Ecology of the Sitatunga

(*Tragelaphus spekei selousi* Rothschild, 1898.)

in the

Bangweulu swamps, Zambia, Central Africa.

by

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ABSTRACT

Research into the ecology of the sitatunga (Tragelaphus spekei Rothschild, 1898.) in the south-east Bangweulu, Zambia, was carried out between 1973 and 1976. The sex ratio for sitatunga does not differ significantly from 1:1, although 47.3% of the population are adult females and 25.6% adult males, 12.1% immature males, 4.3% immature females and 10.6% calves. Two conception peaks are related to the onset and cessation of the rains with breeding occurring throughout the year. Sitatunga occur singly (50%), in twos (22.2%) or in threes (16.7%). Females and their calves are the only group with any integrity. The maximum number observed in a group was 7. The minimum home range for males is 0.0363 km^2 and for females 0.176 km^2. Aggression and the mutual avoidance of dominant males suggests territoriality. Sexual dimorphism is marked. Pelage colouration is variable. The white facial markings are important in male agonistic displays. Criteria for relative age determination of sitatunga were derived from eruption and attrition sequences of impressions taken from maxillary teeth. Males reach a theoretical maximum weight of 106 kg at 8.1 years and females 51.5 kg at 7.34 years. Males are 54.6% heavier than females and maximum horn length is achieved at 7.5 years. Age is significantly correlated with weight, horn length and the length/weight index. The mean horn length for adults is 64.2 cm and the mean front hoof length, for both sexes, is 7.6 cm. The impact of man on sitatunga in the Bangweulu is minimal.

INTRODUCTION

The sitatunga (Tragelaphus spekei) is a member of the Tragelaphini, a tribe of spiral horned antelope noted for their beauty and shy retiring habits. The species is widely distributed in Africa where suitable wetland occurs. Their importance as a source of protein for subsistence agriculturists, and the extreme paucity of knowledge concerning their life history gave impetus to this study.

Specifically, I decided that a knowledge of the species habitat requirements, movements and behaviour was a necessary adjunct to Phase 1 of the Black Lechwe Project. This project was a 4 year ecological investigation of the black lechwe antelope (Kobus leche smithemani) conducted by Grimsdell and Bell (1975) in the Bangweulu basin of Zambia. The project was administered by my employers, the Department of National Parks and Wildlife. I carried out this research, in addition to other research and conservation duties, between May 1973 and February 1976, in the south-east Bangweulu. (Figure 1).

OBJECTIVES

1. To classify the main vegetation types within the sitatunga's habitat.
2. To describe their habitat requirements.
3. To capture, examine and mark a large sample of sitatunga.
4. To define age criteria from the eruption and attrition of maxillary teeth.
5. To describe the general morphology of the subspecies.
6. To compare their morphological features with those of other subspecies.
7. To classify the population with regard to sex and relative age.
8. To assess the sex ratio of the population and that of the different age groups.
9. To derive a theoretical body growth curve for use in the field.
10. To assess which physical parameters are closely correlated with age.
11. To define the breeding peaks in relation to environmental factors.
12. To estimate the density of sitatunga.
13. To define their movements in relation to vegetation phenology, rainfall and water depth.
14. To define the sex and age structures of different group sizes.

15. To define the influence of their specialized habitat on their social organization.

16. To make observations on social behaviour.

17. To define their spatial behaviour

18. To assess interspecific competition.

19. To make suggestions on the species's management.

THE BANGWEULU BASIN.

The Bangweulu basin (Figure 1) is located in the biome known as the Central African Plateau which straddles much of present day Zambia and Tanzania. It is comprised of a large shallow lake of some 3016 km^2 which is connected with 3900 km^2 of permanent swamp, all of which spreads out into the river estuaries in the rains inundating a total area of some 11,700 km^2. This vast area is a flat mass of swamp grasses and reeds, dotted with countless lily covered lagoons and intersected by many open or semi-open channels (Brelsford, 1946). The swamps are drained by the Chambeshi river which enters in the north-eastern corner and flows down the lake to its meeting with the Luapula river in the south-east at Kapata, the sole exit point. The Chambeshi flows through the swamp changing both direction and gradient in response to local accumulations of water (Debenham, 1946). Features of this area are the numerous channels dug by the Colonial Administration and the canoe tracks leading to the villages of the sand and termite-mound islands within it. South towards Matongo and in the east towards Masala, are the extensive seasonally flooded peat swamps (Brelsford, 1946). Beyond the swamp toward the woodland, are the estuaries of the rivers which enter from the secondary miombo (Brachystegia sp; Isoberlinia sp.) and tall grass chipya, open canopy woodland. Associated with the estuaries are the flood plains and water meadows with which most of the wildlife of the region is associated.

STRUCTURE AND GEOLOGY

The central and East African region is characterized by a series of ancient and stable land surfaces riven by geologically active belts, a pattern that has major geological and economic consequences (Grimsdell and Bell, (1975). In this case the Bangweulu basin is the ancient, stable land surface, surrounded by areas exhibiting less stability: the Luapula/Lake Mweru rift; the Lake Tanganyika/ Lake Rukwa rift and the Luangwa valley rift. This area has been called the Bangweulu craton (Vail, Snelling and Rex, 1968, in Grimsdell and Bell, 1975), an area stable for 2,200 million years. Much of the area is overlain by ancient quartzites, slates and dolomites with an extensive zone of granite on the plateau between the Luapula valley and the western shores of Lake Bangweulu. The acidic nature of these parent rocks is held to be responsible for the low cation exchange capacity of overlying soils (Italconsult, 1970). This, coupled with their extreme age and excessive leaching, has produced soils of low agricultural capability.

Grimsdell and Bell (1975) postulate the occurrence of a continuous downwarping of the basin along the Chambeshi drainage line caused by the orogenic activity of the less stable areas surrounding it. Since this downwarping period, activity has been one of erosion and deposition of alluvium on the extremely flat surface of the basin floor. This recurring phenomenon of enrichment is particularly marked in the estuarine areas lying close to the woodland.

TOPOGRAPHY AND SOILS

The Bangweulu craton is flat with gradients of the basin slope being less than 1^0 (Mansfield _et al_., 1975). The total area encompassed approximates 20,000 km^2.

a. Soils

The soils of Zambia have been classified by Trapnell (1953) in terms of soil-vegetation relationships, by Italconsult (1970) who related soil types to agricultural quality, and by Mansfield _et al_. (1975) for the Northern and Luapula provinces.

b. The Plateau Soils.

The soils of the north-east plateau are of low agricultural capability, a fact not surprising in view of the practice of Chitemene agriculture in the region. The soils tend to be sandy with a low cation exchange capacity. They are also acidic and have acute phosphorus deficiencies. Mansfield _et al_. (1975) describe them as soils of low fertility with no macro-structure below an organic horizon.

c. The Floodplain Soils.

The soils of the swamps and floodplains are of low fertility but the floodplain soils have high organic carbon values and greater cation exchange capacity (Grimsdell and

Bell, 1975). The floodplains therefore have a higher relative fertility than the surrounding sandveld of the plateau.

Italconsult (1970) states that the floodplain soils, seasonally waterlogged soils and swamps were potentially non-arable. A feature of the area is the building of sand levees by the rivers as they enter the floodplain, and the deposition of alluvium behind them.

RAINFALL AND HYDROLOGY

The Central African area is characterized by the division of the year into a dry season (April - November) and a rainy season (November - April). It is the latter which causes the flooding of the Bangweulu basin and the adaptation of all life to this dynamic covering and uncovering of the basin's periphery.

The catchment of the basin has an area of about 190,000 km^2 with the mean annual rainfall lying between 111 cm and 134 cm isohyets on a general gradient increasing from south-east to north-west (Grimsdell and Bell, 1975). The craton is fed by 17 rivers, the largest of which is the Chambeshi, the ultimate source of the Congo river. The only exit point is via the Luapula river in the south-east which accounts for 10.3% of the total precipitation (Grimsdell and Bell, 1975). The balance of the precipitation is lost to evapotranspiration. Balek (1970) suggests that the high water loss is primarily from wet mud as opposed to open water.

