is given in Table 20, which includes Terminalia randii and T. prunioides, which were not present on the island, but had recently been denied to Impala in nearby flooded areas. Comparisons of the acceptability of these species were made in two ways. Similar samples of two species at a time, offered to between five and seven, seven-month old calves. As soon as one of the penned calves began feeding the position of the two species was reversed. Excepting for the last four species listed, all samples were eaten to some extent, depending upon the combinations in which they were offered. Fresh samples of C. apiculatum were preferred to H. spinescens and T. brachystemma in that order, although it was difficult to obtain similar leafy branches of H. spinescens, because of its growth form, and the preference for it over T. brachystemma, on the ten occasions when the two plants were given together, was less pronounced than between any two other species. There was usually no doubt which of the two species was preferred as, after sampling both, most of the leaves were eaten from one before an Impala moved to the second. Diospyros quiloensis and T. prunioides were not compared adequately but, on the occasion they were presented together, T. prunioides was preferred by both calves tested.

In addition to fresh material, dry samples of C. apiculatum and dry mopane leaves were compared with other samples. As shown, dry C. apiculatum was taken in preference to all plants below E. zambesiacum, but the dry mopane leaves were not eaten, even after 24 hours in the pen. This was interesting, as these leaves are often described as useful livestock food in dry parts of Rhodesia, (see for example de la Hunt, 1954), and occurred in several stomachs autopsied at the end of October, in the south east of Rhodesia where the main diet was grass.

Other comparisons were made from the feeding of Impala on freshly felled browse. Approximately equal amounts of mopane, E. zambesiacum and jesse were brought within reach of Impala. After two days, 98% of the E. zambesiacum had been eaten compared with 12% mopane and 1% jesse, and only Impala spoor was evident on the swept ground. In the same way, D. quiloensis was preferred to Commiphora spp.

Most general works describe Impala as predominantly browsers, which take fair amounts of young grass during the rains, but the relative year-round importance of grass to browse varies

Table 20.

The Order of Preference shown by Impala for Different Browse Plants on Island 17

SPECIES	Order of Preference
Combretum apiculatum (fresh material)	1
Homskioldia spinescens	2
Terminalia brachystemma	3
Combretum apiculatum (dry material)	4
Erythroxylum zambesiacum	5
Terminali prunioides	6
Diospyros quiloensis	7
Colophospermum mopane (fresh material)	8
Commiphora spp	9
Terminalia randii	
Combretun elaeagnoides	
Colophospermum mopane (dry material)	

locally with population density and the conservation status of the veld. In six areas in Rhodesia, where the grass cover has been severely down-graded, Impala live on browse for much of the year. Lamprey (1963) has found they are mixed feeders, taking a reasonable proportion of both, while in two areas in the south east of Rhodesia they are predominantly grazers. On Buffalo Range, perennial grasses are generally reasonably well conserved and provide Impala with most of their food. This is shown clearly in Table 21, based on 353 stomach samples taken by African technicians, who preserved a convenient handful in 10% formalin, between March 1962 and April 1963. Small particles were floated out in a sieve and the proportion of browse was estimated and recorded as zero or a trace, 10%, 20 to 50% or over half a sample. Grass tended to wash out more readily than browse which loads results in favour of browse, including fruits and seeds, of which there were a fair proportion seasonally, especially marula, Sclerocarya caffra, fruits and Acacia seeds. June was the only month sampled adequately, in which browse made up over 10% of the stomach contents in most animals, as even in October, just before the rains, 68% of the animals had eaten 10% or less browse. Preserved material retained its colour surprisingly well, from which it was clear that late in the season Impala were feeding mostly on dry grass. Mr. C. Savory (pers. comm) biologist in the Department of Wild Life Conservation, obtained similar results on this ranch at the end of 1961 dry season. Only one of the nine stomachs examined in September had more than 10% browse, and in October there was only one of 16 which had eaten less than 60% grass, when Impala were feeding largely on dry grass. This was the case before any rain fell at the end of a very dry season at Chipinda Pools, where the grasses were in even better condition. Forty eight stomachs were examined in the field and all contained over 90% grass, in most cases with only a trace of browse. Early in the month, most of the browse consisted of dry leaves, including mopane, but the proportion of green leaves increased as more plants came into leaf towards the end of the month, just before the beginning of the rains. The Impala here fed almost exclusively on dry grass and, although the majority were in poor condition after a very dry year, they had better developed fat reserves than specimens which had subsisted on browse alone at the end of the dry season in less severe years elsewhere. This was particularly noticeable in the better quality bone marrow.

Impala lived almost exclusively on browse on islands at Kariba. As the islands became more and more over-populated, they ate less and less palatable foods, but starved on Island 17 before eating large quantities of the readily available mopane and jesse. Of these two species, mopane was preferred and yet, on Ukubula Island there was a well-defined Impala browse line in jesse (Fig. 20),

Table 21.

The Proportion of Browse in Impala Stomachs from Buffalo Range.

Month	Sample	% Browse				% Stomachs with 10% or less browse.
		< 10	10	20 - 30	>50	
Jan.	31	31				100
Feb.	42	41	1			100
Mar.	87	72	13	2		98
Apr.	57	37	15	5		91
May.	26	5	13	7	1	69
Jun.	13	2	2	7	2	31
Jul.	1	1				
Aug.	2	1	1			
Sept.						
Oct.	28	10	9	8	1	68
Nov.	32	30	2			100
Dec.	34	26	5	2	1	91
Total	353	256	60	32	5	92

while the mopane, which was less plentiful and therefore would have been expected to show heavier use, was hardly touched. On this island the extensive use of jesse was largely responsible for the prolonged survival of the population in 1962, as it was abundant and had been browsed almost as heavily as more palatable forms. This may have resulted from its being more palatable than on Island 17, either because it had been cut back to ground level during bush clearing operations, or because of some soil factors, as the island had relatively sandy soils compared with the heavy mopane soils on Island 17. Coetsee (1964) found Impala making extensive use of grasses which grew in the soak zone in the 1963 dry season.

It is also noteworthy that dry mopane leaves, although plentiful on Island 17, formed a very low proportion of the food in the 62 stomachs analysed. This material is frequently found in stomachs from the late dry season, and Mr. D. Rushworth (pers. comm) estimated as much as 20% in two samples from the Beitbridge area at the end of the 1964 dry season, following a severe drought.

Similar species to those on Ukubula Island and Island 17 were heavily browsed on Island 144, but here depletion of the habitat was less complete on 28 and 29 May, than on the other two islands later in the year. On Island 203, two large Terminalia prunioides trees had been stripped of all leaves within reach, but the abundant jesse on mopane soils had hardly been touched, although the Impala were losing condition and there were no alternative foods.

The wide range of foods taken, which enabled Impala to survive on islands such as Ukubula Island, indicates one of the reasons Impala are so successful in marginal areas. They can subsist almost entirely on grass, apparently the preferred food when available, or can take a wide range of browse plants. Dasmann and Mossman (1962,c) suggest they are a successional species, particularly well adapted to areas where the vegetation has been disturbed and down graded through human agencies. Here they compete for any available grass, but can tide over critical periods by subsisting on browse which, incidentally, would further aggravate scrub encroachment in down-grading veld, unless numbers, which tend to increase greatly under such conditions, are managed to within safe limits. Lamprey (1963) found they favoured transitional zones between woodland and open grassland, and this was very apparent on the east bank of the Lundi River in the Chipinda Pools Area in October 1964. In this area, which shows few signs of disturbance, there is a reasonably dense, but short, perennial grass cover in open mopane woodland, intersected by open, recently bush cleared water courses, the edges of which attract Impala.

Impala have been found to prefer reasonably dense cover only during the lambing season, although shade is important during the heat of the day at all times. In seven widely separated areas in Rhodesia and two in Zululand Game Reserves, they appear to favour habitats where their vista is not impeded by tall grass or dense low scrub. They have never been contacted in tall grass, which is possibly another reason they favour areas over-stocked with domestic stock, and the only Impala found in dense thickets have been females about to calve or with calves only days old. For example, during the 1961 calving season on Buffalo Range, very gravid females left the herds in small numbers not exceeding four, and made for the densest available thickets in generally open country. Lone calves were never seen during the day, although 10 were observed at night, suggesting the calves are left at night for the first week or so, and that after dark the mothers rejoin the herds, when there were noticeably few calves in herds of non-pregnant, adult sized females.

Impala were marooned on two islands at Kariba with extensive thickets, where they remained in mopane veld where food was scarce, although abundant browse was available in the thickets. On one island this may have represented a reluctance to leave an established area, but on the other, they moved through a thicket to alternative mopane veld when the first area became submerged.

It is, therefore, unlikely that shortages of cover, arising from over-browsing, had any effect on Impala marooned on islands except, perhaps, Ukubula Island where the population was trapped during the calving season. Shade was readily available on islands at all seasons, due to the effect of the soak zone.

Food was scarce on Islands 14 and 15 where most of the trees were out of reach of Impala, which had to compete with Bush-buck and Kudu in terrain which was not typical of Impala habitat in the Kariba Basin.

The habitat on Islands 17 and 144 was similar, although as noted, the former was more heavily used, due to the fact that there was a greater density of animals and that it had taken five to six months to reach its June size, compared with Island 144, where animals had been marooned for under six weeks. Although fat measurements show little difference, it was obvious that animals, particularly adult rams, were in better condition on Island 144.

As to be expected, Impala lost condition more rapidly on islands than is generally the case. This culminated in a considerable die off on Island 17, which affected some sex or age classes more than others. Differences in physical condition showed that a similar pattern of mortality would have taken place on other islands, had the animals not been rescued. However, before the significance of this mortality can be gauged, it is necessary to outline briefly the role of the different classes in the year-round reproductive pattern of the species.

Impala have a well-defined calving season and most young are born within two to three weeks. The timing of the season varies with locality and, to some extent, from year to year. Ansell (1960,b), for example, has described late September and October for the peak on the Zambian plateau and November for the Luangwa Valley, and Child (1964a) cites November to early January for four areas in Rhodesia. On Buffalo Range, the peak was in the latter half of November in 1961 and few pregnant females remained by the 30th. November, while in 1963, the season was about two weeks later, according to Mr. G. Style, the ranch owner. The timing of the season is not a simple question of altitude or latitude, as Doddieburn Ranch is similar in these respects to Buffalo Range, and yet Dasmann and Mossman (1962,c) describe the peak of lambing there as the latter half of December, with few births after January 6th. in 1959 and 1960. Calving at Ukubula Island took place during the second half of November (Rescue Reports) and was complete by 11th. December, 1962, when no pregnant females could be found among some 200 to 250 females examined.

Dasmann and Mossman (op. cit) found lactating females as late as August, six weeks after the rut, which occurred mainly between 15th. May and 15th. June. On Islands 17 and 144, females ceased lactating soon after the rut, which may have acted as the final stimulus to wean their calves. Females with developed udders produced a fine stream of wholesome-looking milk, when tested on 8th. June on Island 17, but after 18th. June, yielded only a few drops of watery milk. Udders tested later in the month had an increasing amount of waxy material adhering to the mammae, indicating that they were no longer being suckled, whereas those tested on the 8th. were relatively clean. About half the adult females caught on Island 144 on 28th. May had wet udders, which, in a number of cases, were clearly going dry.

Udder development has only been recorded in females over two years old, both at Kariba and elsewhere in Rhodesia. The udders of yearlings are small and resemble those of calves, in that they show no signs of previous development, such as stretch lines, which are common in older females, even when not lactating.

The timing of the rut probably differs in different parts of Rhodesia in the same way as the calving season, but this requires more precise definition from a number of localities, as there is some contradiction in the lengths of the gestation period quoted in the literature. Asdell (1964) gives 195 to 210 days, Kenneth and Ritchie (1953) 150 to 210 days, Stevenson-Hamilton (1947) 195 to 210 days, and Dasmann and Mossman (op. cit) suggest between 195 and 210 days from observation on Doddieburn Ranch. There was strenuous rutting activity in 1961 on Island 144 between 15th. May and 27th. May, but this subsided markedly towards the 27th. The rutting activity included vigorous fights between adult males, which were frequently seen chasing females although only two copulations were witnessed, both by Haslam. Five foetuses found on the 28th. measured two to 13 mm. from crown to rump, while 12 from Island 17 on 8th. June, 1960, measured three to 13 mm; indicating a similar rutting period there the previous year. With a peak in calving activity in the second half of November on Ukubula Island in 1962, this indicates a gestation period of 180 to 200 days.

The weights of the testicles graphed in Figure 21, indicate males reach sexual maturity during their third year, although Kerr (1965) has found some active sperm in younger animals. It seems likely, however, that mature males are only sexually capable for a limited period each year (Figure 22.) Serious fighting forms part of the rutting behaviour and Stevenson-Hamilton (1947) has noted that these fights may lead to bad wounds, so that horn development (p.15)provides useful supporting evidence for rams not generally taking part in breeding before they are two and a half years old. There was no evidence to infer that fighting was more strenuous under the restricted conditions on islands, as no wounds were noted and, although three adult rams on Island 17 had broken horns, these were old wounds and the stumps had been worn smooth.