The highest seasonal fluctuations in the Bangweulu basin occur at the Chambeshi inlet and at the Luapula exit, followed by the Lake and the Chambeshi channel in the region of Ncheta island, and finally, by the central swamp and the Lukulu estuary. In the latter, the average fluctuation over 5 years was 43 cm.

THE STUDY AREAS

With the exception of a few behavioural observations made in area 1 (Figure 2), all the work on sitatunga was carried out in the Lukulu estuary (12^0s, 30^0 25'e) in the south-east Bangweulu. Here two areas were chosen for intensive study (area 2 and 3; Figure 3).

The Lukulu Estuary (Study Areas 2 and 3

The Lukulu estuary is situated between two strips of woodland: the Lukanga and Mandamata. It consists of high quality floodplain and the marshes associated with the river.

At the inception of the study in 1973, the Lukulu estuary provided little or no water to the main swamp. However, a canal dug by the Department of Water Affairs linking the Lukulu with the main swamp has changed this.

Levels of water in the Lukulu estuary are a function of the following features:

1. increased flow in the Lukulu during the rains.
2. the draining effect of the Water Affairs canal.

3. local rainfall.
4. the overflow and backing of water in the main swamp derived from the Chambeshi channels around Ncheta island which affects the rate of the Lukulu's escape.

Water levels recorded in the river channel (quiescent) near the field station show that the level begins to rise in the middle of November, the onset of the rainy season, reaching a peak in mid-March. Actual inundation of the floodplains usually occurs at the end of December. This phenomenon takes place with extreme rapidity and appeared to be induced by heavy local rainfall once levels had reached a certain height. Indeed, flooding on the plains appeared to be very much a function of local rainfall with the highest water levels being recorded after peak rainfall.

Study Area 1 (Figure 2)

The Kang'omba marsh associated with the junction of the Lulimala river and the Kang'omba dambo (drainage area) exhibits a similar flooding regime as a result of increased run-off and resistance in the flow wrought by the large beds of papyrus and marsh further down. This marsh lies on the edge of the village of Chiundaponde.

VEGETATION

The vegetation of the Bangweulu is clearly defined in relation to water depth and duration of flooding, going from the dryland conditions of the miombo and chipya through the various stages until the open deep water of the lake is attained. The principal zones are:

1. Miombo and chipya woodland and dambos.
2. Peripheral grassland.
3. Intermediate grassland.
4. Shallow water floodplains.
5. Seasonal swamp.
6. Permanent swamp.
7. Open water.

These zones (Grimsdell and Bell, 1975) were further subdivided by Verboom (1982) (Appendix A).

BURNING

Indiscriminate burning of the countryside occurs in response to the location and movement of people. Fires are traditionally set as early in the year as possible, and are not uncommon in the Lukulu estuary in April, a month which signals the end of the rains. Although fire is an extremely important tool when properly applied, this is rarely done, and may be partly responsible for the low biomass of wildlife in the miombo woodland. Verboom (1982) recommends a rotational burning regime of most of the vegetation types in the Bangweulu, including papyrus, although burning of sedge marsh can have deleterious effects on animals by drastically altering the vegetation composition.

TERMITES AND LEVEES

A feature of the Bangweulu floodplains is the variety and adaptation of species of termites to the flooding regime. Since the general rise in the water level, these mounds have become partially flooded where they are a most valuable resting place and source of minerals for a number of wildlife species. The Luitikila swamp which lies north of the Lukulu is a large area dotted with flattened mounds on which sitatunga are often to be seen.

THE STUDY AREA

Study Area 2 (Figure 4) Plate 1)

The main study area lies between the field station on Chikuni island and the Lukulu river, and consists of most of the vegetation types found within the Bangweulu wetland area. Where possible, I have related the vegetation types to Verboom's classification (1982) - Appendix A.

a. Open Water and Rivers (Chambeshi class)

These areas support a diverse array of aquatic plants. Water depths do not exceed 2.5 m.

b. Recent Levees (Akambizi class)

These 'islands' within the area are usually not flooded except during an exceptionally high rainfall and are the result of the mechanical building action of the river through the millenia. An exception to this classification is the Lubavu levee which corresponds more to the water meadow class (Luiya class). It is flooded annually and receives the constant attention of ungulates.

c. Cyperus papyrus

This species is not an important component in any of the study areas. It is found in water depths of around 2 m and requires permanent water for sustained growth.

d. Phragmites communis

This species occurs at depths of up to 2 m and grows in dense stands throughout the year.

e. Miscanthidium teretifolium (Chisongo class)

This species occurs at depths up to 2 m. It grows principally in anoxic water.

f. Water Meadow (Luiya class)

The water meadows are flooded annually to depths of 0.33 m for approximately half the year. The Lubavu levee, due to its flat profile, resembles the true water meadows which lie within the floodplains further away from the river.

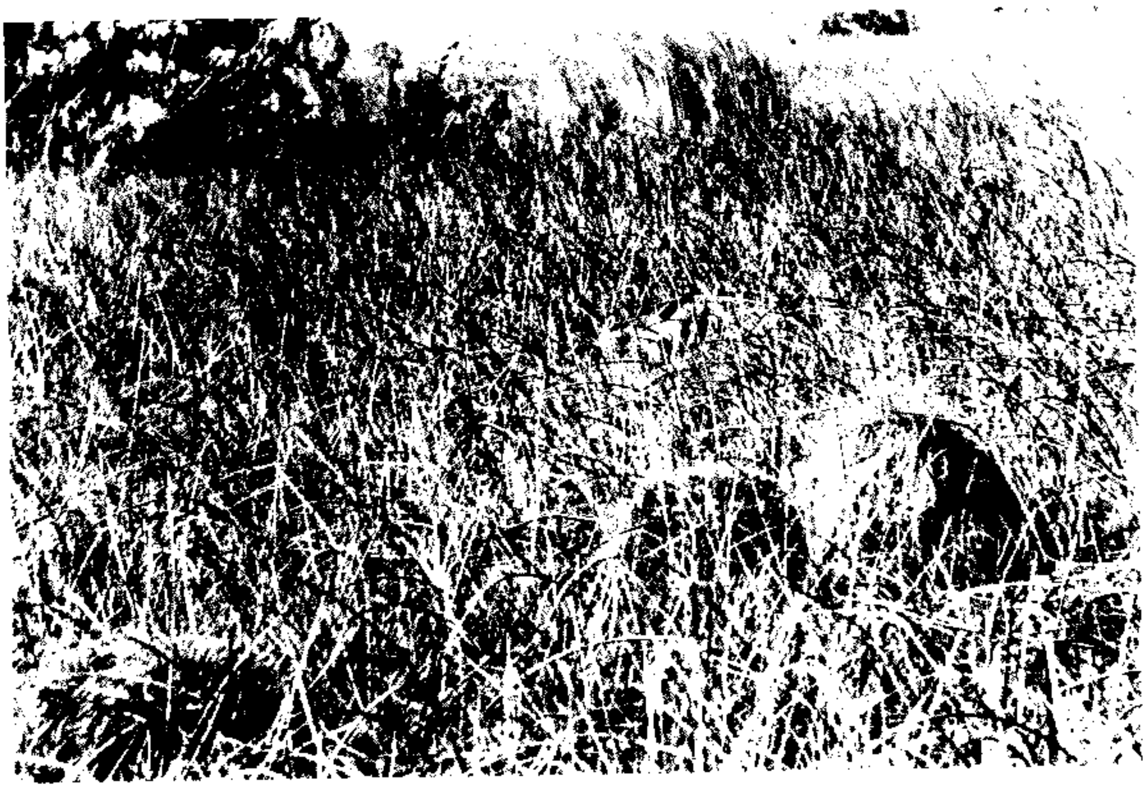
g. Intermediate Grassland (Mayengele class)

These grasses are of a coarse variety compared to those of the water meadow. Found on the sandy leached soils peripheral to deposits of alluvium, they are flooded annually to a depth of 0.16 m.