A high proportion of adult and yearling females conceive. Dasmann and Mossman (op. cit) obtained 97% adult and 85% yearling pregnancies on Doddieburn Ranch and the present author found 14 of 15 (93%) adults, the exception being an old female in very poor condition, and all three yearlings, to be pregnant at Chipinda Pools, while at Kariba 94% of the 35 adults autopsied after the rut were pregnant, as were four of five yearling casualties. These results suggest an annual reproductive potential approaching 100% of females over a year old, as examples of multiple births have never been found and must be rare, and no examples of pregnant calves, which have small uterae, have been recorded. It is significant that even under unfavourable conditions, which prevailed on Island 17, 29 of 31 (93.5%) adults and three of four yearlings conceived, which suggests that a temporary low plane of nutrition does not affect conception to any marked extent, although if prolonged, it would probably retard maturation and so limit the number of sexually mature yearlings. It was particularly noticeable

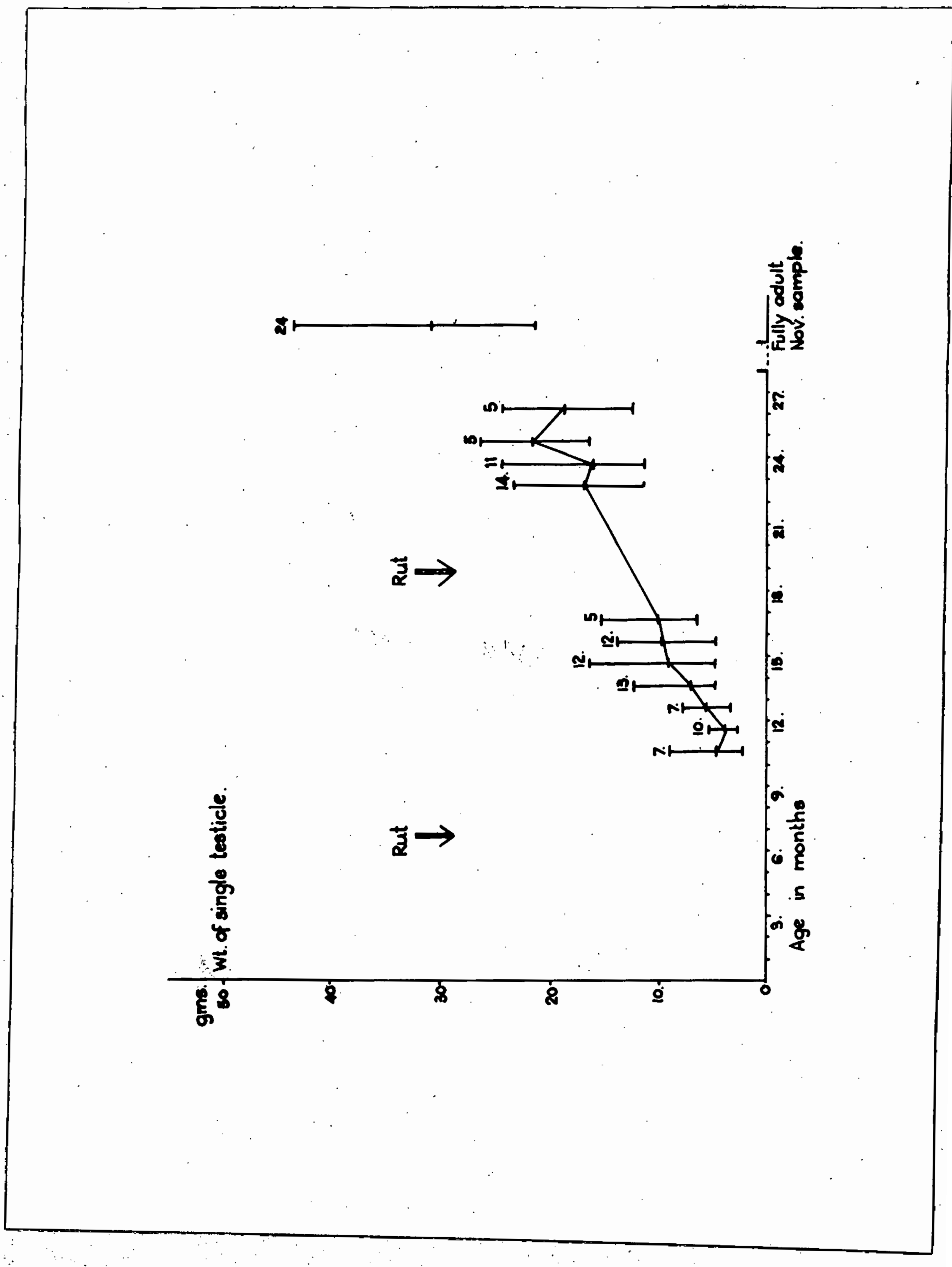


Fig. 21. The growth of the testicles in Impala, showing the minimum, mean and maximum and size of sample for each age group.

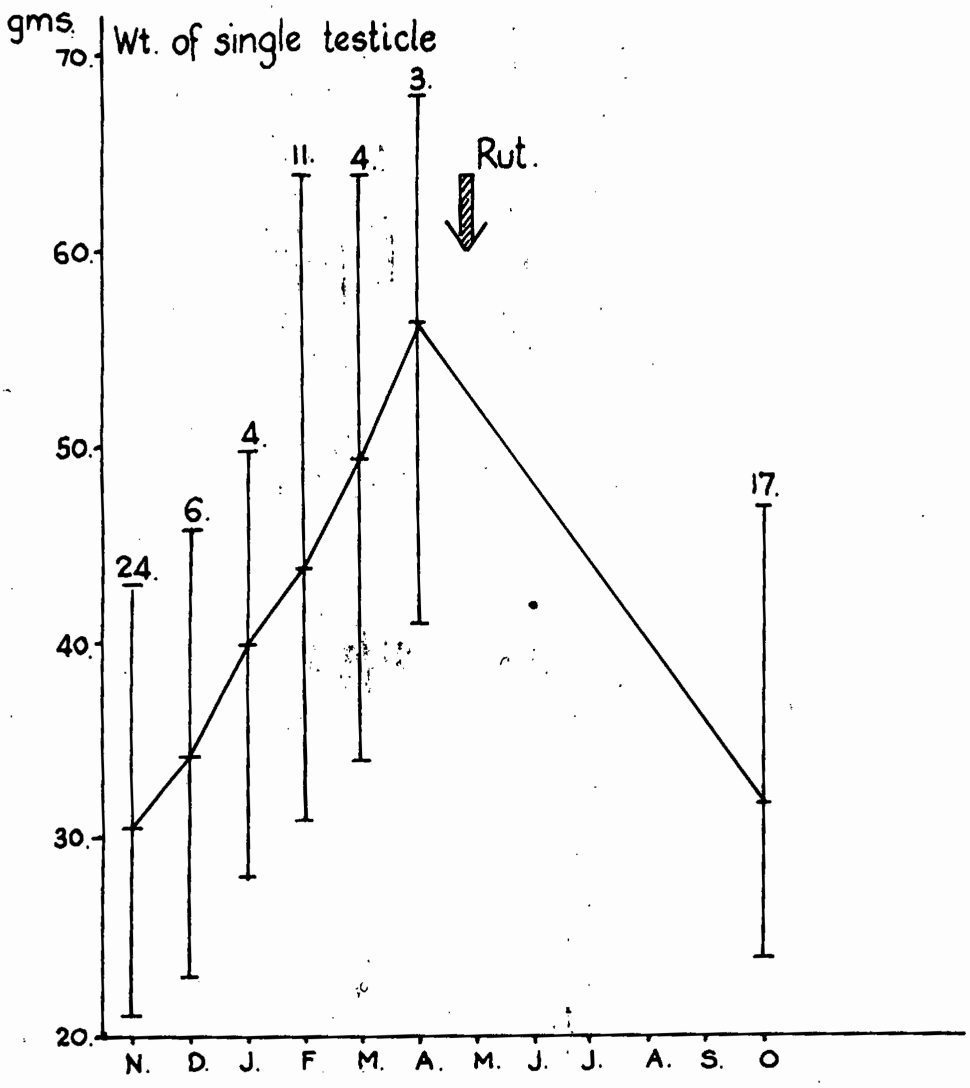


Fig. 22. Seasonal changes in weight of adult Impala testicles, showing minimum, mean and maximum weight in the monthly samples whose size is shown for each month.

on Ukubula Island that yearlings were smaller than usual at 13 months of age.

Conditions on islands led to shifts in the sex and age class composition of Impala populations. These are difficult to compare with free-ranging populations for, as previous workers have noted, there is obvious sex and age segregation between herds, and even within herds, of this highly gregarious species. Preliminary results suggest a further partial ecological segregation of older males and females, which is supported by Anderson (*in press*) from the Hluhluwe Game Reserve. These factors are probably responsible for the impossibly high calf ratios often obtained from classifications of free-ranging Impala. Dasmann and Mossman (*op. cit*) mention no precaution against this possible bias, when describing population structure on Doddieburn Ranch, so that it is difficult to judge what relationship their sample had to the actual population, especially as they acknowledge some segments were probably inadequately sampled at certain times of the year. Another difficulty is that Impala often run in herds of over 50 head, which predominate with one sex or age class, so that the chance of contacting or overlooking such a herd could seriously alter samples ranging from 152 to 564, such as these authors used.

The only mainland sample, therefore, used for comparative purposes in this paper, is based on a collection of skulls from the Cewali Tsetse Control Hunting Area. This sample was fairly small, but represented kills from 14 months in an area of about 300 square miles, made by 30 to 40 hunters, after 12 years hunting in the area. Animals were extremely wary, and 14 hunters interviewed all stressed the necessity of shooting the first animal seen, so that the sample was as unbiased as could be expected. Even so, it is used with caution as it is not known what effect such prolonged shooting would have on Impala. Most conclusions of changing trends in population structure are, therefore, based on comparisons between different islands, where the whole population could be observed together with the habitat. It is unlikely that ecological segregation of males and females would have been sufficient to affect samples compressed onto islands from several square miles for, as noted, both sexes were very localised in this area. This is borne out by the insignificant difference ($\text{Chi}^2 = 0.779$) between the sex ratios of the 129 Impala released and the 76 re-caught on the west bank of the Bumi River (p. 81). There is no significant difference between the proportions of males at successive levels of sampling on Island 17 (Table 22), although the tendency towards more males in later samples, giving a significant difference between the first and last quarters ($\text{Chi}^2 = 4.87$, $P > 0.05$), when the proportion of males

Table 22.

The Sex Ratio at Different Sampling Levels in Impala Marooned on Island 17

% of Total Population	Sample	M	F	% Level of Population	Sample	M	F
25	66	10	56	25	66	10	56
25	66	17	49	50	132	27	105
25	66	19	47	75	198	46	152
25	67	21	46	100	265	67	198

M = Male
F = Female

in the population was declining, was attributed to males being a little more difficult to catch than females.

Table 23 compares the proportion of calves in marooned samples with that from Cewali, which indicates a heavy loss from this group on most islands. As noted, yearlings were smaller than adults in December on Ukubula Island, and so could still be easily separated from them. This sample included only complete herds, while another herd in which only adult females and calves were classified, brought the total to 20 calves and 91 adult females (22:100). This herd is mentioned as it contained a higher proportion of calves than any other, so that it is obvious that the proportion of this age class was very low, four to six weeks after the calving season.

Robinette et al (1957) review the human as well as the large and small mammal literature on the effects of nutrition on pre and post natal mortality. Generally there is a reduction in the proportion of male foetuses, which potentially exceed the number of female foetuses, when the plane of nutrition is low. The number of implantations is lower, the average birth weight is reduced and resorbtions or abortions increase. The reduced birth weight lessens the survival rate of the young calves, which are at a further disadvantage due to the impaired milk supply of their mothers. The first calves on Ukubula Island were stillborn (Rescue Reports) and it is probable that pregnancy failure was the prime cause for the low proportion of calves, as no carcasses were found when the island was thoroughly searched.

There were 298 Impala on Island 17 on 3rd. June, including those which were later rescued, casualties from rescue operations, natural deaths and an adult ram which was left on the island. There were 197 females, 96 males (48.7 males : 100 females) and five full grown animals which were not sexed. The total included 11 female and 12 male calves, seven to eight months old. The calf to adult female ratio in Table 23 was calculated from the proportion of yearling females in the rescue casualties, which apparently were not selective. Four of 37 adult-sized females were yearlings and if this ratio is projected to all mature females, it gives approximately 165 females capable of having bred, or 14 calves:100 females.

Impala were dying on Island 17 by 3rd. June, when two-week-old adult ram carcases were found. Thereafter six more died between 4th and 10th June, seven between 11th and 17th and 10 between 18th and 24th, by which time most of the Impala had been rescued. The first two female carcasses, an adult and a yearling, were found on the 23rd and two calves died between 21st and 24th.

Table 23

A Comparison of the Calf to Female Ratio of Impala Samples From Islands with that from the Cewali Tsetse Area

Locality	No. in Sample 1)	Calves			Females			Calves/100 F Over 1 yr.old	Calves/100 Ad. F.
		M	F	Total	Yr.	Ad.	Total		
Cewali	55			11	4	22	26	42.3	50
Island 17	298	12	11	23	21	165	186	12.4	13.9
Island 144	75	9	4	13			30	43.3	-
Island 201-205	14			0			8	0	-
Island 21	11			0			8	0	-
Ukubula Island	161			7	33	59	92	7.7	11.9
Total on Islands.	559	21	15	43	54	224	324	-	-

M = Male, F= Female, Ad = Adult, Yr = Yearling.

1) Includes males over 1 year old in the sample.

However, the calf ratio on this island showed that, as to be expected, the die off of adult rams had been preceded by a heavy loss of calves, although both groups had very depleted fat reserves. Between 8th and 16th June, no adult ram or calf casualties had any kidney fat and all had poor bone marrow, while other groups had better developed fat deposits (Table 24). On Island 144, where food was less critical about the same time of the year, adult males were in obviously better condition than the calves. The absence of calf carcasses on Island 17 indicated that losses among them had taken place over an extended period and that the carcasses had been submerged or removed by scavengers, whereas the male die off was sudden.

Rutting activity, which placed an additional burden on the rams, was probably responsible for this, as in his discussion on Impala, and in broad agreement with Fitzsimons (1919), Stevenson-Hamilton (1947) notes that females are in poorest condition in summer, but pick up in winter when "herd rams" are thinnest. He concludes that the improvement in condition of females results from the removal of the strain imposed by lactation, while the demands of the rut causing the decline in condition of rams may be read into the term "herd rams". Observations on Islands 17 and 144 support this hypothesis and it is a pity that neither author presents evidence for his conclusions or recognises more than the three sex and age classes of calves, males and females.

As noted, yearling rams were not yet fully mature at the time of the rut, while yearling females conceived for the first time and could not, therefore, have suckled the previous summer. On the other hand, the physical condition of yearlings was probably impaired to some extent by growth, as Child (1964a) has shown that females reach adult size when about 18 months old. He also suggests that the greater size of adult rams over similar aged females resulted mainly from a longer growing period in males, although growth in the second year was much slower.

There was no marked difference between the conditions of adult and yearling females on Island 17, but male yearlings, in general, were the class in best condition. The sample of males from Island 144 was small but suggested that here, too, they were in better condition than the thinnest adult rams after the rut. This was probably due to the strain of rutting activity, as Leopold <u>et al</u> (1951) recorded a rapid deterioration in male Mule Deer during the rut, due to energy demands of copulation coupled with less feeding by rams competing for females, and Darling (1956) records the same for Red Deer, which is supported by Riney (1954) who demonstrated the decline in fat reserves. Further, the five adult rams, whose condition was assessed before the rut, were in better

Table 24. Fat Reserves in Different Sex and Age Classes of Impala on Islands 17 and 144, Showing the Poor Condition of Males and Calves Relative to that of Females Whose Condition Deteriorated Rapidly During June on the First Island.