STUDY AREA 3

This area is roughly circular and lies between the Mandamata woodland and the Lukulu swamp thickets. It falls

Plate 1. Sedge marsh in study area 2 with sitatunga calf in middle ground.



within the intermediate grassland type (Mayengele class), but is, in fact, sedge marsh. It is bounded in the north by beds of Typha capensis and Phragmites communis and by the raised levee known as N'go. The area is 4.3 km^2 in extent.

The area (Figure 3) is fairly homogeneous sedge marsh consisting of extensive Cyperus digitatus and patches of Sesbania microphylla pockmarked with small levees and old termite mounds on which immature stands of Phragmites communis are supported. It is dry throughout the dry season while in the rains it is covered by approximately 0.66 m of water. A fire in the dry season of 1975, resulted in a massive invasion of the woody plant Sesbania microphylla.

STUDY AREA 1 (Figure 2)

Study area 1 is a marsh situated at the junction of the Lulimala river and the Kang'omba dambo. It is approximately 4 ha in extent forming a depression in the surrounding secondary miombo woodland (Mupundu class). It is isolated from other pockets of marsh both up the Lulimala and down the Lulimala at the estuary.

The marsh is a microcosm of the seasonal flooding regime of the basin resulting from the Lulimala and the Kang'omba stream, the resistance of the system which aids in 'backing up' the waters, and from local rainfall.

The vegetation in the marsh is intermediate in type, combining certain features of the Mikanshi class and the Luiya class. Principally, it is sedge marsh, interspersed with beds of grass but with no trees or shrubs present.

MAN

HISTORICAL PERSPECTIVES

The earliest known inhabitants of the Bangweulu are the Batwa (Wildmen) who today survive on some of the islands in the region of the Luapula/Chambeshi confluence such as Mbo (Figure 2). When the main migration of the Luba people took place in the eighteenth century from Kola (Angola), an offshoot of the main group, the Baunga, arrived at the lake only to discover the existence of another people. The Batwa were then forced to take up a nomadic existence in the swamp and their former position on the shores of the lake and swamp was taken by the new immigrants who were skilled agriculturists.

In recent times the tribes have intermarried a great deal although something of the tribal traditions and belief in certain totems remains.

THE POPULATION

The overall human population density of Zambia is low (5.6 km^2), a function of low soil fertility and the shifting form of agriculture known as Chitemene. Chitemene can only be operated in perpetuity in areas of low human density (Grimsdell and Bell, 1975).

The Northern and Luapula provinces of Zambia are populated by 22% of the country's population. Of a total 1969 population of 4,056,995 people, 143,694 people were found on the margins of the Bangweulu basin (Grimsdell and Bell, 1975).

The demographic distribution of people in the basin has been affected by a number of factors in recent times (Grimsdell and Bell, 1975):

1. The permanent flooding of a large part of the basin at the end of the 1930's.
2. A steady movement away to the Copperbelt mining area.
3. The decline in soil productivity as a result of population settlement on the basin's periphery.
4. The decline in the vast herds of lechwe and other wildlife.
5. A declining source of firewood.

THE LUKULU ESTUARY

The islands within study area 2 show evidence of recent human occupation and agricultural activity. The total coverage of Lubafu island (Figure 5) with its long mounds, and the other islands with the clumped mounds typical of cassava growing, provides the evidence. According to my staff, all of whom were local tribesmen, Lubafu island was occupied from 1945 - 1961. The people vacated the area due to the excessive high water period of 1961 and because of the depredations of elephant (Loxodonta africana) and eland (Taurotragus oryx) they moved to N'gungwa village.

CHIUNDAPONDE VILLAGE AND STUDY AREA 2 (Figure 2)

The village of Chiundaponde occupies the south bank of the Lulimala stream, extending as far as the Kang'omba stream and the road which crosses the Lulimala to the west of the village. Some 500 - 1000 people live here under Chief Chiundaponde. The general area was included in the proposed Livingstone Memorial game reserve (Pitman, 1934), an area never promulgated. There is little wildlife in the area other than the sitatunga of the Kang'omba marsh, and these appear little affected by the people.

HUNTING

The subsistence hunting of sitatunga is impossible to quantify. That it plays an important part in providing protein and skins for villagers is certain, although the large drives of yesteryear are now past. The effect of past hunting on sitatunga was minimal (Hughes, 1933). Ansell (pers. comm.) is of the opinion that sitatunga are little affected by human predation today.

CONSERVATION AND PROTECTION

In the Bangweulu, sitatunga fall well below the black lechwe as a conservation priority, for they may well be the most populous animal there. Their habitat and use of their home range, in addition to the presence of the occasional wildlife patrol and the steady exodus of people away to the mainland, insures their protection.

THE WILDLIFE.

HISTORICAL PERSPECTIVES

The earliest reports of wildlife in the Bangweulu originate in the journals of David Livingstone (Waller, 1973) in which he mentions lion (*Panthera leo*) and the vast herds of black lechwe. These reports were followed by the detailed descriptions of Hughes (1933) who lived in the Bangweulu for 18 years and wrote: "the numbers of lechwe must be seen to be believed". He described in great detail the profusion of other wildlife inhabiting the area. This work was followed by the faunal survey of Pitman (1934), which also chronicled the abundance.

PRINCIPAL SPECIES OF THE BANGWEULU (Appendix B)

a. Black lechwe (*Kobus leche smithemani*)

Accounts of the numbers prior to the high water period of the nineteen thirties, are, like most early assessments of wild populations, highly subjective. However, Grimsdell and Bell (1975) do estimate there must have been at least 150,000 lechwe. Since that time the population plummeted, the decline further influenced by the flood of the early sixties, until they numbered some 17,000. From this low point, the population rose to the present level of 29,000. The last count was carried out in 1975 (Manning and Moss, 1975).

b. Lion (Panthera leo)

Populations of lion appear to correspond closely with those of their chief prey species, the black lechwe. The early reports of Hughes (1933), Pitman (1934), Allen (1963) and the accounts of others (Mateyo, Rowher and Hanken pers. comm.) confirm the abundance of lion. However, since the flood of the early sixties, lion numbers appear to have decreased drastically, a function perhaps of high water and declining lechwe numbers. I saw and heard few lion during three years of concentrated activity in the south-east Bangweulu.

c. Leopard (Panthera pardus)

Leopard are present in the woodland fringes bordering the swamp. Although only one was seen (found with the remains of a bushbuck Redunca arindinum), regular sign of a large male was noted in study area 3 on N'go island. My assistants stated that the leopard occasionally fed on Clarius sp.

d. Crocodile (Crocodylus niloticus)

Crocodile are common if not abundant in the swamps. They are likely to be an important predator of sitatunga in those areas where open water allows them to swim and hunt for Clarius sp. and other fish.

e. Python (Python sebae)

Python are common in the swamps being occasionally caught in the gill nets of the fishermen. They appear to live principally on fish but probably take sitatunga and lechwe when possible. They were usually encountered in _Phragmites_ thickets when driving sitatunga for collection.

f. Hyena (_Crocuta crocuta_)

Hyena prey mainly upon lechwe and their movements are dictated by the movement of this antelope. Two dens were found which were only occupied when the main lechwe migration arrived back in the wet season range. At this time adult male lechwe are vulnerable due to their defense of leks which allow hyena to approach closer than at other times (Manning, in prep.).

g. Elephant (_Loxodonta africana_)

A small population (c. 150) live permanently on the periphery of the swamps (Grimsdell and Bell, 1975). I frequently observed the same individuals within the Lukulu estuary and a short distance into the main swamp.

h. Buffalo (_Syncerus caffer_)

Grimsdell and Bell (1975) recognized four herds in the area. The two herds found close to human settlement decreased in size between 1969 and 1973. The other two increased.

i. Tsessebe (_Damaliscus lunatus_)

Most tsessebe occupy the large plains south of the Lukulu and the Lulimala river. No estimate of their population is available. They are heavily poached.

THE SITATUNGA.

TAXONOMY

ORDER:	Artiodactyla.
Suborder:	Ruminantia.
Infraorder:	Pecora.
Family:	Bovidae.
Subfamily:	Bovinae.
Tribe:	Tragelaphini.
Genus:	*Tragelaphus* Blainville.
Species:	*Tragelaphus spekei selousi* Rothschild, 1898. (Sidney, 1965; Kingdon, 1982)

The sitatunga is a member of the tribe Tragelaphini and is distinguished from other members of the tribe by its elongated hooves, an adaptation to its semi-aquatic existence. The species exhibits great variability in the colour of its pelage even within a sub-species and this has led to a plethora of races being described. A past worker (Sidney, 1965) has described several but Kingdon (1982), relating the designations to the overall distribution appears to favour three distinct populations, each centred on a river system or drainage basin. They are:

Tragelaphus spekei gratus

Tragelaphus spekei spekei

Tragelaphus spekei selousi

The form found in Zambia is *Tragelaphus spekei selousi* with *inornatus* being regarded by Ansell as a synonym (pers. comm.)

THE TRIBE TRAGELAPHINI

The Tragelaphini are medium to large antelopes with spiral or twisted horns. They exhibit a 'gleaner' strategy (Kingdon, 1982) and are continuously dependent on a constant supply of green, leafy growth and cover. They are also known for their cryptic behaviour and use the vegetation as a prime defence against predation rather than a rush and escape pattern common for open plain grazers. All the species have stripes and similar black markings on the legs, throat and head. According to Kingdon (1982), sitatunga, bushbuck (*Tragelaphus scriptus*) and eland in the drier and colder parts of the continent, show less striping and are generally thicker coated than their northern conspecifics.

Vision and hearing are acute and they tend not to take account of a man's scent (Hughes, 1933). However, the degree of sensitivity related to smell is more difficult to assess and may be the reason for the conclusion that their sense of smell is not as important as it is in other antelopes (Kingdon, 1982; Hughes, 1933). Sitatunga, kudu (*Tragelaphus strepsiceros*) and bushbuck, because of their dense habitat tend to react first to auditory stimulae and then wait for the noise to be confirmed visually. However, where predation from humans is excessive, they move rapidly into the thickest part of the vegetation.

The genus Tragelaphus exhibits marked sexual dimorphism with regard to body size, colour and the presence of horns in males (Plate 2). They make use of severe habitat at times, being found between 2,800 m and 3,600 m in the mountains of Ethiopia (Brown, 1969; mountain nyals, Tragelaphus buxtoni) and in the swamps and forest edges of the vast Congo basin (sitatunga) as well as semi-desert areas such as the Kalahari (greater kudu). Those races or species found in the mountains tend to be much larger in body size.

There are numerous fossils of the T. spekei/T. angasi type, covering a period of over five million years. The sitatunga may represent the most conservative form (Kingdon, 1982) with the tragelaphine pathway tending to radiate away from the moister, forested areas and into the more open and arid savannah and bushveld.

Mutual grooming is highly developed and licking has a placatory function both during mock-fighting and during mating behaviour (Walther, 1964). The mating display is also well developed with the male commonly driving the female before him in a straight line, stretching his neck and laying it on the cow's withers. These ritualized actions distinguish the tragelaphines from other horned ruminants (Walther, 1964).

'Lying out' is a phase common among this group, where the calf is secreted in dense cover for the first 14 days after birth (Walther, 1964).

DISTRIBUTION AND STATUS

The sitatunga is widely distributed. It is found in West Africa, Equatorial Africa, Angola, Zaire, Sudan and the western edge of East Africa, then south through Zambia and into the northern part of Botswana. Isolated populations occur in Lake Chad and the Gambia (Sidney, 1965) but not in Ethiopia (Micheale, pers. comm.) (Figure 6). Within the general range sitatunga may be expected to occur in any marshland area with adequate cover and interspersion of cover types. Anomalies here are the sitatunga of Nkose island in the Lake Victoria region which inhabit a dry, heavily bushed area. Sitatunga spoor has also been observed in the equatorial forest of Zaire although I could not confirm that the sightings were far from a swamp area (Macleod and Callens, pers. comm.).

The species would appear to be allied with large river systems or drainage basins with *T.s. gratus* having its stronghold in the Congo basin; *T.s. spekei* in the Lake Victoria basin and *T.s. selousi* on the Bangweulu, Zambesian and Okovango basins (Kingdon, 1982).

In Zambia, the species is well represented (Figure 7) though absent from the Eastern province, Luangwa valley and middle Zambesi valley (Grimwood *et al.*, 1958). In the Southern province it occurs only on the Kafue flats (Ansell, 1960). Possibly its greatest stronghold is in the Bangweulu swamps and the rivers which flow into the system. Here it

Plate 2. Sitatunga adult male.

may well be the most numerous species (Grimsdell and Bell, 1975) but other workers have tended to regard it as a species nowhere in great abundance (Owen, 1970), or have even failed to register it within a portion of its range (Sheldrick, 1981) as in the case of the Bangweulu where there is at least 650 km^2 of prime habitat (Grimsdell and Bell, 1975).

Sheldrick (1981) states that today it only occurs in three separate areas of Central Africa; in the vicinty of the Niger river, and around the headwater regions of the Congo and Zambesi rivers, but offers no evidence to support this.

Until recently, a sitatunga male was seen on a number of occasions in a small marsh located on the outskirts of Lusaka, Zambia (Uys, pers. comm.), while on the edge of Chiundaponde village on the Lulimala river (study area 1), I was able to observe half a dozen sitatunga on occasion. Sitatunga also occur in small patches of swamp further upstream in the woodland and are found close to Mpika on the plateau, in the Luitikila marsh (Figure 2). Perhaps it is therefore understandable that they are described as a little known species that spends the days underwater with only its nose poking above the surface (May, 1982).

SITATUNGA LITERATURE REVIEW

The sitatunga has received a fair amount of attention from man, but most of it is of a conjectural nature. The earliest quantitative approach was possibly that of Meinertzhagen (1916). He made certain detailed descriptions of the species and took physical measurements of a few adult males. Other reports were compiled by Pitman (1928) and Lydekker (1908) but none of these contained any in-depth details of the biology of the species. Mention was made by hunters of stomach contents (Roosevelt, 1910) and a great deal regarding its swamp habitat in the central Bangweulu (Hughes, 1933). Aspects of its taxonomy, distribution and breeding were considered by Ansell (1960), 1963, 1978). Short descriptions were attempted by Bere (1962), Smithers (1966) and Astley-Maberley in Owen (1970) while details of taxonomy were addressed by Allen (1939). A natural history article by Jobaert (1957), and one comprehensive paper on the distribution of the species (Sidney, 1965) are also available. General behavioural observations carried out in zoos appear in a paper by Walther (1964). However, the first contemporary scientific report was produced by Owen (1970) following her 16 month study of the sitatunga of the Saiwa swamp in Kenya. She paid particular attention to distribution within the habitat, daily activities and food preferences. Since then, one article has appeared (Manning, 1975) in which some of the findings of this study first appeared. A general presentation of the ecology and evolution of the species, culled from published work, personal observation and communications from myself, appeared in a comprehensive review of the wildlife of East Africa (Kingdon, 1982).

MATERIALS AND METHODS.

CAPTURE

Equipment and Techniques

Sitatunga were caught with the use of an Aircat 17/180 airboat which is able to reconnoitre all but the densest vegetation. It is fast and manoeuverable and able to run in depths as low as 2 cm of water. Adult and subadult males were noosed from the front or side of the boat with smooth rope supported by *Phragmites* poles 3-4 m in length attached to the bottom of the driver's seat (Plate 3). Females and smaller males (occasionally adult males) were simply jumped on from the airboat. Care was taken to grasp the rear legs first followed by the head and forequarters. The legs were immediately bound and the eyes hooded with strips of hessian. Animals were then placed in the bottom of the airboat and the legs tied to the struts. A total of 130 sitatunga and 123 lechwe (as part of a separate project) were captured this way. Two sitatunga died from airboat injury.