Location	Date	Sex	Age	Sample	Fat Deposits						
					Back Fat		Kidney Index		Marrow		
					Range	Mean	Range	Mean	Good	Fair	Poor
Island 17	8 June	F	Adult	16	0-Tr	1	0-47	16		1	15
	11 June	F	Adult	7	0-Tr	1	11-42	25		3	4
	16 June	F	Adult	3	0-Tr	2	0-31	17		2	1
	21 June	F	Adult	3	0-0	0	0-0	0			3
	24 June	F	Adult	2	0-0	0	0-0	0			2
	8 June	F	Yearling	2	0-Tr	1	18-20	19			2
	16-21 June	F	Yearling	2	0-0	0	0-0	0			2
	8-21 June	M	Adult	30*	0-0	0	0-0	0			30
	18-21 June	M+F	Calves	7	0-0	0	0-0	0			7
Sub Total				72							
Island 144	28 May	F	Adult	4	0-4	3	0-47	19		1	3
	28 May	F+M	Yearling	4	Tr-8	4	8-50	19	1		3
	28 May	M	Adult	7	0-Tr	1	0-19	6		2	5
Sub Total				15							
TOTAL				87							

* This sample includes 25 animals which died from starvation.

M= Male
F= Female

condition than most females at the same time. These conclusions receive support from the trends that emerged from preliminary work carried out on Buffalo Range immediately before the 1964 rut. Three adult rams had then an average kidney index of 101, whereas in five mature females, all of which were in milk, it was only 13 and yet, later in the year, rams have usually been in poorer condition than females on this ranch. This is clearly demonstrated by the differences in kidney fat indices found at Chipinda Pools in October, 1964, where eight adult males averaged 8.0 (Range 2.1 to 15.0) and 11 adult females averaged 29.0 (range 8.8, in an old and exceptionally thin female (the second lowest was 15.9) to 65.2).

Fat reserves were better developed in adult females with dry udders than in those still lactating after the rut on Island 17. Eight of nine with milk had poor marrow, while this applied only to four of 18 which were not lactating, which supports the hypothesis that suckling is a strain on Impala females. It is unlikely that early pregnancies recorded on the island would have materially affected the condition of females, although pregnancy failures would have been expected had they remained under such severe conditions, judging from the observations on Ukubula Island.

Several authors, including Dasmann and Mossman (op. cit), have remarked on the preponderance of females in Impala herds. Fothergill records a sample of 800 Impala rescued by 30th June, 1961, in which there were 517 females, 264 males and 19 unsexed individuals, giving an overall sex ratio of 51 males per 100 females. On Island 17, the proportion of males was low (48.7:100), even before the heavy die off following the rut. Dasmann and Mossman (op. cit) suggest this results from a differential loss in calves, favouring young females, as Taber and Dasmann (1954) found in deer. On the other hand, Robinette et al (1957) found heavier losses among females in deer elsewhere and there is some contradiction in Dassman and Mossman's reasoning, as they later assume the number of female yearlings in an Impala sample is equal to the number of male yearlings classified. As noted, there were almost equal numbers of male and female calves on Island 17 following a heavy die off, while Mr. G. Stewart (pers. comm) found a sex ratio of unity in a sample of several hundred calves of about 11 months of age in Umkuzi Game Reserve, Zululand.

Evidence from Island 17 suggests that one reason for the low number of males in Impala herds is the heavy mortality among adult rams after the rut in critical years. The ratio of males over one year old to females of the same age changed from 48.7:100 to 35.4:100 in four weeks on the island. Rushworth (1964) records that adult female Impala were in better condition than males at the end of the 1964 drought in the Tuli Circle. A pregnant female shot was in reasonable condition, "although not fat", but three adult males were "in very bad condition indeed; so much so that the meat was unpalatable". He also found a relatively higher proportion of male carcasses, even allowing for the greater distance at which these were sighted. They were not aged unfortunately, but tend to substantiate the findings on the island, and Robinette _et al_ (_op. cit_) found a similar shift in favour of older females in Mule Deer, following severe winters.

Predators selecting for males may further the discrepancy, but this is probably less significant than the innate dispersal mechanism described by Howard (1949) and Riney (Ms.). Howard found that male Prairie deermice, _Peromyscus maniculatus bairdii_ (Hoy and Kennicott,) dispersed more readily and for a greater distance than females, and Riney recognised similar behaviour among deer in New Zealand. These authors found that a proportion of a given age group, usually well grown sub-adults, in the species so far studied, dispersed away from the parental home range, so furnishing a method by which species, which normally occupy restricted home ranges, can spread into new territory. In Impala, dispersion seems to involve animals about 12 months old and takes place during the succeeding calving season. During the 1961 season on Buffalo Range, numbers of these young animals were contacted away from the general concentrations of Impala on the ranch, and were often in unsuitable habitat. They were predominantly lone males, although groups of up to three, including some females, were noted. This is the only season when this normally highly gregarious age group has been found alone. Further evidence for the timing of dispersion in Impala was provided by Mr. G. Stewart of the Natal Parks Board, who found a sex ratio among calves which approached parity just before the calving season in Mkuzi Game Reserve, although the same age group contained many more females after the next crop of calves had been dropped.

Thus, Impala are a highly gregarious species which became marooned on islands in large numbers as they were both poor swimmers and had very localised movements. The consequent food shortages reflected in a decline in physical condition, which culminated in a heavy die off on two islands. This affected primarily the calves, but also led to a marked drop in the proportion of adult rams following the rut.

16. ROAN

Roan, _Hippotragus equinus_ Desmarest, were scarce in the Kariba Basin, where a total of 11 were seen on two occasions, near the west bank of the Umniati River. This probably accounted for their absence from islands, as Child and Wilson (1964a) found that a marked Roan herd in eastern Zambia was much more localised than three herds of Sable, a species which did become trapped on islands. This group of five Roan, including a bull, two cows and their calves, remained within 30 square miles, whereas Sable ranged over a much wider area.

17. SABLE

Child and Wilson (1964a) found Sable, Hippotragus niger Harris, are chiefly grazers which favour areas with an adequate short perennial grass cover. This explains their distribution in the Kariba Basin where most were found in open scrub savannah. Although the grasses here were taller than those with which they were usually associated in eastern Zambia, perennial grasses were better represented than in any other vegetation type. Smaller numbers also occurred in mopane veld, away from dense human settlement, possibly because of the adverse effects of Tonga agriculture on grasses, or the disturbance it caused.

They were not numerous on islands, contributing only 1.6% of the mammals rescued by 30th. June, 1961. The magnitude of the movements described by Child and Wilson (1964a) would, however, tend to make them less susceptible to becoming marooned on islands, which is substantiated by Mr. P. Coetsee (pers. comm), who observed a herd of 10, marked with yellow ear stigs, about eight miles from their release point after about two years. This makes it difficult to judge the relationship between this sample and their actual incidence in the large mammal fauna. Judging from limited work on the mainland, it did appear that they were more numerous than these figures suggest, especially between the Bumi and Umniati Rivers, where they were better represented than elsewhere along the Rhodesian shore.

A. Response to Flooding

Sable became marooned on islands and, although poor swimmers, usually took to the water when humans approached, especially if they were without calves. This general conclusion, based on Rescue Reports, was supported by observations of five bulls caught during the present study. These animals all swam weakly for animals of their size, particularly when pursued, although Junor (1960) reports at least one which swam a mile, and the present author saw one swim 600 yards before crossing a small islet and proceeding a further 120 yards to the mainland.

A herd of Sable was marooned on Island 100, which originated from an area of 25.9 square miles, while another herd of nine, including five juveniles, was trapped on an island on the west bank of the Sengwa River, which formed from an area of 23.2 square miles. On the other hand, two bulls were isolated on Island 101, which had never exceeded 375 acres. This suggested greater localisation than that described by Child and Wilson (1964a), who found that three recognisable herds moved an average of between 0.14 and 0.26 miles a day, between successive contacts throughout the year, in much wider areas. The annual, more or less cyclic movements of one herd of three to five Sable occupied about 200 square miles for the nine months of the year they were in the study area, while two bulls remained within about 30 square miles during a similar period.

These apparent differences between movements in eastern Zambia and the Kariba Basin can be explained by the distribution of suitable habitat. In Zambia the habitat was fairly uniform over large areas, while at Kariba the most favoured vegetation types ran in fairly narrow bands parallel to the Zambezi. This rapidly became dissected as water backed up the numerous stream beds, cutting across it, so that to have remained in favoured habitat and not become marooned, Sable would have had to travel longer distances than observed in Zambia. Further, Child and Wilson found that although Sable occur in grassland, they appear to prefer open woodland and this may have contributed to their being isolated on the second and third islands discussed above, as in both of these water cut through along the edge of a bush clearing.

As Sable move about a good deal and seem to favour open woodland, which usually occurs at some distance from rivers, it seems unlikely that they would be much affected by flooding under normal conditions.

B. Behaviour on Islands

The four Sable handled during this study were in poor condition and this applied to two herds of which there is a cinematographic record. One of these herds was on a heavily trampled mopane veld island, while the second was on an island in open scrub savannah. Some of the latter starved, and when the island was visited seven months later, signs of over-grazing were still very apparent and, in spite of the intervening growing season without grazing, few of the grasses showed signs of life.

A number of Sable, including juveniles, died on islands, but Rescue Reports are inadequate to determine whether or not this led to any definite shifts in population structure, such as could be detected for a number of other species.

18. BUSH BUCK

Bushbuck, *Tragelaphus scriptus* Pallas, constituted 8.7% of animals caught before the end of June 1961, and occurred throughout the Central Zambezi Valley where they favoured thickets, especially those along water courses. They were least numerous on densely settled alluvium, where cover had been greatly reduced through cultivation and overstocking with domestic stock, especially goats, and were most common in broken ground along the foot of the Matusadonna Range.

A. Response to Flooding

Bushbuck were among the first animals affected by the formation of the Lake, when water backed up rivers and streams forcing them out of riparian thickets. They took to the water very readily and were good swimmers, but became trapped on small islands because of their localised habits. Of 57 observed, 50 (88%) entered the water readily, usually at the approach of humans, or after a very short chase. The exceptions were two animals too weak to run, and five on a big island, with ample room to escape on land. Similar behaviour was reported in the presence of a Leopard (Rescue Reports). Sclater (1900) has already noted that "sometimes when hard pressed they take to the water and swim well". Further, as mentioned below, they entered the water to feed and hid in the shallows.

They are fast manoeuverable swimmers and were the most difficult species to catch in the water. Junor (1960) recorded one which swam between one and threequarter and two miles and, during the present study, the following distances were recorded : one over 3,000 yards before reaching land, three over 500 yards before being caught, five over 200 yards, 12 over 100 yards and six over 50 yards. The first animal covered the distance, confirmed on contour maps, in 13 minutes and, although tired, had maintained a speed about twice that of which a man is capable over a shorter distance, and this through choppy water with waves up to 18 inches high. The remainder of the animals showed no signs of tiring when picked up, although several of them were very thin.

Sclater (op. cit), Fitzsimons (1919) and Shortridge (1934) all mention examples of Bushbuck which remained in limited areas for considerable periods but, unfortunately, give no indication of the size of the area. Four marked Bushbuck, three females and a male, were released on the south bank of the Nyamune River on 31st. August, 1960, and recaptured on 16th. and 17th. June the following year on islands which had formed the previous March. Four of these were well within half a mile of the release point, while the fifth, which was retaken on a narrow island 500 yards long, may have wandered up to three quarters of a mile and still been trapped on this island. Two other Bushbuck moved up to 4.5 and 1.5 miles respectively, but in both cases the intervening land was submerged and they were on the nearest land to the release point after 16 and nine months.

Two young Bushbuck were trapped on an island which originated from less than 200 acres, while 33 became isolated on islands which originated from areas of under three quarters of a square mile. In one case a Bushbuck was marooned under adverse conditions within 50 yards of the mainland and 22 were within 400 yards. Further evidence for their localised habits comes from their behaviour when flushed from an island. It was often possible to chase them to alternative land, but they usually showed a strong tendency to circle back to the island from which they had been flushed, although on three occasions they passed close to other islands.

The concentrations of Bushbuck along water courses and their very localised habits, would make them particularly susceptible to abnormal floods, in spite of their considerable swimming ability.

B. <u>Behaviour on Islands</u>

Most authors have found Bushbuck a secretive species of dense cover, especially that along water courses. It is probably the cover and not the proximity of water which is essential, as Shortridge (<u>op. cit</u>) reports them a long way from water, and four contacts at the end of the dry season along tributaries of the Nagupande River, were at least five miles from water. This is significant, as the species was very localised in similar habitat in the Kariba Basin, less than 50 miles away.

Water was obviously readily available on islands, on eight of which cover was sparse, due to the nature of the vegetation or over-browsing. On Island 17 they were often seen crouching in inadequate cover, but flushed more readily than usual. They offset this lack of cover on some islands by hiding in thickets in the in the surrounding shallows. This behaviour was apparently very marked during the 1959 Rescue Season, when most Bushbuck were caught, and was observed by the author on 11 occasions. The animals remained motionless in water ranging from under a foot deep to that in which they could not stand and where an adult ram, in order to remain motionless, had to rest its head on a horizontal branch. Several others had only their heads showing and, thus concealed, Bushbuck did not flush until approached to within 20 to 30 yards by a motor boat.

It is unlikely that shortages of cover, unless accompanied by food shortages, would have had any effect on physical condition as three of five adults caught on islands with limited cover, but adequate food, were in fair condition. They would, however, have been more susceptible to predation.

It is generally agreed that Bushbuck are mainly browsers and Wilson and Child (1964) have described some of the plants eaten by them in eastern Zambia. Grass is taken when green and two, kept in captivity, did not eat it after it was about 18 inches high. There was some grass available in the soak zone on two islands, but on others they were limited to browse, including Combretum apiculatum, Holmskioldia spinescens, Terminalia prunioides, T. stuhlmannii, Diospyros quiloensis, Ximenia americana, Boscia matabelensis, Mundulea sericea, Gardenia resiniflua and Acacia pods, as determined from direct observations of undisturbed feeding and the contents of 10 stomachs. An unusual observation was the presence of 20% Salvinia auriculata in the stomach of a female from Island 204 where there was adequate browse available in April, 1961.

The physical condition of 54 Bushbuck from eight localities is related to the status of the habitat in Table 25. They starved on Islands 17 and 106, due to competition from Impala on the former and through the destruction of their own habitat on the latter, where there were 11 Bushbuck confined to less than a third of an acre by mid-June 1961. Eight of these were dead by the 15th and the remaining three were in a very weak condition, but decomposition was not advanced in any of the carcasses, so that all 11 would have died within about a week of each other.

There were five Bushbuck on Island 17, one of which was removed and another, with very depleted fat reserves, died on 4th July and the remaining three had died before the Unit returned in August. These animals were all in poor condition on 8th. June, and became progressively weaker during the month. On this island, a female was seen feeding on Holmskioldia spinescens in the shallows, where it was protected from Impala, while another competed for food with a Rhino, an Impala and a Grysbuck (p.55).

There was a clear Bushbuck browse line on Island 107, which was about an acre on 16th. June, 1961. Here food was less critical than on Islands 17 and 106, but most Bushbuck were in extremely poor condition. The habitat was similar on Island 109, but on the remaining islands there was adequate food when the animals were removed. The status of the habitat reflected in the condition of the animals (Table 25).