I attempted to capture as many animals in as short a time as possible as the noise of the airboat eventually caused sitatunga to move into the dense cover adjoining the river.

Tranquillization

Following capture, sitatunga were injected in the rump with a tranquillizer using a Gilette 1 ml (Tuberculin) syringe and No. 17 needle which, together with the blind-folding, produced a suitably tranquillized state. Initially, the drug Rompum was used (made by Bauer, Germany). This drug works well with lechwe at dosage rates of 0.5 - 1 ml per 100 kg live weight and acts as an analgesic, a muscle relaxant, and a sedative. However, the state of tranquillization and immobilization of sitatunga with Rompum was poor even at dosage rates of 5 ml per 100 kg live weight. Thus the drug Combelen was used successfully, at dosage rates of 3 ml for animals weighing up to 30 kg, 4 ml for those weighing between 30 and 70 kg and 5 ml for those heavier than 70 kg.

SHOT SAMPLE

A small sample was shot with a light calibre rifle (.270) fitted with a 4x telescopic sight. Animals were either shot from the airboat or, when dry conditions prevented this, were driven from thickets by beaters and shot as they attempted their escape.

EXAMINATION AND MEASUREMENT

Physical Measurements.

The captured and shot animals were ferried to a nearby anthill or other dry area. As it was possible, especially

Plate 3. Shortly before the capture of an adult male sitatunga in study area 3.

during the early stages of a capture exercise, to capture half a dozen or more animals in short order, examination only ensued after six or more animals had been captured. The information collected, and methodology used, followed Grimsdell and Bell (1975) from whom I took over the field station.

a. Live weight

All sitatunga were weighed from a specially made lightweight tripod, fitted with a block and tackle and a Salter 200 kg spring balance. A canvas sling, with metal rings in each corner, was used to weigh the animals.

b. Measurements

The following body measurements were made with a steel tape measure.

1. Heart girth, measured immediately behind the forelegs.
2. Neck girth, measured half way along the neck.
3. Shoulder height, measured firstly from the highest point of the wither to the base of the hoof, and secondly to the tip of the hoof.
4. Body length, measured along the mid-dorsal curve from the tip of the nose to the base of the tail.
5. Tail length, measured from the base of the tail to the tip, excluding terminal hair.
6. In males: horn length, spread and base diameter.

In addition, measurements of frame size were taken following those made on sheep (Turner *et al.*, 1953).

1. Wither to pinbone: from the most anterior palpable spinous process of the thoracic vertebra, commonly found in front of and between the scapulae, to either sciatio tuber.
2. Width at hips: from the point of the ilium which is furtherest from the midline of the back (i.e. the tuber coxae) on one side to the corresponding point on the opposite side.
3. Width at ribs: the maximum width through the level of the second last rib (care being taken to place the tips of the calipers on the ribs and not let them sink in between).
4. Width at shoulders: from the lateral tuberosity of one humerus to the corresponding part of the other.
5. Depth of chest: the vertical distance from the highest point of the wither, at the point used to measure wither height, to the ventral surface of the sternum.
6. Wither height: from the top of the olecranon process to the mid-lateral point of the coronet.

These frame size measurements were made with a wooden sliding metre-rule scale.

c. Body Condition Scoring

This follows the system given by Russel et al. (1969) for the subjective assessment of body fat in live sheep. The method entails assessing the prominence of the spinous and transverse process of the anterior lumbar vertebrae by palpation. As found by Grimsdell and Bell (1975), reference to subcutaneous fat (absent in lechwe and sitatunga) has been

been omitted in the list which follows. The condition scores are:

Grade 0: extremely emaciated on the point of death.

Grade 1: spinous processes prominent and sharp; transverse processes also sharp, the fingers pass easily under the ends, and it is possible to feel between each process; Mm. longissimus dorsi shallow.

Grade 2: spinous processes prominent but smooth, and individual processes can be felt only as fine corrugations; transverse processes smooth and rounded, and fingers can be passed under ends with little pressure; Mm. longissimus dorsi of moderate depth.

Grade 3: spinous processes have only a small elevation, are smooth and rounded, and individual processes can be felt only with pressure; transverse processes smooth and well covered, and firm pressure is required to feel over ends; Mm. longissimus dorsai full.

Grade 4: spinous processes can be detected with pressure. Transverse processes cannot be felt; Mm. longissimus dorsi full.

Grade 5: spinous processes cannot be felt even with firm pressure. Transverse processes cannot be felt; Mm. longissimus dorsi very full.

Marking

All captured sitatunga were marked with collars if they were adults or ear tags if they were anything else. The collars used were Dalton cattle collars (yellow, white, red and blue) and the tags used were Ketchum 'visa' ear tags. Recaptured animals received an additional collar or ear tag. The tags were assigned an order related to colour and position on the ear so as to facilitate recognition from a distance.

AGE DETERMINATION

Introduction

Methods for determining the age of mammals have been dealt with at length by Morris (1972) and Spinage (1973). In a population such as the sitatunga, for which no age criteria have been previously presented, and for which, with the exception of maxillary row of a known-age zoo animal, I was unable to obtain any evidence from known age animals, the methodology had to follow an arbitrary sequence of impressions (made from one maxillary row). Age classes were then related to the eruption and attrition sequence. These result in a sequence of relative age only. It was not possible to determine absolute age for reasons previously mentioned as well as the fact that sitatunga breed throughout the year. However the aids available did allow for reasonable precision, especially for use by the field worker (Spinage, 1967 and 1973) (Appendix C).

Eruption and Attrition.

As most animals handled were released after examination it was necessary to collect impressions of the teeth in order to determine age. This is easily carried out in the field. A metal tray, with a handle, was covered with well kneaded plasticine and placed between the maxillary and mandibular tooth row with the aid of a sliding gag. An impression was then taken of the maxillary row. Positive casts were made later with plaster-of-paris giving a permanent record of the particular animal handled. The impressions were then divided as to sex and placed into rough categories related to weight. In the case of the males, further divisions were made with the use of horn measurements and photographs taken to record horn development (Figure 8). This rather rough sequence was further refined by placing the sample of animals in a sequence related to the eruption and replacement sequence for artiodactyls (Thomas and Bandy, 1975). Comparison with published data on the nyala (Tragelaphus angasi), a species anatomically similar to the sitatunga (Kingdon, 1982) also helped in determining the sequence. This was particularly helpful with regard to the eruption and replacement sequence (Anderson, 1978), and the more general, subjective aspects of age assay (Tello and van Gelder, 1975: Rowe-Rowe and Mentis, 1972 and Vincent et al. 1968). Further refinement was attained with the use of animals which had been recaptured at yearly intervals and, in one case, recaptured twice.

The final sequence of relative age encompassed seven eruption and replacement groups, and ten wear groups (Appendix

C). Information on longevity, birth weights and weights at specific age was obtained from seven zoos which allowed greater accuracy in determining relative age.

REPRODUCTION

All captured females were tested manually to determine their lactational status and udder size.

All foeti present in the shot sample were collected, sexed if large enough, and then weighed. A note was made of their general development, pelage growth, and colouration.

Foetal Growth.

In order to arrive at an estimate of foetal age the formula for mammalian foetal growth, derived by Huggett and Widas (1951) was used. The formula is:

$$\sqrt[3]{W} = a(t - t_0)$$

W is foetal weight, a is the "Specific foetal growth velocity", t is foetal age and t_0 is a numerical value estimated by analogy with other mammals for which foetal weight and age data are available.

This formula has found practical application in a few African herbivore studies (Allsopp, 1971; Anderson, 1978; Bradley, 1977) although the latter has criticized the careless manner of its application. Foetal growth constants a were calculated and the formula used to derive foetal age from the sample.

FIELD SEX AND AGE CLASSIFICATION

Field sex and age classification were based on parameters of body size, pelage colour, and horn growth and development in study areas 1, 2 and 3. The sex and age criteria for such a classication appears in Table 1.

For females it was necessary to combine the classes of juvenile and subadult into the single class of immature due to the difficulties of discriminating any further. Adult males were not further divided as in Anderson (1979), due to the difficulty of doing so in the field. As a result, certain males which might better be described as subadult were included in the adult classes. This is crucial when discussing the question of territoriality.

Sitatunga were further classified in study area 2 and 3 using the age determination methods outlined. This covered the majority of the animals in study area 3 and a percentage of those in study area 2, as well as a few outside both areas but within the Lukulu estuary.

Table 1. Field sex and age criteria.

Class		Sex	Description
I	Calf	F	Body height below belly line of adult female.
II	Immature	F	Animal larger than I but smaller than III.
III	Adult	F	Animals larger than II and obviously large and mature.
I	Calf	M	Body height below belly line of adult female.
II	Juvenile	M	Horns with no obvious twist, usually less than two ear lengths.
III	Subadult	M	Animals with horns of adult bushbuck type i.e. those that have just completed the second twist but have not begun to point to the side. Obvious large size.
IV	Adult	M	Large males with mature sets of horns.

OBSERVATIONS

The vast majority of observations of sitatunga were made from the airboat which enabled me to collect the necessary information on the movements, aggregations, sex and field-age criteria classifications, habitat preferences and behaviour. This information was added to observations made on foot (described later) while aerial surveys gave information on distribution and habitat use.

GROWTH

Weight curves were derived for a sample of 119 sitatunga, and a horn curve for 51 males using a computer derived polynomial regression equation based on relative-age criteria (Tosh, pers. comm.). The curves were fitted by eye. Computer derived correlations were also obtained for various parameters of isometric growth in males and females, and for males and females combined.

RESULTS AND DISCUSSION.

PHYSICAL CHARACTERISTICS.

The sitatunga is noted chiefly for its long hooves which affords it purchase in its swamp retreats. The species, as for other congenerics, exhibits marked sexual dimorphism, with only the males carrying the typical spiral horns of its tribe. Males are much larger than females. The coat is long (5 - 7 cm) and shaggy, unlike the silky coat reported for the East African variety by Lydekker (1908). It is also coarse and variable in colour, ranging from the chestnut shades of some of the younger animals and females, to the dark brown and grey for the adult males (Manning, 1975; Jobaert, 1957). In general, the degree of colouration and the presence of white markings is not as marked as reported for <u>T.s. gratus</u>, which is strongly striped and patterned in both sexes (Kingdon, 1982). The sub-species <u>selousi</u> was differentiated from <u>gratus</u> due to the erroneous report that the sexes were of the same colour (Lydekker, 1908).

Sitatunga, in common with their congenerics, 'cross-walk', a primitive pattern of locomotion (Sheldrick, 1981) where the front and hind legs on the same side of the body move forward together. Although able to move swiftly within a marsh they are ponderous on a firm surface and were never observed trotting.

PELAGE

The predominant pelage colour tones are dark brown, grey and chestnut, with some scattering between. Calves of both sexes as well as immature and adult females are evenly distributed between these two poles of the colour phase. Juvenile males are mainly dark brown (84%), while subadult and adult males are all brown/grey tending, with increasing age, toward a dark grey colour over the body and charcoal/ black on the face and legs. About 10% of females and juveniles, and calf males exhibit the typical spots and stripes of the bushbuck but not as marked as those found in T.s. gratus. Spots or stripes are not apparent in the old males.

The only white colouring found in the population is the nose chevron and facial marks of the cheek, throat and chest band, and the marks at the point where the forelegs meet the chest. Not all animals possess the nose chevron. The colour of the belly hair is the same as the predominant pelage colour and not white as in most other antelope. The skin of the belly and udders is either pink or black.

HORNS (Figure 9)

The horns of sitatunga while adhering to the general lyre shape, do show great variety. Horns may be fairly straight, or have the twists of bushbuck males, or they may describe the outline of a graecian urn (Figure 8). All the varieties were observed. The different horn shapes described by Meinertzhagen (1916), as distinguishing the Nkose island, Entebbe and Bugalla sitatunga are also found in the Bangweulu.

The horns are indistinguishable from those of the nyala, although Lydekker (1908) believes them to be dissimilar. The horns which I have observed in other parts of Zambia, from the Okovango delta of Botswana, from zoos in Europe and the United States appear to conform strongly to type.

The record length of horn, measured along the front curve, is 91.12 cm ($35^{7/8}$") shot by J.E. Hughes (Best <u>et al</u>., 1962.). The longest measured in the Bangweulu during this study was 77.41 cm (30½") and the mean length for the adult population sampled (n=18) was 64.18 cm (25½").

A comparison of the horn lengths of three sitatunga populations is provided in Table 2.

Table 2. Comparative horn measurements ($\bar{x}$) for three populations of adult sitatunga (cm) (Meinertzhagen, 1916; this study)

Place	Sample	Length	Base girth	Tip to Tip
Bugalla *	5	59.94	19.20	38.81
Nkose *	5	54.86	18.66	20.70
Bangweulu	18	64.18	18.41	30.14

* <u>sylvestris</u> (Meinertzhagen, 1916)

The difference in mean horn measurements between the Bugalla and Nkose populations combined, and that of the Bangweulu population, is not significant ($x^2 = .38$; d.f = 1; $p>0.05$.). There would therefore appear to be little validity for the erection of the race sylvestris on account of its smaller horns as reported by Lydekker (1908).

HOOVES

The hooves of sitatunga have attracted considerable attention and have been responsible for separating the species from the bushbuck (Lydekker, 1908) and for the unjustifiable creation of a new race T.s. sylvestris (Kingdon, 1982), on the basis of a population inhabiting a dry heavily bushed island. According to Meinertzhagen (1916), these animals possessed slightly shorter but stouter and stronger hooves than the specimens from elsewhere. With the passage of time, this race was described as having stouter and shorter hooves (Sidney, 1965; Allen, 1939; Owen, 1970; Kingdon, 1982) although the latter recognized them as being marginally shorter.

Comparison of the Bangweulu data with those of Meinertzhagen (1916) is difficult since measurements were not taken of hoof breadth in this study, and where measurements of hoof length were recorded they differed from those of Meinertzhagen. Meinertzhagen took measurements of the top curve of the true hoof while I took the lower. However, the length of the top measurement is less than that of the bottom measurement by approximately 23%. Table 3 provides a comparison of the race said to have shorter hooves than those of other sitatunga.

Table 3. Comparisons of front hoof length of adult males for three populations of sitatunga (cm)

Place	Sample	Upper curve	Lower curve
Bugalla *	5	7.65	
Nkose *	5	7.70	
Bangweulu	17		7.55

*"sylvestris"

There is little difference in the lengths of the hooves in the Bugalla and Nkose populations and both tend to be larger than the mean front hoof length of the Bangweulu sample. The corrected values (+ approximately 22.33%) for these two populations are: Bugalla 9.43 cm and Nkose 9.49 cm.

From observations in zoos, sitatunga hooves tend to curl back and do not wear down as might be expected. Table 4 provides comparisons of hoof width for two populations of "sylvestris".

Table 4. Average hoof widths of two sitatunga populations (Meinertzhagen, 1916).

Bugalla	(n=10)	4.30 cm
Nkose	(n=10)	5.76 cm

In common with lechwe, sitatunga possesses no hair at the back of the hooves.

TRANQUILLIZATION.

The first few captured sitatunga were injected with the drug Rompum at dosage rates of 5 ml per 100 kg live weight. This drug has little effect on sitatunga, a finding corroborated by the Paris zoo (Densmore, 1979). Rompum is effective however on the black lechwe at dosage rates of 1 ml per 100 kg live weight (Grimsdell and Bell, 1975; this study).

The drug Combelen was then used, producing satisfactorally tranquil states in the captured sample at dosage rates of 5-9 ml per 100 kg live weight. Early trials showed that a minimum dosage of 3 ml was required for the smallest animals. Later in the capture programme, 4 ml of the drug were used on all but the adult males, suggesting that application rates were of necessity much higher for small animals than for large ones.