Shortridge (op. cit) and Stevenson-Hamilton (1947) indicate Bushbuck associate in breeding pairs or pairs consisting of a female and her latest calf. Fitzsimons (op. cit) gives an example where only one adult ram was flushed with 11 does, but Jackson (1899) cited by Shortridge, considers two or three females per ram is usual in East Africa. Wilson and Child (op. cit) found singles, made up 53 of 74 contacts, and a breeding pair 14 of the remainder. The over-all sex ratio of 39 males to 35 females approached parity, but among adults with all permanent teeth, females outnumbered males by

Table 25.

A Comparison of Availability of Food and Physical Condition in Bushbuck.

Location	Date	Sample	Physical Condition												Status of Habitat.
			Calves			Adult Males			Adult Females			Total			
			G.	F.	P.	G.	F.	P.	G.	F.	P.	G.	F.	P.	
Island 17	June/July 1960	5						2			3			5	Very over-populated
Islands 201/205	April 1961	9			1		2	1		4	1		6	3	Adequate Food
Island 101	March 1961	4					2			2			4		Adequate Food
Island 151	June 1961	1					1						1		Adequate Food
Island 106	June 1961	11						2			9			11	Critically over-populated
Island 107	June 1961	15			1		1	5			8		1	14	Over-populated
Island 109	June 1961	3									3			3	Over-populated
Islands 111/113	June 1961	6			1			1		3	1		3	3	Adequate Food
	TOTAL	54			3		6	11		9	25		15	39	

G = Good condition
F = Fair condition
P = Poor condition

19 to 15. These authors show that females which had not replaced the deciduous teeth, but had well grown third molars were sexually mature, while rams probably did not reach maturity until tooth replacement was complete. Their sample would, therefore, give 15 mature males with 25 mature females (60 males:100 females).

A sample of six Bushbuck from the Cewali Tsetse Area all had permanent dentition and included four females and two males. There were 18 males and 19 females shot in the Nagupande between October 1962 and November 1963, so that it appears that Bushbuck populations contain about equal numbers of males and females, although mature females outnumber mature males.

An analysis of the sex ratio of Bushbuck from 62 islands or groups of islands, from which the whole population was apparently removed, gives a total of 269, including 76 rams and 152 (50:100) does classed as adults, and 19 males and 21 females recorded as juveniles. Ageing by personnel on the Rescue Unit was based on size (p. 17),so that an unknown number of young animals of either sex may have been classed as adults, but it is unlikely that any adult would have been recorded as a juvenile.

There were only six islands where males outnumbered females, on four of which two rams were with a single doe, while on the other two, there were four males and two females, and five males and three females. Adult females outnumbered adult males at 16 localities, but on seven islands there was a single breeding pair. The greatest predominance of females was on an island where there were eight with a single ram, while on Island 106, there were nine females (all sexually mature) with two mature rams.

A comparison of the sex ratios obtained from Tsetse Control Hunting, with those on islands, indicate a lower proportion of males at Kariba. Whether this difference was induced by the abnormal conditions at Kariba or not is open to some doubt, as few Bushbuck carcasses were found and the discrepancy was also apparent on islands with adequate food. On the other hand, it was apparent on Island 106, where two of the oldest carcasses were rams, and on Island 17 the two rams, one of which died, were weaker than the three does. Whether prevailing conditions during the formation of Lake Kariba led to a shift in the sex ratio of the population or not must, however, remain in abeyance until the behaviour of Bushbuck populations under adverse conditions is understood better. Nevertheless, these shifts, if they did in fact occur, were not as clearly defined as in Baboon, Impala or Buffalo.

Little is known of the breeding biology of Bushbuck, but it seems that there was a very high juvenile mortality on islands. Three young, less than three quarters grown, were handled by the author in a sample including 34 full grown females (9 young : 100 females) while Wilson and Child (op. cit) obtained 20 juveniles about this size or smaller with 25 mature females (80 : 100 females). The hiding of young, which could more easily be overlooked in a game elimination scheme than on islands, makes this difference even more significant.

Shortridge (op. cit), quoting several authors, suggests that except for the coastal regions of South Africa, Bushbuck calve mainly in summer (September to March), which would reduce the number of very small calves expected on islands, but Ansell (1960a) and Wilson and Child (op. cit) found breeding throughout the year in Zambia, and Brand (1963) recorded births in all months of the year, except February, in the National Zoological Gardens of South Africa.

The low calf ratio can be attributed to post natal losses as at least three Bushbuck were born on islands, on two of which food was scarce, and all six females which died on Island 106 were pregnant. Four foetuses from over-populated islands in this area weighed between $1\frac{1}{4}$ and $6\frac{1}{2}$ lbs., and at least nine of 16 other females were gravid, the majority of which were very thin.

Thus Bushbuck are more or less solitary, predominantly browsers, which appear to calve throughout the year. The over-all sex ratio tends to parity between the sexes, but females predominate in older age classes. They are accomplished swimmers which entered the water readily, but became marooned on islands at Kariba on account of their localised habits. Food became critical on several of the islands affecting primarily the juveniles, but although there was a lower proportion of males on islands than has been recorded in other samples, its cause cannot be gauged until more is known about Bushbuck populations under stress.

19. KUDU

Kudu, Tragelaphus strepsiceros Pallas, occurred throughout the Kariba Basin, where 153 were removed from islands before the end of June, 1960. This represented 4.1% of the mammals rescued, which was probably lower than their actual proportion in the fauna, because of their movements to and from islands.

A. Response to Flooding

Kudu were intermediate between species which became marooned on islands and those which swam to islands freely to feed. They were among the first to take to water when men landed on an island and only six of 35, whose capture was observed, were caught on land, and these included three small calves. There were 17 Kudu on Island 17, but they disappeared following the first game drive in which a very young calf accidentally tangled in the game nets. Spoor showed where the group, including two other small calves, had entered the water and swum over a mile to the mainland. It was interesting that young calves could swim this distance, although it was not remarkable that older females and juveniles did so, as Junor (1960) records them swimming 1½ miles. He rightly points out that Kudu are strong swimmers, which can easily outpace a man, although adult rams are handicapped to some extent by the weight of their horns.

It is not surprising that Kudu took to the water readily, as they will do so to avoid Wild Dogs and, according to Shortridge (1934), may do so when followed by Domestic Dogs.

Kudu moved back and forth between an island and the mainland during 1960 and early 1961, but did not become trapped on the island, which was never over 200 yards from shore. In 1960, there was a reasonably well developed soak zone with green vegetation, that may have attracted them in September and October, but in the following June the vegetation on the island was similar to that on the mainland. Junor relates a similar example of Kudu moving to an island, apparently to feed, and Parnell (1963) actually witnessed this behaviour, and yet Kudu became marooned on islands as feeding conditions deteriorated.

Little is known of their seasonal movements and evidence from Kariba is not conclusive, but 20 of 22 which took to water readily, did so over the most recently submerged land between two islands. The partially submerged vegetation around these islands was similar in all directions and alternative land was seldom visible through the trees, so that the behaviour resembled that of a localised group, observed with Riney, in the Wankie National Park. This group of six Kudu was recognised by its individual markings and followed the same devious route when crossing a vlei in the dry season, as they used to avoid shallow depressions which held water for a few months during the rains. Riney kept this herd under regular observation for over 18 months, during which time it was contacted only along one particular stretch of road 0.6 miles long. This is supported by observations on the recapture of 10 tagged Kudu. Two adult females, whose release point was not very accurately defined, were recaptured on an island which formed within two miles of the release point six months later, by which time about half a mile of the intervening distance had been flooded. Two females, one adult and one half-grown, were retaken after 21 months within 1½ miles, of which three-quarters of a mile had been submerged, and three adult females had been marooned for a second time within three miles of the release point, after 20 months. An adult female and two adult males were recaptured after 10 months within 3.75 miles, of which 1.25 miles was submerged. The last were on very big islands and may, in fact, have moved less than half a mile of their own accord.

If Kudu are localised, their tendency to leave islands such as Island 17, which necessitated a swim of over a mile, indicates that in the Kariba Basin they were either less localised than the group at Wankie, or they can be shifted from their home ranges more easily than most other ungulates discussed so far. The readiness with which Kudu took to the water and their ability to swim long distances, make it unlikely that they would be affected by the gradual flooding of an area, unless they became trapped on islands some distance from land. This distance would depend largely on the position of the island in relation to their former home range.

B. Behaviour on Islands

Kudu were found on only one island where they were critically short of food. This resulted from their tendency to leave islands when feeding conditions deteriorated too much, and because they were the tallest browsers found on most islands. Wilson (1965) has described how this species, which feeds almost exclusively on browse from a variety of plants, attains maximum reach by standing on its hind legs. This was borne out on Island 17 by the patchy browse lines eight to 10 feet from the ground on *Erythroxylum zambesiacum* and *Holmskioldia spinescens*.

These were the only two species which showed marked signs of Kudu browsing and both were taken readily by a captive calf which refused *Combretun apiculatum*, *Terminalia brachystemma* and *Colophospermum mopane*. The condition of the Kudu on this island was not assessed, unfortunately, before they disappeared, as one Kudu per 6.7 acres was the densest concentration found. Haslam counted 49 Kudu in mid-1962 on Ukubula Island, before habitat conditions deteriorated. By December, 27 of 28 animals, whose condition was gauged, were in poor condition and seven carcasses were found. The latter consisted of five females and one male with fully adult dentition and a second male with permanent incisors, but otherwise all deciduous teeth. Some of the youngest animals had been removed from the island, but those remaining included a fair proportion of sub-adults, most of which were estimated to be in their second or third year.

A large proportion of Ukubula Island had been bush cleared and much of the vegetation was not over nine feet tall. Below five feet, there was a well marked Impala browse line, so that Kudu were limited to the vegetation between these two levels, where they experienced competition from Buffalo.

Two Kudu were in poor condition on Island 21, but neither was fully mature, and this applied to the three of four females classed as poor on Islands 11 to 13. But on islands 201 and 204 to 207, seven of 13 Kudu were in fair condition. These included six females and a male, of which three females and the male were mouthed and found to have all permanent teeth. The seven in poor condition included four small calves, three with the first molar erupting, a juvenile with M_2 just cutting the gum and a female with adult teeth. This indicated that condition on these islands, where there was no sign of over-browsing, was largely determined by age.

There was apparently little change in the sex and age class composition in the Kudu sample found on islands, which was as to be expected from their swimming ability and the species' habit of moving to and from islands. Of 119 sexed Kudu rescued before the end of June 1961, 84 were females and 35 males (42 males : 100 females). These included 17 males and 66 females (26 males: 100 females) classed as adult in Rescue Reports, 16 males and 15 females (107 males : 100 females = parity) recorded as under three-quarters grown, five animals whose ages were not noted, and one very small unsexed calf. A collection of 133 skulls from the first 13 months of hunting in the Nagupande Tsetse Area, gave 75 females and 57 males (76 males : 100 females), but among adults with all permanent teeth, there were 50 females and 29 males (58 males : 100 females), while in juveniles with the second molar erupting or younger, there were 11 males and 13 females (85 males : 100 females).

There was a significantly higher proportion of males in the Nagupande sample ($Chi^2 = 10.22$, $P>0.01$), but Wilson (1965), who obtained 86 males and 72 females (119 males : 100 females), concludes that Tsetse shooting tends to select for males, as hunters usually shoot only one animal from a group, and males generally associate in smaller groups. Further, there was evidence of little increased juvenile mortality at Kariba and calves would be expected to be more susceptible than adult males. The calf ratio recorded at Kariba was 31 to 84 (37 : 100) females of all ages, whereas there were 24 young calves with basal skull lengths up to three-quarters of that of adults of their respective sexes, and tooth formulae up to M_2 erupting, at Nagupande, in a total sample of 75 females (ratio 32 : 100 females). Calves with skulls about three-quarters the length of those of adults are relatively small and would probably have all been classed as calves in Rescue Reports, so that the similarity between these two samples is good evidence of normal losses on islands.

This evidence suggests Kudu populations generally predominate with females, and that this becomes more pronounced in older age classes, so that in the light of present knowledge, there was little to suggest shifts in sex or age structure of the Kudu sample from Kariba.

20. ELAND

Eland, Taurotragus oryx Pallas, were contacted in small groups between Chete and the Umniati River, but none was marooned on an island before the end of June 1961, although Dr. H. H. Roth (pers. comm) reports a herd with young calves, which became isolated in the Sengwa Basin in 1963, over eight miles from the Zambezi River. Little is known of this species' movements in Rhodesia, although they are probably quite extensive, judging by the way groups of a few to over 100 appear and disappear from an area. Eloff (1959 a and b, and 1962) suggests they are nomadic in the Kalahari Gemsbok National Park in South Africa, but recognises the need for prolonged observations of recognisable individuals to determine whether or not their movements follow a regular pattern.

Benson (1960) gives an observation in Zambia, where for several successive days, an officer of the Game and Fisheries Department witnessed Eland move out more than two miles in the morning, only to return in the evening. This represented only a part of each day's movements, but if Eland wandered to this extent in the Central Zambezi Valley, they would tend to have moved off most islands as they were forming. This was supported by fresh spoor and droppings on three islands, which were visited within a week of their separating from the mainland.

21. BUFFALO

Buffalo, Syncerus caffer Sparrman, were common on the southern shore of the Lake east of the Masumo River and became very conspicuous in bush clearings between the Sibilobilo and Umniati rivers, where there were several herds of over 200. Only nine were recorded on six islands worked before the end of June 1961, although they were also known to be marooned on Sampakaruma Island where, judging from spoor, there was a fair number. Later in 1961, however, a herd of about 20 to 30 were found on Island 100 and about 200 became marooned on Ukubula Island in 1962. This herd was observed in December 1962 after a number, mostly juveniles, had been rescued, and 71 mandibles of the surviving animals, which were shot in June 1963, were forwarded to the author by special arrangement. These were accompanied by flesh measurements and the sex of the specimen.

A. Response to Flooding

There were apparently two reasons why so few Buffalo were found on islands. Little is known of their seasonal movements beyond the fact that they range over fairly large areas (a marked Buffalo, released from Ukubula Island, killed an African some 15 to 18 miles from its release point about two years later, Mr. P. Coetsee pers. comm.), and while doing so numbers appear to fluctuate as groups break away and reunite. Apart from the small groups which appear to have been composed entirely of old males, Buffalo occurred only on large islands derived from large areas. Ukubula Island arose from between 24.8 and 29.5 square miles; Island 100 from 25.9 square miles and Sampakaruma Island from 7.9 square miles, which separated from the mainland very quickly. These areas may have exceeded the home ranges of the Buffalo, but suggest movements are extensive. Large herds often moved up to three miles across portions of clearings in the space of an afternoon, so that there was little chance of their being trapped on any but the largest islands.

A less important reason for the few Buffalo found on islands was the readiness with which they took to water and swam to the mainland as islands diminished in size, although there is no evidence of their having swum to islands. With the exception of an animal shot in self defence, all the smaller groups behaved in this way although, like Elephant and Rhino, they never did so while humans were present. This applied to the herd on Island 100 even while a number were run down on foot, and on Ukubula Island, five were drugged and 34 were captured from a Land Rover after extensive chases, spread over two weeks, before the first animal took to the water.

This behaviour was probably due to their vulnerability in the water, which is borne out by four reports of high casualties when herds have been stampeded into a river by a predator. On the other hand, when unmolested, they were strong swimmers. One was observed to swim over two miles from an island to the mainland, by personnel employed on bush clearing operations, and two others swam 1½ miles and one mile respectively. The only drowned Buffalo found by the Rescue Unit was trapped in thick Salvinia.

Gradual flooding would probably have little effect on this species unless large areas were affected. They would either move away or swim from islands on which they became isolated. This is borne out by the absence of recorded losses in the Zululand Game Reserves during the 1963 floods (Natal Parks Board Records).

B. Behaviour on Islands

Buffalo left most islands before food became critical but, on Ukubula Island, there was a marked decline in physical condition ending in 47 deaths between mid-November and mid-December, at the end of the 1962 dry season, when the island was severely overstocked. The Buffalo trapped on the island are broken down by sex and age classes in Table 26, depending on whether they were rescued or survived the population crash, when 36.4% of those on the island died.

The sample is aged according to the state of tooth eruption. Sixty calves were rescued late in 1962 for restocking other game areas in Rhodesia, of which six were examined by the author, including two females considered too big for restocking purposes. Four males were 90 cm at the shoulder, had hind feet measuring 483 to 486 mm and all deciduous teeth, with the first molar erupting. The two females were 30 cm taller, had hind feet of 535 and 544 mm and all deciduous teeth, but the molars could not be examined. A female shot in June, however, had a hindfoot of 545 mm and the second molar in an early eruptive state, so that it was safe to conclude that none of the calves removed from the island was older than those with M_2 erupting and they were, therefore, placed in Class 1.

The remaining sub-adults were divided into Class 11, which were older than Class 1, but still had all their deciduous teeth, or Class 111, in which permanent tooth eruption was in progress. Class IV included specimens with fully permanent dentition.

In Table 26, there is a slight tendency towards males in Class 1, but a greater number of females in Class 111 or older, where there were 50 males and 72 females. There were 160 Buffalo on the island, when the first died of starvation, of which 31 calves were removed during the following two weeks. Of the remaining 129, 45 died of starvation and two calves were stillborn at the end of 1962, and 84 survived until June 1963, when 71 were shot. These do not include five calves born after mid-December and omitted from further discussion on population changes, as they were not confronted with the 1962 dry season.

In these two samples there were seven small calves, two of which died, while two others died at birth, but it is probable that a much higher proportion of calves would have died had 60 not been rescued, as those left on the island probably included the strongest and most difficult to catch. Three of the six (50%) Class 11 and and 39 of 50 (78%) Class 111 animals survived, but only 28 of 57 (49%) fully mature animals lived. This showed a definite shift in favour of Class 111, mainly at the expense of Class IV.

Table 26.

Population Structure and Fate of Different Sex and Age Classes of Buffalo on Ukubula Island

Age Class	Removed Before Population Crash				Died				Survived				Total			
	M.	F.	?.	Total	M.	F.	?.	Total	M.	F.	?.	Total	M.	F.	?.	Total
I	34	25	1	60	2		2[i]	4[i]	3	2	3	8[ii]	39	27	6	72[iii]
II					2		1	3	1	2		3	3	2	1	6
III					6	2	3	11	16	23		39	22	25	3	50
IV					3	26		29	11	14	3	28	14	40	3	57
Full grown, i.e. III or IV but not separated	10	3[iv]		13					4	4	2	10	14	7	2	23
TOTAL	44	28	1	73	13	28	6	47	35	45	8	88	92	101	15	208

M = Male
F = Female
? = Sex not recorded

i) 2 Calves born on island
ii) 5 Calves born on island after crash
iii) 7 Calves born after sampling began
iv) Includes one female which swam from the island.

This shift in age structure, due to starvation, resulted largely from the heavy die-off, amounting to 65%, in Class IV females and small losses, 8%, in Class 111 females. It was also noticeable that tooth wear was generally less marked in the Class IV female survivors, several of which had only just completed tooth replacement. On the other hand, there was a slight tendency for old males to survive better than those in Class IV, although this was less marked and, at this level of sampling, was not statistically significant. It was, however, apparent in December that some of the biggest bulls were more alert and in generally somewhat better condition than the rest of the herd.

The sex ratio in Classes 111 and IV changed from 36 males and 65 females to 27 males and 37 females which, although not statistically significant, showed the same trend towards a higher proportion of males which Christian et al (1960) and Woodgerd (1964) found for islandic populations of Sika Deer, Cervus nippon Temminck, and Big-horn Sheep, Ovis canadensis Shaw, respectively, when the habitat became saturated. The relative proportions of Class 111 male and female Buffalo involved in reproduction might make this trend more pronounced as, in most bovids, females mature earlier than males.

The most significant shift in population structure, however, concerned sexually mature females, which apparently form the core of Buffalo herds, as this favoured younger animals with a longer potential reproductive life ahead of them. If numbers are reduced during a catastrophe, this mechanism would favour a rapid regeneration of the herd when conditions improve.

The limited calving observed on the island may have favoured mature females in general and, therefore, the younger adults in particular. Two calves died at birth during the population crash and only five were born to 41 (12 : 100) Class III and IV females early in 1963. There is little data on breeding and calving rates in Buffalo, but Asdell (1946) suggests an extended season with most births between September and March in South Africa. Thus, the low number of calves born between September and mid-December indicates an interruption in normal breeding, which is supported by the small number of calves born on the island compared with 64 Class 1 animals : 72 Class 111 and IV females (88.6 : 100) or, if all the unsexed adults were females, 77.7 : 100, when the herd was first marooned. To have been born by early 1963, calves would have been conceived early in 1962 (gestation period 11 months, Kenneth and Ritchie, 1953), before feeding conditions had had time to deteriorate too far, so that pregnancy failure seemed the most likely cause for the low number of calves. These embryos would have been about half term when food became critical, which is the stage in development when the foetus begins to compete with the mother for nutrients (Hammond, 1960).

DISCUSSION

The behaviour of large mammals during the marked habitat changes associated with the construction of Kariba Dam, demonstrated some characteristics of species native to the Central Zambezi Valley. Observations relating to the spreading out of Lake Kariba and the readiness with which a species took to the water, or their relative swimming ability, have limited application, although Kennerly (1963) has indicated the importance of swimming for ensuring gene exchange between the two parts of a population separated by a perennial river. Other information is of more general interest.

Species which were readily trapped on islands generally had localised habits and would, therefore, be more sensitive to local catastrophes such as food shortages or flooding of their habitat, than those with greater home ranges, including forms which moved freely to and from islands or did not become marooned at all.

The rapid over-population on some of the islands led to a marked decline in habitat resources, which facilitated the observation of behaviour of the animals under conditions of stress, although it is unlikely that their behaviour differed basically from that of free ranging populations under adverse conditions. For example, it would be expected that limited space would elicit the same type of aggressiveness between individuals which occurs normally, but on a somewhat exaggerated scale.

This discussion deals with three main topics : (a) the fauna of an area of typical mopane veld in the Zambezi Valley and its animal density compared with other areas; (b) observed relationships between a number of species; and (c) mechanisms that assist some populations to regain their numerical strength as quickly as possible following food shortages.

1. THE LARGE MAMMAL FAUNA OF AN AREA OF MOPANE VELD

Mopane veld dominated the Kariba Basin and is widespread in many good game areas in Rhodesia. This description is of an area on the east bank of the Bumi River and falls within Region VA of Vincent and Thomas' (1961) agricultural land classification of Southern Rhodesia. This is the second lowest category recognised, exceeding only Region XX, which they consider unsuitable for any form of agriculture.

The area was in flat country where slight undulations governed the pattern of flooding and determined its extent, thus eliminating human bias in selecting its limits. It was chosen for its uniform habitat and because it was one of the few large areas, in which game became marooned, for which there is an accurate tally of numbers.

Islands 17 and 18 and a number of islets (Fig. 7) arose from 15 square miles and were cut off in February 1960, at the height of the rains and just as the Lake level began to rise rapidly for the season (Fig. 12). The separation, which was rapid in this flat country, was further ensured by thick Salvinia which soon developed, and took place when there was the maximum food available to animals which became marooned. The pattern of flooding was such that about half the original area gave rise to Island 17, so that animals listed in Table 27 may be taken as originating from 7.5 square miles (± 0.2 square miles).

Chance may have determined which side of a depression animals happened to be when water backed up and so, initially, whether they were isolated in the whole area or, later, on Island 17. Similar objections apply to any census method based on a single series of observations in a sample area, which is all that most authors, with the notable exception of Lamprey (1963), have been able to achieve. The objection in this case is largely answered by the fact that, apart from Zebra, all important species on Island 17 were also marooned on Island 18 and other adjacent islands. Animals which became trapped on islets around Island 17 can be ignored, as none had more than the odd Grysbuck or smaller species on them, which is not surprising for, as noted in the species accounts, most animals did not become marooned in such small areas.

The vegetation was uniform mopane woodland, with scattered Commiphora trees and scrub thickets, especially on Island 17 (Fig.10) where the vegetation achieved its greatest complexity. Rivers were flanked by a thin riparian fringe, chiefly Acacia spp, and there were a few small intrusions of open scrub savannah along the Makuzapela River, too limited to detract from its being typical of good mopane veld in the Zambezi Valley. Settlement was very light in the region (Fig. 11), so that there was very little disturbance, apart from occasional signs of a light, primitive shifting agriculture. Occasional fires from outside may have modified the vegetation slightly, but effects of domestic stock were limited by the presence of tsetse fly, so that the area was almost undisturbed by humans.

Similar habitat on the adjacent mainland was in a healthy state with no signs of over-population or veld deterioration, indicating that the animals found in this area represent those of undisturbed mopane veld. This basic information is difficult to obtain in Rhodesia because of widespread human influence, which may cause animal populations to increase or decrease (Riney, 1964a).

The animals found on Island 17, and their original stocking rates, are listed in Table 27 where two alternatives are given for Zebra, which probably occupied most of the original 15 square miles, as this gives a similar density to that found in an area on the opposite bank of the Bumi. Elephant, Buffalo and Waterbuck were known in the area, but did not become marooned, and Eland occurred just beyond its limits. Others in mopane veld within 10 miles of the island, excluding small mammals, were Leopard, Lion, Honey Badger, Wild Cat, Side-striped Jackal, Hippo, Klipspringer and Sable. This gives 26 species, the size of a Jackal or bigger, including two large cats and 16 large herbivores. Dasmann and Mossman (1962,b) also obtain 16 species of herbivore on Doddieburn Ranch, where the habitat is also predominantly mopane veld, although their spectrum of species was slightly different. They include Giraffe, Wildebeest and Steenbuck, whose geographical ranges do not extend into the Kariba Basin, but had no Sable, Hippo or Rhino which have, apparently, been exterminated on the ranch.

It was interesting that such a wide range of large mammals, particularly large herbivores, was found, at least occasionally, in one small area of mopane in the Zambezi Valley. Classifying mammals as large, medium or small is, at best, an arbitrary process and it is often not certain whether authors include all the large species in an area, but nevertheless Table 29 shows mopane habitat supports a considerable number of species, even when compared with more diverse habitats. Klipspringer are dependent on rocky outcrops, but all the other species make some use of the general vegetation.

Eight herbivores trapped on Island 17 were resident within 7.5 square miles and this applied to Zebra in 15 square miles. The density figures in Table 27 are low, as they do not include animals which died and whose carcasses were lost, particularly those of young Wart Hog and Impala. Nevertheless, these losses would not account for the density being only about a third of that described by Dasmann and Mossman, when their Buffalo, Eland and Waterbuck are excluded. It is interesting, however, that their figure of 42 Impala per square mile was similar to that obtained at Kariba, both of which are very much lower than the 200 per square mile they calculated near Fort Tuli, where Impala are severely overstocked. They found Impala, Zebra and Wildebeest were the dominant species in the south western lowveld of Rhodesia, but Wildebeest become much less numerous towards the east, where Kudu are plentiful in some areas. In the Zambezi Valley, there are no Wildebeest and Zebra are relatively scarce (Table 1), but Wart Hog numbers are much higher than in the south, where they are not especially common.

Klipspringer and Hippo were uncommon in mopane veld in the Kariba Basin and Sable favoured open scrub savanna, probably seldom

Table 27.

The Original Density of Mammals Marooned on Island 17.

Species	No. on Island	Animals/Sq. mile.
Monkey	2	0.27
Baboon	79	10.53
Pangolin	1	0.13
Genet Cat	1	0.13
Aardwolf	1	0.13
Hyaena	5	0.67
Antbear	4	0.53
Rhino	3	0.40
Zebra	41	2.74) 5.47)
Bush Pig	18	2.40
Wart Hog	77	10.27
Duiker	7	0.93
Grysbuck	6	0.83
Impala	298	39.73
Bushbuck	5	0.67
Kudu	17	2.27
Hare	1	0.13
Porcupine	1	0.13
TOTAL	567	75.60 - 72.81
Large Herbivores	472	62.81 - 60.27

lingering in mopane, as this was their habit in the Nagupande Area, where they favoured open woodland on Kalahari sands. Elephant, Buffalo, Waterbuck and probably Eland, used Island 17 for part of the year, but had ranges which extended beyond its limits. Excluding these species, the biomass of all the species recorded in Table 27 was over 8,100 lbs per square mile (Table 28), of which large herbivores contributed c 7,700 lbs. These figures are conservative as they make no allowance for the lost carcasses and are based, as far as possible, on weights obtained at Kariba, where many animals were in very poor condition.

The weight of animals on Island 17 is related to that from other areas in Table 29. Such comparisons are rough, for as others (Stewart and Zaphiro, 1963: Lamprey, 1964) have noted, there is little standardisation between the methods used by different workers and no allowance is possible for populations being at different stages in eruptive cycles, such as those described by Riney (1963,a). The comparison does, however, indicate relative differences in the amount of game recorded in different vegetation types, suggesting that mopane, which has hardly been disturbed, can carry reasonably large game populations, and this is significant in view of its low assessment for agricultural purposes. It is also interesting as mopane veld is relatively uniform with few associated plants and mopane, which is leafless for several months of the year, was itself eaten by few animals, even when they were starving on islands. It may, therefore, be significant that chemical analyses of grass samples from the Luangwa Valley, carried out on behalf of the Zambian Game and Fisheries Department (Anon. undated), show that some annual species retain a higher food value in the stems during the dry season than perennials, whose energy reserves are in the root.