In instances when individuals had to wait for more than an hour to be measured, they were injected with a further full dose. No ill effects were observed due to sustained tranquillization.

Pregnant females, or animals which were not tired when caught, required a higher dosage in order to produce the desired state of tranquillization. Animals which were not blindfolded or handled quietly and gently, also required a higher dosage than normal. In a number of cases, animals were blindfolded, but not tranquillized and, provided they were handled carefully, lay still for the period necessary to extract the data.

When an adult male reedbuck (Redunce arindinum) was caught (weight, 77 kg) and injected with 5 ml of Combelen it became deeply sedated and showed evident signs of stress by a greatly increased heart rate and heavy salivation.

POPULATION PARAMETERS.

SEX AND AGE CLASSIFICATION

Sitatunga observed or captured within the three study areas were assessed by the field methods described, as well as by the relative age determination methods. The field method allows for rapid assessment but is highly subjective.

Field Criteria

Study Area 1 (Kang'omba marsh)

The total observed sample within study area 1 is shown in Table 5.

Table 5. Study area 1: sex/age composition (Field criteria)

Number (n)	Sex	Field Age Class
1	M	IV
2	M	III
1	M	II
3	F	III
1	F	II
1	? (calf)	I
	sex ratio (excl. calf)	1:1

a. Study Area 2 (Lukulu estuary)

All animals observed over a period of three years are classified according to the field criteria in Table 6.

Table 6. Study area 2: sex/age composition (Field criteria)

Number	Sex	Field Age Class	Percentage of sightings
33	M	IV	25.8%
7	M	III	5.4%
8	M	II	6.2%
67	F	III	52.3%
6	F	II	4.7%
7	? (calf)	I	5.5%

Sex ratio (excl. calves): 40M:60F

($X^2 = 4.0$; d.f = 1; $p > 0.05 < 0.02$; difference from a sex ratio of 1:1 is barely significant)

The results of Owen's (1970) observations are difficult to relate to the Bangweulu situation as the methods of field classification are not defined. However, there is close correlation for Class III females (Adults 52.3% - 50.5%) and overall, for combined males (37.4% - 31%) and combined females (57% - 65.8%). Far more Class IV males (Adults) were classified for this study (25.8% - 13.1%), though far fewer for Class III males and Class II females (5.4% - 17.9%) and (4.7% - 15.3%) respectively. Some of the variation may be ascribed to differences in field criteria.

b. Study Area 3.

A more accurate picture is probably presented by Table 7 which is based on field criteria accorded a population captured over a short period each year at the onset of the rains, for three consecutive years.

Table 7. Study area 3: sex/age composition (Field criteria)

Number	Sex	Field Age Class	Percentage of sightings
20	M	IV	25.0%
4	M	III	5.0%
7	M	II	8.7%
11	M	I	13.7%
31	F	III	38.7%
3	F	II	3.7%
4	F	I	5.0%

Sex ratio: 42M:38F

(x^2 = 0.16; d.f = 1; $p > 0.05$; difference from a sex ratio of 1:1 is not significant.)

The percentage sightings for calves of 18.7% is indicative of a population with a healthy base, but is in marked contrast with the 5.5% of study area 2. This may be due to the avenues of escape available in study area 2 where cover interspersion is in marked contrast to the more open and uniform vegetation of study area 3.

c. Combined Data.

The percentage composition of the sex and age field classes for the Saiwa swamp (Owen, 1970) and for area 2, 3, and 2 and 3 combined in this study is shown in Table 8.

Table 8. A comparison of the sex/age composition (Field criteria) for Study Area 2 and 3, and for 2 and 3 combined, and for the Saiwa swamp (Owen, 1970)

Sex/Age and Field Class	Owen %	(n)	Area 2 %	(n)	Area 3 %	(n)	Area 2+3 %	(n)
Adult male IV	13.1	(85)	25.8	(33)	25.0	(20)	25.5	(53)
Imm. Male III/II	17.9	(116)	11.6	(15)	13.7	(11)	12.5	(26)
Adult female III	50.5	(327)	52.3	(67)	38.7	(31)	47.1	(98)
Imm. female II	15.3	(99)	4.7	(6)	3.7	(3)	4.3	(9)
Calf I	3.2	(21)	5.5	(7)	18.7	(15)	10.6	(22)

Sex ratios (excl. calves)
32M:68F (Owen) and 42M:58F (This study)

A Chi square test shows that the difference of my sample from a sex ratio of 1:1 is not significant: $x^2 = 2.56$; $p > 0.05$; d.f = 1; while that of Owen is highly significant: $x^2 = 13$; $p < 0.005$; d.f = 1.

The sex ratio for the sample based on relative age criteria (n = 119) is 51 males to 68 females. ($x^2 = 2.42$; d.f = 1; $p > 0.05$).

Based on the total observations (n = 208) there were 96 males and 112 females, if the 22 calves are split according to the total sexed sample of 79M:107F. ($x^2 = 1.38$; d.f = 1; $p > 0.05$).

Birth records from the Antwerp zoo reveals 50 males to 66 females (n = 116; x^2 = 2.20; d.f = 1; p>0.05).

The consistency of the ratios with those of the Antwerp zoo, and with each other, suggests that my sample is representative of the total population.

RELATIVE AGE AND SEX COMPOSITION

The population pyramid for study area 3 (Figure 10) reveals a population having a broad base and tapering gradually until group F. From this point there is an abrupt drop which continues on until group J. The very large representation of males over females in Group 1 (Figure 10) may be a sign that differential mortality exists with regard to males; for as can be seen, males are underrepresented from group E onwards. This is amply illustrated in Figure 11 where males from group A onwards comprise 23.5% of the sample in comparison to 43.7% for females. This is also the case for the total sampled population (Figure 12). Although group B and D are underrepresented (Figure 11 and 12), this may be ascribed to the difficulty in differentiating those groups lying between A and E.

AGE DETERMINATION

A total of 120 impressions of maxillary teeth was obtained from the captured and shot sample. These are assigned to seven groups based on the eruption and replacement sequence of the deciduous and permanent teeth. A further ten groups are defined based on the progressive attrition with age of the permanent molariform teeth (Appendix C).

a. Maxillary Age Determination Criteria.

Group I.

Full term foetus (6 kg) had Dp I, Dp II and Dp III partially erupted. This is taken as the likely situation at birth as zoo records give birth weights ranging from 1.8 kg - 4.6 kg.

Group II.

In the youngest animal of 8.5 kg, Dp I, Dp II fully erupted and Dp III still not at full height. In the older animal of 14.5 kg, Dp I, Dp II and Dp III fully erupted and in use.

Group III.

MI erupting or fully erupted. Information from zoos would place this group in the three month class.

Group IV.

M2 partially erupted in youngest animals or, in the case of the older animals, has not attained full height. Dp I concave and Dp II showing signs of wear.

Group V.

M2 at full height. Dp II and Dp III present. Dp I worn smooth on occlusal surface. Infundibula absent. Wear on Dp III.

Group VI.

M3 not at full height. Dp II worn smooth. Dp III worn, with greatly reduced infundibulum, usually on posterior side.

Group VII.

Pm 2, Pm 3 and Pm 4 erupted or not at full height.

Group A.

All permanent teeth in use but Pm 4 not at full height in younger animals. In the older animals Pm 4, Pm 3 and Pm 2 have deep infundibula.

Group B.

Infundibula of Pm 2 and Pm 4 still deep.

Group C.

Pm 2 has spot of exposed dentine. Infundibula of Pm 3 and Pm 4 shallower.

Group D.

Pm 2 concave and worn with infundibulum absent. Infundibula of Pm 3 and Pm 4 slightly shallower.

Group E.

Pm 3 and Pm 4 have shallower infundibula. Secondary infundibulum (spot) of MI smaller, occlusal surfaces broader.

Group F.

Pm 3 and Pm 4 occlusal surfaces worn with infundibula smaller. On MI the secondary infundibulum now absent. The decrease in size of the infundibula and the general increase in wear is marked between group E and F in comparison to the degree of wear found between A and D.

Group G.