Dasmann and Mossman's (1961) figures for the Henderson's ranches give an ungulate biomass of c 25,100 lbs per square mile on an area characterised by "open mopane woodland", devoted entirely to wild animals. If non-residents in the Island 17 area are deducted from their figures, by reference to Dasmann and Mossman (1962,b), the figure is reduced to c 23,800 lbs or about three times that on Island 17. They ascertained populations by means of road strip counts (Dasmann and Mossman, 1962,a) and, although they made no allowance for the possible attraction of roads towards game and calculated the width of the strips from the vertical distance from sighted animals to the centre of the road, instead of the longer diagonal distance to the animals from where they were first seen, they are satisfied that their figures are conservative. In any case, there is little doubt that, in spite of a lower rainfall (c 20 inches a year), the ranches supported a substantially higher weight of animals than the area around Island 17.

Table 28. The Biomass of Large Mammals Marooned on Island 17.

Species	Number	Total wt. lbs.*	Biomass lbs./sq. mile	% Biomass	Basis of weight calculation.
Impala	298	24,430	3,258	40.1	186 Ad.+ Yr.F, 84 Ad.+ Yr.M, 5 Ad.?, 23 calves at 80.2, 93.2 and 54.5 lb. av. of 79, 28, 29 at Kariba.
Zebra	20.5	13,535	1,805	22.2	1/2 wt. of 41, 37 Ad. and 4 foals at 710 lb. per Ad.(av. wt.17 in N.M) & 200 lb. per foal, estimated.
Wart Hog	77	8,375	1,117	13.7	34 Ad.+ Yr.M, 35 Ad.+Yr. F, 3 Suck. at 118.8, 112 & 34.8 lb. av. of 12, 26 & 2 at Kariba.
Rhino	3	5,000	667	8.2	2 Ad.+ 1 juv. at 2,000 & 1,000 lb (Child & Fothergill, 1962)
Kudu	17	4,885	651	8.0	Av. wt. of unselected sample of 12 F. & juvs. from Chipinda 287.4 lb.
Baboon	79	2,120	283	3.5	Av. wt. of 11 of all ages from Island 17, 26.8 lb.
Bush Pig	15	700	93	1.1	6 Ad. 4 juv. 7 suck. at 116.8, 90, 30 lb. av. of 7 Ad. 4 juv, at Kariba. suck. estimated.
Hyaena	5	640	85	1.1	5 at 128 lb. wt. of Ad. F. collected by author.
Antbear	4	440	59	0.7	4 at 109.4 lb. av. 5 at Kariba.
Bushbuck.	5	410	55	0.7	2 Ad.M, 3 Ad.F at 108.7 & 65.2 lb. av. of 6 & 6 at Kariba.
Duiker	7	245	33	0.4	7 Ad. at 37.7 lbs. av. wt. 58 Ad. Cewali.
Grysbuck	6	120	16	0.2	6 Ad. at 20 lb. p.16.
Porcupine	1	35	5	0.1	1 Ad. av 2 at Kariba.
Aardwolf	1	20	3	-	1 Ad. av. 2 in N.M.
Monkey	2	20	2	-	2 at 9 lbs. av. wt. 6 (Head+Body >17 ins.) at Nagupande.
TOTAL			8,130*	-	

N.M. = National Museum, Bulawayo. Ad.= Adult, Yr.= Yearling, juv.= juvenile, M=Male, F=,Female, suck = suckling.

* Weights to the nearest 5 lbs.

Although the habitat on the ranches is chiefly mopane veld, parts have been greatly modified through human occupation. Water has been manipulated by the construction of dams and there are clear signs of misuse in the form of scrub encroachment and deteriorating grassland, with trampling particularly severe near the water. This trampling is now caused by game, which is certainly too numerous to allow the habitat to heal, although the original cause of the trouble was probably the mis-management of domestic stock. The result has apparently been an increase in animals, but a decrease in species, with the extinction of Sable and Reedbuck, both grazers of healthy grassland.

Riney (1964,b) has described the sensitive nature of mopane veld to the mis-management of fire and domestic stock and, in another paper, (Riney, 1965) has shown that the time lag between cause and effect may take decades to become abundantly obvious, by which time reversal of the trend may be difficult to achieve. These observations indicate that stable mopane can support a reasonably dense and varied game population. Practices detrimental to its long term stability may increase the standing biomass temporarily, but lead to a decrease in the range of species. It would be interesting to know whether this is triggered by disturbances increasing annual grasses at the expense of perennial species, for, as Riney's work shows, mopane is sensitive to this change, which would make its proper management very critical.

2. INTER AND INTRA-SPECIFIC RELATIONSHIPS

Extreme over-opoulation on islands accentuated competition between animals of the same and different species and, to a limited extent, the effects of predation on prey populations. Naturally, relationships varied with the species present and with their relative numbers, and, as to be expected, intra-specific competition was more pronounced than that between species. Under these critical conditions, however, it was possible to gauge the maximum extent of certain relationships between species.

A. Competition for Food

The critical food shortages on Island 17 in June, 1960, forced animals, most of which were in very poor physical condition, to eat any available food plants, thus reducing the effects of different food preferences discussed at length by Lamprey (1963). The first adult deaths on this island were among Baboons and Impala. The latter, as noted, contributed the greatest biomass (40%) and had defoliated most plants to a height of 60 inches. Impala deaths were due almost entirely to intra-specific competition.

Competition from Impala resulted in critical food shortages for most other species. Kudu could reach above the Impala browse line and enhanced this by standing on their hind legs, but they generally swam off islands before food became too critical. This also applied to Waterbuck and Elephant, both of which were known to have returned to over-populated islands after the animals had been cleared and the vegetation allowed to recover.

Bushbuck, on the other hand, were very localised and starved on Island 17, where they made up only 0.7% of the total biomass. It was surprising that they were never recorded standing on their hind legs, as by doing so they could have reached above the Impala browse line, and this behaviour on Island 106 led to the removal of all food to a height of 66 to 69 inches before the population starved. They did, however avoid some competition by feeding in the shallows, where the vegetation was protected from Impala. Grysbuck and Rhino also did this and the latter were able to obtain food above the browse line by breaking down branches.

These observations emphasise the importance of special anatomical or behavioural characteristics for the survival of a species faced with direct inter-specific competition for the same food plants. Duiker, which are chiefly low browsers, were shorter than both Impala and Bushbuck, but remained in relatively better condition, in spite of the virtual absence of forbs and other low browse on Island 17. This is obviously a very hardy little species which no doubt accounts for its widespread success throughout much of Africa.

On this island, shortages of Grysbuck food were due mainly to Impala, although on Island 110 it was attributable solely to Bushbuck.

Wart Hog and Bush Pig rooted extensively on Island 17, where the latter remained in reasonable condition while the former starved. This may have been partly due to the differences in their respective numbers, but the main reason seemed to be the use Bushpig made of carrion, which Wart Hog seldom touched, in spite of their being known to eat dead animals.

Zebra remained exclusively grazers, apart from occasional fragments of dry leaf taken in error, and experienced competition for any available grass with most species on the island. It was remarkable that, with their high biomass (22.2%), they survived so long. The possession of upper incisors enabled them to bite off the few tufts of perennial grass shorter than other species, but the main reason seemed to lie in their use of dead trampled annual grasses.

Baboons competed very little with other species for food as, when they began eating leaves and bark, they took mostly mopane, and starvation resulted from competition between themselves.

Collias (1944) stresses the importance of the peck-order dominance in vertebrate animals, especially during adverse conditions, for determining which individuals succeed in obtaining food, a mate or a territory, so that it was surprising that no aggression was observed between undisturbed Impala outside the rutting season. This applied even when individuals were dying and yet seven penned calves attempted to "horn" each other, particularly while feeding, and this behaviour was performed with equal intensity by the hornless females as by the horned males.

There was also very little aggression noted between members of other species, while feeding, although Wart Hog competed with each other to a limited extent for suitable burrows. This even applied to Baboons, in which there was a general breakdown in the social organisation of troops, which is discussed further on pp. 119 and 122.

The pushing down of trees by Rhino was beneficial to other species and leaves seldom remained long on these branches, and, as noted (p.55), an Impala, a Bushbuck and a Grysbuck were seen feeding on food brought within reach, in spite of the Rhino's attempts to drive them away. This was the only case of aggressiveness recorded between species while feeding, although the Impala calves attacked humans in their pen, once they had become accustomed to them, in the same way as they butted each other, and an adult Bush Pig charged and forced a full grown Wart Hog to yield during a game drive.

It is perhaps surprising that so little aggressiveness was shown between species and individuals, including species like Rhino (p. 126), when animals became crowded into small areas where food was so critical. Lamprey (op. cit) noted that under less severe conditions species which tended to compete in the same habitat, associated peacefully in mixed groups and observations at Kariba suggest this is generally the case among large mammals, although there are obvious exceptions, such as when Elephant chase Wildebeest, Buffalo or Giraffe. This is very different from the aggressiveness shown between different species of birds feeding on a rich source of food (see for example Petrides, 1959, and Child, 1964,b), or when birds of the same species feed together.

Deaths from competition were all attributable to starvation as, with one exception, carcasses had very depleted fat reserves. This exception was the Bushbuck which, although it had no back fat and very poor red watery bone marrow, had a kidney fat index of 89.

Christian (1950) describes a stress syndrome which causes death and inhibits breeding when animals became too crowded, even if there is adequate foot. Christian <u>et al</u> (1960) correlated the mass mortality of an islandic herd of Sika Deer, when the population reached one animal per acre, with over stimulation of the adrenal glands and found no indication that the die off was due to food shortages, as animals still possessed reasonable amounts of fat. Impala reached a density of over one animal per half acre on Island 17 without interruption to the breeding cycle and it seemed unlikely that stress, due to over-crowding, caused losses in this species, as greatly depleted fat reserves pointed to plain starvation. This also applied to Bushbuck on Island 106 and many species calved on over-populated islands. Some stress factor may, however, have inhibited breeding in Baboons and Buffalo, although losses in these two species also resulted from starvation.

B. <u>Predation</u>

There were a few observations of the relationships between large mammal predators and their prey. Lion were noted on three islands containing reasonably sized groups of Buffalo, and in at least one instance the Lion had swum over 1¼ miles to the island, although once on the island they preyed on other species. The only island where predation was allowed to proceed almost unchecked was Island 21, where a Leopard eliminated all the Wart Hog and most of the Impala before leaving the island after the 11 surviving Impala had been rescued.

As suggested on p.45, it is unlikely that a Leopard would eliminate Wart Hog in an unrestricted habitat with adequate burrows, which, incidentally, highlights the relationship between Wart Hog and Antbear, which was so obvious on a number of islands, as Antbear were absent from Island 21. Further, there does not appear to be an authenticated case of a free-ranging large mammal population being seriously curtailed by predation alone. Even the frequently quoted example (see Allee <u>et al</u> 1961, P.707) of predator control causing an eruption of deer on the Kaibab Plateau, described by Leopold (1943), may have been over-simplification. According to Mr. L. Robinette (<u>pers</u>. <u>comm</u>.), historical records indicate deer were not numerous in the area until it was temporarily over-stocked with cattle, which resulted in improved deer habitat as scrub encroached into grassland. Deer numbers increased and eventually overtaxed the range and crashed during two severe winters. Had predators not been controlled, they may have cushioned the eruption, but it is debatable whether they would have prevented an upsurge, triggered off by marked changes in the habitat.

Wright (1960) considers Baboons may have increased in parts of East Africa due to the heavy poaching of Leopards, but leads little evidence in support of this. Leopold (1950) feels predators are usually well adjusted to their prey, unless man has interfered with the equilibrium, and it is generally accepted that the prey populations benefit from predation (see Allee _et al, op. cit_, p.374 ff). A. Murie (1940 and 1944) and Borg (1962) have shown that predators attack mostly sickly or weak animals and have no adverse effects on the prey, which benefits from the removal of animals which are already doomed. Murie notes that this would tend "to quicken the adjustement of deer (also Caribou, _Rangifer arcticus_ (Richardson), and Dall Sheep, _Ovis dalli_ Nelson) populations to conditions of the range", and Allee _et al_ quote other ways in which predation might benefit populations of animals other than large mammals.

Culling or cropping of large ungulates on a sustained yield basis demonstrates how many wild populations can withstand an increased annual mortality, while Riney (Ms.) and Child and Wilson (1964b) have shown that certain intensities of hunting may stimulate an increase in numbers so that it is reasonable to assume predators could have similar effects under certain circumstances. An analysis of Wright's (_op. cit_) and Mitchell _et al_'s (_in press_) data shows that in East Africa and the Kafue National Park, there was a marked selection for males. Wright obtained an overall sex ratio of 60 males per 100 females in a sample of 67 sexed kills, which are, unfortunately, not broken down by species. Mitchell _et al_'s ratio for 30 prey species was 100 males to 84 females in 254 kills, of which the nine principal species are shown in Table 30, taken with slight modification from their paper. The selection for males is more marked than these results suggest at first glance, as most wild populations predominate with females and Robinette _et al_ (1959), who found that deer constituted 77% of Cougar, _Felis concolor_ (Linnaeus), diet by weight in winter, obtained a significantly higher proportion of males in a sample of 148 winter kills than occurred in the deer population, although the two ratios were almost identical in summer. The tendency to increase the number of females in polygamous species, such as Impala and Buffalo, which particularly concern this paper, would raise the reproductive potential per unit of population in the prey species, thus providing the mechanism for an increase in the population through the removal of surplus males.

Predation of Impala on Island 21, which reduced the herd from about 35 and eliminated all calves and adult males, therefore had two effects. It reduced the population pressure in a restricted habitat, but favoured the rapid re-growth of the prey population if the restriction were removed, by increasing the proportion of sexually mature females. Three yearling males survived and would have matured by the following rut, so that the effects of predation on this island

Table 30.

The Sex Ratio of Significant Prey Species in the Kafue National Park. (After Mitchell *et al*, *in press*).

Species	Sample	Females killed per 100 males killed.
Buffalo	94	63
Hartebeest	77	88
Reedbuck	41	5
Puku	40	122
Wart Hog	33	32
Duiker	25	79
Impala	18	50
Roan	16	60
Sable	14	133
	Average	70.2

the long term maintenance of species in marginal areas subjected to periodic shortages of habitat resources due to fluctuations in rainfall.

Changes in population structure may arise through a higher mortality of some sex or age classes, through the suspension of breeding activity or pregnancy failures, or a combination of both. Selection favouring these changes might be expected to have a greater effect on gregarious species where the herd and not the individual, or breeding pair, is the basic unit of the population and would depend to some extent on the individual species' sociology. It was, therefore, not surprising that the greatest shifts in population structure found in samples faced with extinction occurred in the most sociable species.

Among Baboons, there was a breakdown in the social organisation of troops leaving a residue of old sub-adults or young sexually mature animals. This was caused by a cessation of breeding activity, high juvenile losses and possibly pregnancy failures on the one hand, and the dispersal away from the troop of the oldest animals, including the largest males, on the other. The remaining segment which maintained troop cohesion for a considerable period after most of the troop had perished, was potentially the most fecund group. Its members had survived the rigours of early growth and were on the threshhold of their reproductive life. Had they survived the catastrophe, they would have provided the most efficient nucleus for re-establishing the troop when environmental conditions improved.

Impala are highly gregarious and very successful in marginal areas in Rhodesia. Feeding patterns are probably of great importance in this respect (p.86), as are compensating mechanisms which operate during a decline in numbers in critical years. Starvation on islands favoured the survival of sexually mature females and yearling males at the expense of calves and adult males. There was the expected heavy calf mortality which generally favours adults, especially lactating females, as was shown by the slightly better conditions of those with dry udders compared with those still lactating shortly after the rut.

Sexually mature rams were the next most sensitive group and died in fair numbers on Island 17 soon after the rut, which took place early in the dry season. By then, most of the females were pregnant, so that the loss of rams had the beneficial effect of reducing population pressure at the onset of the most critical time of the year. The additional strain on males of rutting behaviour is, therefore, beneficial to the population, as there are probably always more males than necessary to cover the females, and yearling males, which were among the animals in best condition, would have matured by the following rut.

There was no significant lowering of the proportion of pregnancies on Island 17, although the small size of the yearlings on Ukubula Island in December, 1962, after several months of severe conditions, suggests that a drought might lower the proportion reaching maturity by the time of the rut. No indication of abortion or resorption of foetuses was found on Islands 17 and 144, during the first few weeks of pregnancy, but evidence from Rescue Reports suggests some pregnancy failures on Ukubula Island. This or a heavy loss of young calves reflected in the low calf to female ratio, when calves were four to six weeks old.

In this species, the shift in population structure favouring mature females and yearling males provided a good mechanism for the rapid re-establishment of numbers when conditions improved. There was no evidence of a change in the proportion of young to old females of breeding age and it seems unlikely that this would materially have affected the breeding potential of the survivors, as the high pregnancy rate found in this species suggests few females survive to post breeding age. It might be argued that over-crowding on islands intensified competition between males seeking harems, so accelerating their loss in condition during the rut, but this was not noticeably the case and Stevenson-Hamilton (1947) describes similar losses in condition under unrestricted conditions. Further, the small sample of carcasses found by Dasmann and Mossman (1962,b) and the larger unaged sample collected by Rushworth (1964) in the Tuli Circle, fit the pattern observed at Kariba remarkably well.

Selection for sexually mature females would raise the reproductive potential of the herd, so that a succession of poor years, which allowed sufficient interval between them for numbers to build up, could actually result in a potential increase in the population, provided the level of food shortages during the critical time of the year were of the right magnitude. The marked differences in the physical condition of adult males and females at the beginning of the dry season, would mean that the severity of food shortages could vary within fairly wide limits and still lead to a greater loss of males and an upward trend in the population. This leads to the hypothesis that mismanagement of the veld results in conditions which approach the threshold, where slight depressions in climatic conditions will lead to an increase in Impala. Further deterioration of the veld, either by the Impala or continued mismanagement, would approach the threshold at which females were affected and eventually the collapse of the entire population.

Little is known of growth and maturity in Buffalo or of the role of different sex and age classes in the reproductive cycle or general social organisation of the herd. They are, however, highly gregarious and a definite shift in population structure was evident on Ukubula Island. There was little successful calving on the island and a heavy juvenile mortality was prevented by the removal of most of the calves, but in older animals, young fully grown individuals were favoured. This resulted from a heavy die-off of females with all adult teeth and small losses among full grown females in which adult tooth replacement was not yet complete. This led to a slight over-all increase in the proportion of males, which has been observed in other saturated islandic populations (p. 108), but the high proportion of young adult females which survived would have been of particular significance to the potential re-establishment of the herd had it been under unrestricted conditions improved after a drought for example.

Zebra are gregarious, but neither differences in physical condition nor a differential mortality between different sex or age classes was manifest on Island 17, when the sample was critically short of food. A lower proportion of juveniles could, however, be expected under severe conditions, although the close adherence to parity in the sex ratio of Zebra, culled on cropping schemes in dry marginal areas of Rhodesia, suggests there is no differential mortality between the sexes.

Wart Hog are semi-gregarious and associate in groups or family parties of up to about 12. Over-crowding led to a rapid die-off among sucklings and, to a lesser degree, yearlings, thus favouring individuals over two years old.

There was a lower proportion of males in Bushbuck trapped on islands than in Tsetse kills, which may indicate greater survival in females, but the only clearly defined shift in structure among other small, solitary antelope (Klipspringer, Duiker and Grysbuck) was a lowering of the proportion of juveniles, although all three species calved after prolonged isolation under adverse conditions. On the other hand, Roth and Child (<u>in press</u>) have shown that heavy losses among juvenile Rhino could not be attributed to conditions on islands, as they did not apply for long enough to alter the composition of the population to any extent, if at all. Calves were born on islands so that the normal reproductive pattern of this slow breeding species was also probably unaffected.

These patterns of mortality are summarised in Fig. 23, which shows that it is obviously a different phenomenon from that shown by populations growing towards maximum numbers. In seven species there was the expected heavy loss of juveniles, but the proportion of males and females was little changed. In the three most gregarious species, however, in addition, there were definite

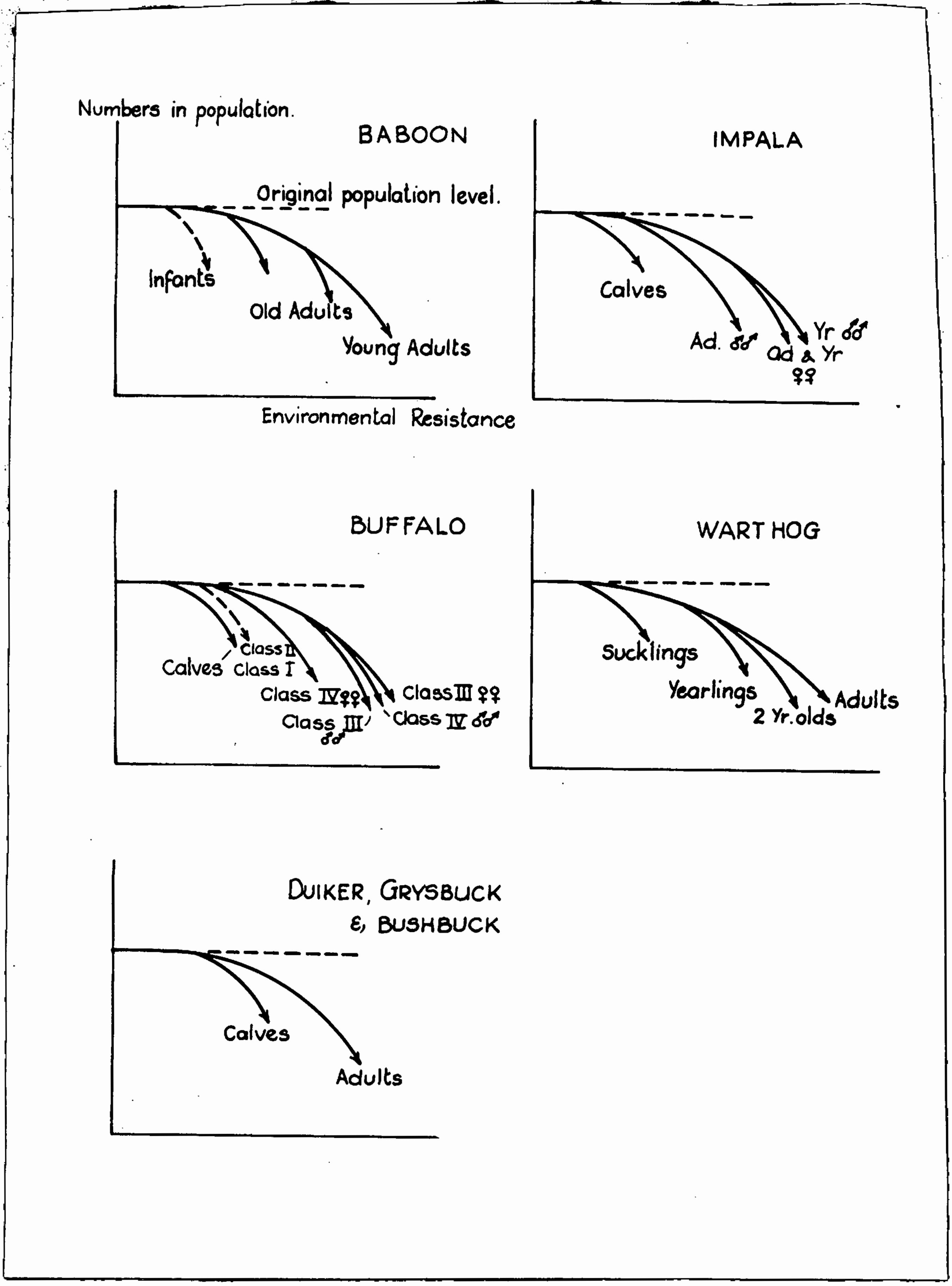


Fig. 23. Diagrammatic representations of mortality patterns observed during the decline in populations marooned on islands and faced by declining habitat resources, showing the relative losses from different sex and age class.

shifts in the age composition of the adult population, which would have enhanced the population's return to original numbers after a catastrophic food shortage. A high proportion of young adult females survived at the expense of older females in Baboon and Buffalo, although in Impala, the survival rate of all mature females was similar. There was a reduction of old males in both Baboon and Impala where a high proportion of young, well grown males survived, although this may not have applied in Buffalo where a slight trend towards old bulls was apparent. The mechanism effecting these shifts was only determined for Impala, although in all three it favoured the survival of the most fecund segment of the population. Hunting of a certain intensity would have the same effect of reducing the average age in the breeding herd, and, as Wilson (1965) has shown, increasing the proportion of females in some species. This offers an explanation as to why some species increase under certain intensities of hunting as Riney (1963) has described.

Similar mechanisms were not apparent for Zebra or Wart Hog, or for the more solitary species, possibly because the populations are more spread out. A retention of the proportion of males and females to within fairly narrow limits may be necessary to ensure adequate contacts for breeding purposes in such species as Grysbuck, which have restricted home ranges and an adult sex ratio approaching parity. This would apply particularly after a population had been thinned out and when maximum reproduction among survivors is desirable to re-establish numbers.

Duiker females can calve at least twice a year and this may also apply to Grysbuck, as it is known in the congeneric Steenbuck, and Bushbuck, all of whom calve throughout the year. This means losses can be made up more easily by reproduction alone than in species with a lower annual reproductive potential, such as Rhino, in which Roth and Child have shown survival of a population to be largely dependent on the longevity of the adults.

Wart Hog, however, have a very high fecundity among large placental mammals, equalled by few except other suidae and the carnivores. Stevenson-Hamilton (1947) indicates litter size in lion may adjust in response to the availability of prey in the way Lack (op. cit) describes for a variety of smaller animals, and it would be interesting to know whether a similar mechanism applies in Wart Hog whose unborn litters vary from one to eight.

A high proportion of sucklings usually die, but provide the means whereby a depressed population could soon build up. The habit of females adopting orphaned sucklings would enhance the build up and seems the only plausible explanation for this behaviour. If the majority of the young die in a stable or declining population, there would be no advantage in a female having added competition against her own young, unless there was some inherent benefit to the whole group in certain circumstances. The pattern of mortality at Kariba suggests that this behaviour can only be widespread in an expanding population, as the juveniles were the first affected by a reduction in numbers and most disappeared before starvation affected their parents, so that environmental resistance would produce few orphans. Obviously culling a population lifts the environmental pressure on the survivors so that adoptions can become more widespread, as they did in parts of the Zululand Game Reserves.

Zebra may associate in large herds, especially in open country, but Klingel (1964) found these very unstable, and that the population consisted of small family groups, made up of a male and one to five females and their offspring, and bachelor parties. These sociological units are rather similar to those of Wart Hog and, in both species, populations tend to have similar numbers of males and females, suggesting this is necessary for sociological reasons. In many truly gregarious species, however, a few males can serve many females, but in none of the three species in which a homostatic mechanism was observed at Kariba, involving changes in the adult sex and age structure, is the reproductive potential greater than 100 young per 100 mature females per year, as multiple births are exceptional.

Baboons and Buffalo mature slowly, limiting the rate at which populations can grow, so that these mechanisms are of particular importance after a set-back. This indicates another value,besides protection, for the gregarious habit in marginal areas as, to act efficiently, the mechanisms require a fairly large well co-ordinated group.

It is therefore interesting that Talbot and Talbot (1963) found a similar state of affairs in the highly gregarious Wildebeest in Masailand. There were about 52% males in a stable population on "optimum" range in Western Masailand, compared with 32.8% males in Eastern Masailand, where Wildebeest habitat has deteriorated. Calving was delayed in the latter area in 1961, when few calves were born and juvenile mortality was high, at a time when adults also died in large numbers from the effects of several successive years of drought. However, rainfall was heavy and food plentiful in 1962, which resulted in a heavy and successful calf crop the following year.

The pattern here appears to show a remarkably close parallel to that of Impala. The sex ratio for Eastern Masailand was taken by Lamprey (quoted by Talbot and Talbot, 1963) before 1962 and appears to have been based on counts over the previous five years, including 1961, "the height of a series of drought years". It therefore appears that the optimum sex ratio in Wildebeest is over 50% males, but that during droughts in poor habitat, this proportion is reduced in favour of females. These are seasonal breeders, with a reproductive potential approaching 100 calves per 100 mature females, but this potential is greatly reduced in poor years. However, the greater survival of females was obviously beneficial to the Wildebeest population on poor range after the good rains in 1962, which resulted in a heavy calf crop and the early stages in the regeneration of the population.

In a smaller sample of 79 Mule Deer, which are not highly gregarious, however, Leopold et al (1951) give figures which follow the same trend, indicating that the mechanism may also sometimes apply to species with a different social organisation. They obtained a sex ratio of 58 males : 100 females, excluding fawns in the fall of 1948, and located 79 carcasses at the end of the severe winter, of which 11 were bucks, 15 does, 31 fawns and 22 unsexed adults, but calculated an overall loss, from an area of 304 square miles, well in excess of 2,000 deer. Again, there was a tendency for a greater proportion of males to succumb during a catastrophe and it is interesting that no yearling or prime adult (2-5 years of age) carcasses were found in the sample, which included 60% old adults and 40% fawns. It is also interesting that they found an inverse correlation between the number of bucks per 100 does and the number of fawns per 100 does.

Silberbauer (1965) found a similar age structure in Kalahari Bushman populations following a severe smallpox epidemic in 1950-1951. He attributed the high proportion of children under 10 years old (33.5 to 35%) to post epidemic breeding and notes that the age group which was between five and fifteen years during the epidemic had a high survival rate compared with both younger and older age groups. He concludes that "this differential mortality during the epidemic is responsible for the curious frequency-distributions through the age-groups and for the presently abnormally high rate of increase indicated by the high proportion of young children".

In five species, including three from Kariba, and in a primitive human society, compensating mechanisms, evolved by selection on social groups, tend to ensure a high reproductive potential over a maximum period in the individuals which survived a critical period. This interpretation differs from the explanation suggested by Wynne-Edwards (1962). He emphasises the importance of social mechanisms and community structure as a control preventing wild populations from exceeding the carrying capacity of their habitat. Essentially, he claims that besides its role in reproduction and defence, sociology is vital for spacing individuals, so that at no time will their requirements exceed the resources of their habitat, especially as regards food. Numbers tend to adjust to optimum density in a stable habitat and, fundamental to the theory is some "feed-back" mechanism that ensures the population will not exceed available resources, which may not currently limit the population. Wynne-Edwards points out, however, that self regulation by special homostatic adaptions cannot be expected to apply in areas with unduly fluctuating climatic conditions. Here "Dispersionary Control would be temporarily lost and starvation and resource damage might occur".

Resource damage attributable to wild populations of large mammals is widespread in many parts of the world, especially in marginal or semi-arid regions, but also where the climate is less severe. In Africa alone, Petrides and Swank (in press) report over-populations of wild ungulates in parts of the Queen Elizabeth National Park, Uganda, Petrides (1956) near Nairobi, Kenya, and Savory (in press) in the lower Zambezi Valley in Rhodesia. Game is at least locally overstocked in the Wankie National Park and Tuli Circle in Rhodesia, culling of Elephant, Hippo and Buffalo is considered necessary in the Luangwa Valley Game Reserves in Zambia, and culling has been carried out for some years in the Zululand Game Reserves. These areas show a considerable variation of habitat and have average annual rainfalls from about 10 inches toover 35 inches.

The observed effects of game on their habitats would, therefore, place these areas outside the region in which Wynne-Edwards would expect his theory to hold, and yet he finds supporting evidence from the migrations of Springbuck, Antidorcas marsupialis Zimmermann, a species of the semi-arid regions of Southern Africa.

There are certain other inconsistencies between observations at Kariba and Wynne-Edwards' theory, which places considerable emphasis on social hierarchies for maintaining the optimum stocking rate in a habitat. The behaviour of adult Baboons, which broke away from the troop to forage individually when food was scarce, appeared to be a social mechanism which promoted the survival of the young adults, by reducing population pressure in the troops' accustomed range. There is a well disciplined hierarchy in Baboon troops (Hall, 1962) headed by the older and bigger animals under normal conditions, yet these animals, including the largest males, were among the first to break away. This is contrary to the situation described by Wynne-Edwards, who suggests that in times of stress, the lower levels of the hierarchy are eliminated successively from the population. He further predicts that social activity will mount as a prelude to major changes in population density, but both Hall (1960) and the present author found the opposite, while individuals were emigrating from the troop's range. Squabbles and vocalisations which are important in maintaining the hierarchy diminished in intensity and frequency to vanishing point.

There are a few observations of aggressive behaviour by adult Wart Hog, especially against yearlings, but its relative intensity cannot be gauged until the frequency of such behaviour under less densely populated conditions is known. It is probable though, that it was fairly normal as there were few observations, even on Island 17, and few had wounds which could have arisen through intra-specific fighting, considering the severe competition for food and burrows on some of the islands.

Similarly, in Impala mature rams died of starvation after the rut. This loss was not as complete as in Baboons, but favoured yearling rams which were presumably lower in the social scale, and yet the only aggressiveness recorded was associated with the rut. Even the commonly observed fighting between immature males, which is probably a form of play, was never seen on over-crowded islands.

Rhino are described by Hutchinson and Ripley (1954) as territorial, as they apparently often fight between themselves and yet there were only two possible cases of aggression between individuals confined on islands. One was a fairly old carcass with a large wound in its side, which may have been caused by another Rhino, while the second involved a short fight after a partially drugged animal blundered into another.

The initial shock absorber to deteriorating habitat resources, shown by all species, was a general loss in physical condition, followed in most cases by a heavy juvenile mortality. The latter was apparently supplemented by a suspension of breeding activity or pregnancy failures in Baboon and Buffalo and, to a lesser extent, Impala. These three mechanisms all have a physiological basis and probably arose from the low plane of nutrition to which the animals were subjected, as this is known to inhibit ovulation or induce pregnancy failures in domestic stock and humans. Leopold <u>et al</u> (1951) cite Stoddart and Rasmussen (1945) who found a higher fawn production on good ranges and Cheatum and Severinghaus (1950) showed that ovulation rate is related to the plane of nutrition, and as Hart and Guilbert (1933) and Miller <u>et al</u> (1942) have found, particularly to the intake of Vitamin A. Morton and Cheatum (1946), Taber (1953), Taber and Dasmann (1958) and Julander <u>et al</u> (1961), all demonstrate that the plane of nutrition before and during the rut affects the fecundity of deer, and Robinette <u>et al</u> (1957) quote evidence that the weight at birth and pregnancy failures are also related to nutrition and, as noted (p.40) the human cycle is interrupted under severe conditions. Hammond (1960) has examined the literature relating to this subject in domestic animals and comes to the same conclusion as do Robinette <u>et al</u> (<u>op. cit</u>) in their review of the human literature.

Growth is a severe strain and, in most species, limits the deposition of fat reserves necessary to survive critical food shortages (See for example Brody, 1945; Riney, 1954). That these mechanisms were not sociological, as Wynne-Edwards infers, is borne out by the fact that at Kariba the young were in the same habitat and feeding on the same plants as their parents, without the latter showing any resentment towards them.

In Baboons, the loss of adults was preceded by a break-down of social bonds, while in Impala "courtship behaviour" influenced the pattern of mortality among males. In these two species, sociology acted in homostatic mechanisms resulting in as rapid a return of the community to its original numbers, after a critical food shortage, as possible. Whether or not it would also act to inhibit population growth after the optimum density for the sustained maintenance of the habitat has been reached, as Wynne-Edwards suggests, is not known. However, it has been noted that large mammals, including Impala and Buffalo, may increase beyond the capacity of the range, often as a result of some manipulation of the environment. This may follow the introduction of domestic stock or the mismanagement of fire (Riney 1963), or through the manipulation of water in dry marginal areas, which suggests that the control of numbers in maintaining a long term equilibrium between animals and their habitat may be essentially a function of environmental resistance. In this case, and in the light of present understanding, it does appear that periodic droughts may be an important factor in maintaining a stable ecology.

Browsing and grazing animals survived for remarkably long periods while food was critical on islands at Kariba, where they had ready access to water. Similar effects on the vegetation occur around artificial water holes in the Wankie National Park and other marginal areas, where large mammals are clearly locally overstocked. Some species, native to dry marginal lands, can survive extended periods without water, but increase in numbers when water is available, suggesting it may be equally as important as food, which Lack (1954) has emphasised, in controlling numbers in some dry marginal ecosystems.

Periodic local droughts may then spell vegetation from high concentrations of some resident species which are adapted for rapid recovery from food shortages. The wanderings of Wildebeest in western Masailand in quest of green grass which flushes after local rain, found by Talbot and Talbot (1963), has a similar effect. The same result is achieved by the formation and eventual silting up of pans, described by Weir (1960), or occasional floods which gouge out water holes and silt others up in rivers which flow seasonally, as this would shift the intensity of animal pressure in a given region.

This hypothesis, coupled with observations on islands in Lake Kariba, suggests several different but often inter-related factors, Which harmonise in the maintenance of an animal environment balance in dry areas. Water, or the lack of it, may influence numbers in otherwise suitable habitat. The availability of food or cover can obviously limit populations, either through basic shortages of the necessary types, or through competition from other species. This relationship between the numbers of one species and those of another is but one of the numerous ways in which one species can influence the well-being of others.

Ill-judged hunting or the mismanagement of the land can, for example, easily upset these delicate balances with results which may be deleterious to the continued maintenance of conservation values. A better understanding of the mechanisms operating to achieve this balance are therefore desirable for the intelligent management of marginal areas, as they are especially sensitive to mis-use. The exploitation of research opportunities, such as those found at Kariba after the removal of the people, or during the rapid destruction of vegetation in incipient fishing grounds, or those associated with the formation of the Lake, can provide much of use to students of animal behaviour or ecology, or conservationists concerned with one or more aspects of protection or management.

SUMMARY

Lake Kariba covers 2,109 square miles in the Central Zambezi Valley and formed in five years following the damming of the Zambezi River. The evacuation of the primitive native inhabitants, whose local over-population on fertile alluvia was downgrading the veld; the clearing of vegetation from incipient fishing grounds, and the filling of the new Lake, all led to changes in the habitat of this dry marginal area, dominated by mopane veld and occupied by extensive populations of large mammals.

The present paper deals primarily with the behaviour and response towards lake formation of 21 species of large mammal, and the conditions to which a number were subjected when they became marooned on small temporary islands. This is, however, preceded by a brief description of the methods and results of measures taken to save these animals and of the effects of flooding on the habitat and on other groups of animals. Aquatic organisms benefitted from the Lake, but reptiles and some birds became marooned on islands and eventually perished, even when the latter were within flight distance of the mainland.

A population eruption of rodents, observed during the first year of Lake formation, was apparently not due to the effects brought about by the Kariba project, although the absence of woody vegetation in bush clearings apparently hastened the crash in these areas.

The accounts of the responses of large mammals to flooding and the behaviour of those found on islands, are prefaced by comments on the species distribution and general abundance in the Kariba Basin and on the possible effects of human settlement on this. They contain pertinent aspects of the species' biology including new information from field studies carried out elsewhere in order to evaluate data from Kariba.

Troops of Baboons became marooned because of a reluctance to leave established home ranges, as they showed little fear of water and could swim well. Food shortages on islands led to a rapid deterioration in physical condition, a suspension of breeding activity and heavy juvenile losses. There was also a partial breakdown in troop cohesion as social behaviour diminished and adults broke away from the troop and perished, so that the last survivors in three troops were young more-or-less full grown individuals.

Hyaena, Leopard and Lion were all strong swimmers and one pride of Lion swam 1¼ miles to an island. These three species benefitted from the concentrations of game on islands and showed a tendency to leave of their own accord when food diminished.

Antbears swam well, but were difficult to drive into the water as they sheltered in their holes. On two islands conditions were unsuitable for burrowing, due to the proximity of the water table or the rocky soil, and on several islands they were short of food.

Elephant, Waterbuck and, to a lesser extent, Kudu swam to islands to feed on vegetation which flushed out of season, but usually left again when feeding conditions deteriorated and, consequently, encountered few of the adverse effects experienced by species marooned on islands.

Roan were never trapped on islands, Eland were only known from one, while Zebra and Buffalo were found only on islands which formed from large areas. Zebra were poor swimmers, but showed remarkable resistance to deteriorating habitat and, although they became thin, there were few natural deaths and no change was detected in population structure. Buffalo tended to swim off islands but, in one case, a herd of over 200 became marooned and would eventually have perished. There were indications of reduced breeding and a heavy mortality followed the rescue of most calves, and favoured young mature females and mature males at the expense of old females.

Rhino were very weak swimmers and their condition deteriorated on island before they could be rescued. Bush Pig had little fear of water, swam well and were adept at avoiding capture, so that many drowned when islands submerged, although they survived remarkably well under adverse conditions. Wart Hog, on the other hand, were more reluctant to go into the water, although they were strong swimmers. They were the second most numerous species on islands where food and cover was limited and were often in poor condition. This led to heavy losses in successively younger age classes, which affected both sexes similarly. The presence of these three species on islands was attributed to their localised habits.

Duiker, Grysbuck, Klipspringer and Bushbuck became marooned on small islands as they are apparently very localised. Apart from Klipspringer, they took to water readily and could swim well. Klipspringer differed from the other three in that they became limited to their most favoured habitat, which reflected in their better physical condition. Few young were noted for any of these species, however, suggesting a heavy juvenile loss and, in Bushbuck, there may have been fewer males than usual.

Sable were easily chased into the water, but were relatively weak swimmers whose condition deteriorated markedly on islands. This culminated in deaths, but the sample was inadequate to detect any shifts in population structure.

The most numerous species on islands was Impala whose localised habits and poor swimming ability are described. The wide range of foods taken affected other species on an island adversely, and indicate one reason for the success of Impala in down-graded marginal habitat. Declining physical condition culminated in a heavy calf mortality affecting both sexes evenly, and following the rut, when most mature females conceived, there was a heavy die-off of males. This, and the tendency for more young males to disperse, explains the preponderance of females in many Impala populations. The loss of adult males raised the reproductive potential per unit of population which survived a crisis, which suggests another reason for their success in deteriorating veld which is more sensitive to fluctuating climatic conditions.

Conditions on one island allowed a description of the fauna in an area of almost undisturbed mopane veld. This showed that in spite of its low agricultural potential, it supported a reasonably dense and varied ungulate population, even compared with that in some other game areas in Africa. Nevertheless, it was not as high as that reported from mismanaged mopane veld, possibly on account of changes in the grasses which temporarily favour more animals, although of fewer species.

Extreme over-population led to severe competition which resulted in little aggressiveness between members of the same or different species, but emphasised the importance of special anatomical or behavioural characteristics. Most significant was the absence of any indication of social hierarchies acting to ensure animals highest in a "peck order" obtained most food and, in three species, animals lower in the social order survived best.

Leopard eliminated Wart Hog on one island, but it is argued that predation is usually ineffective in controlling populations of large mammals, and probably raises the reproductive potential in some, as there is a tendency to kill a higher proportion of males. This and the effects of dispersing a population from local centres of over-population are ways, in addition to those mentioned in the literature, in which predation may favour a prey species.

Patterns of differential mortality between different sex and age classes in Baboon, Impala and Buffalo marooned on over-populated islands favoured a rapid regrowth of the population from the survivors of a calamity. This apparently applied in other species away from Kariba and indicates the importance of social selection, acting on a group, in the survival of populations in marginal areas, where periodic droughts may be one of several significant factors in the maintenance of an equilibrium between animals and their habitat.

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