Pm 2 increasingly concave. Pm 3 infundibulum shallower with increased wear on occlusal surface. Pm 4 anterior infundibulum shallower. M2 secondary infundibulum slightly smaller.

Group H.

Increased wear on MI occlusal surface from the mid-point of the tooth to the posterior end with a small circular area of infundibulum remaining.

Group I.

M1 posterior infundibulum greatly reduced or missing. General evidence of increased wear. M2 secondary infundibulum reduced in size.

Group J.

Posterior side of Pm 3 concave. M1 occlusal surface concave. Secondary infundibulum on posterior side reduced. Secondary infundibulum on M2 missing and greatly reduced on M3.

b. Discussion.

Using the methods and aids so described, the sample of 122 animals covers the years 0 - 11+. Although sitatunga have been recorded living to 17 years, 5 months and 5 days (Flower, 1931) and in another case 14 years (Manton pers. comm.), it would appear unlikely, from the sample, that they live much beyond 12 years in the wild.

The wear groups A, B, C, and D were difficult to differentiate, the degree of wear being barely noticeable as seen from recaptures. Wear increased considerably from group F making it appear easier to classify those groups, although this has not been found to be the case elsewhere (Thomas and Bandy, 1975).

The single known-age animal was classified as a sub-adult after seeing its horns and was placed in group C according to its degree of wear. This may lend some credence to the theory that the wear of teeth is determined solely by aspects of tooth physiology and not by differences in diet as may be experienced by sitatunga in zoos as opposed to those in the wild (Spinage, 1973). The known-age animal was 3 years and 10 months old and although it fitted into group C, which roughly corresponds to the four year old class, the wear on M1 did appear to be greater than for teeth in either the A, B, C or D groups.

GROWTH

The following computer derived polynomial regression equations for growth in live weight with relative age, were derived by Tosh (pers. comm.)

Males: $\text{Weight} = 108.67 - 1.42(\text{age} - 8.01)^2$

$(n=51)\ r^2 = 95.3\%$

Females: $\text{Weight} = 51.5 - .497(\text{age} - 7.344)^2$

$(n = 68)\ r^2 = 69.4\%$

Description: $\text{Weight} = W_\infty - \text{shape}(\text{age} - \text{max. wt. at age})^2$

The quadratic growth curves are shown in Figure 13 for males and Figure 14 for females. The maximum theoretical weight for males of 106 kg is achieved at 8.01 years of relative age, while for the females maximum weight of 51.5 kg is reached at 7.34 years. The maximum live weight of males is 54.59% heavier than that for females, which illustrates the extreme sexual dimorphism of the species. It is also clear that the females reach maximum growth faster than males. Males therefore continue to grow in size to a greater age than females.

As the bulk of the data used to derive the curves were collected at the height of the rains, it is likely that this is representative of the season where maximum growth occurs. It has therefore not been necessary to omit data collected from animals measured in the winter due to the lowered growth rate (Jeffrey and Hanks, 1981; Anderson, 1978)

a. Horn Growth

Growth of horns with age is shown in Figure 15 with the curve being fitted by eye. This clearly shows that horns become progressively worn with age due to the 'horning' action of the males during agonistic displays. Maximum growth is reached at 7.5 years.

b. Relationship of Growth Parameters

Computer derived linear correlations for males (n = 51) and females (n = 68) are shown in Table 9-10. Significantly high correlation coefficients for males, of weight to length/ weight, and of weight to horn length, and horn length and weight to age are evident. Poor values are obtained for the condition indices.

Table 9. Linear correlations of physical parameters for males.

	Age	Len/wt	horn	weight	height	length
Len/wt	.869					
Horn Length	.901	.953				
Weight	.898	.989	.972			
Height	.623	.817	.736	.791		
Length	.795	.864	.865	.903	.724	
Condition	.226	.275	.211	.227	.149	.086

(r = 0.229 is significant at the 0.05 level.)

Table 10. Linear correlations of physical parameters for females.

	Age	Len/wt	Weight	Height	Length
Len/wt	.602				
Weight	.678	.953			
Height	.600	.689	.687		
Length	.649	.631	.823	.537	
Condition	.134	.147	.112	.011	.027

(r = 0.195 is significant at 0.05 level)

c. Discussion.

As it has become increasingly necessary to set maximum sustainable yields for the exploitation of populations, it is important to make objective assessments of growth. There are two important aspects of quantitative growth studies, allometry and isometry (Hanks, 1972). The first means a change of proportion, with increase in size (Reeve and Huxley, 1945); and the second is a linear relationship of relative growth, covering such body measurements as weight and length.

In an attempt to treat growth in an objective mathematical manner scientists have sought the universal growth equation, described by Medawar (1945) as a fiction. There are many growth models and, of the simple ones, none fit perfectly or are able to accommodate anything but monotonic increases of weight with age (Georgiadis, pers. comm.).

An equation which has been put to much use for African ruminants is the von Bertalanffy growth equation (Bertalanffy, 1938), derived by Beverton and Holt (1957) and used by Hanks (1972), Grobler (1980), Anderson (1978), though Caughley (1971) considered it provided a poor fit for the younger age classes.

An attempt was made by Tosh (demons. Comm.) to apply the von Bertalanffy equation to the sitatunga data. When calculations were performed on the growth data for males (weight v age), we attempted to fit the model;

$$W_t = W_\infty \ (1 - e^{-k(t-t_0)})^3$$

This presented two problems. First, the estimate of W_∞, the "maximum weight that an animal can attain under given conditions", was 103.06 kg for the males. As 7 males out of the sample of 51 exceeded this weight they were discarded. Having thrown out all the males between 6.5 (relative age) and 9.5 years inclusive, the non-linear regression still gave a poor fit and yielded an R^2 of 56% ($R^2 = 1$ is a perfect fit and that of $R^2 = 0$ provides no information at all). This highlighted the second problem. An inspection of the male curve revealed that the model was unable to account for the weights of very young animals, a finding similar to that of Caughley (1971), and the lower weights of the very old animals. Because of this a simple polynomial model was fitted to the data provided by the quadratic model $W_t = k_0 + k_1 t + K_2 t^2$. This equation provided a very good fit with an R^2 better than 95% for the males and 69.4% for the females. On repeating the exercise for the females the same results applied.

Body Condition

Indices obtained by palpation showed a poor linear correlation with other parameters of isometric growth. However Grimsdell and Bell (1975) did find it satisfactory when used in conjunction with kidney fat indices.

REPRODUCTION

In the Antwerp zoo females breed at more than 2 years and males will first mate with females at 18 months, but only in the absence of an older, more dominant, male. This highlights the mechanism whereby the young males of some mammal species, though sexually mature, are prohibited from mating by the presence of an older male, either because they are socially inferior or because they do not possess a territory, an essential prerequisite for mating to occur (Manning, in prep; Buechner, 1961; Leuthold, 1966). Anderson (1978) found that only nyala males of 5 years or older mated, i.e. those individuals which had reached asymptotic size.

The data from Wroclaw zoo (Table 11) suggest that sitatunga parturition first occurs at 24 months, and first conception at 1.5 years (Gucwinski, pers. comm.) (Table 12). This is confirmed by Whipsnade zoo (Manton, pers. comm.). A report from the Hanover zoo states that sitatunga and nyala become fertile at the end of their first year or at the beginning of the second year (Grzimek *in* Dittrich, 1971).

Table 12. Ages at first conception, calculated from age at parturition of captive sitatunga.

Conception Age	Parturition Age	Source
1.5 - 2 years	?	V.J.A. Manton Whipsnade zoo (1975, pers. comm.)
13.5 - 22.5 months	21 - 30 months	A. Gucwinski (1975, pers. comm.)
2+ years	?	R. Verlaeckt Antwerp zoo (1975, pers. comm.)

Table 11. Parturition intervals and time of first parturition at Wroclaw zoo (Gucwinski, pers. comm.)

Mother	Mother's Birthdate	Mother's Age at Birth	Calf's Birthdate	Calving Interval
A	1964	5 years	14/3/69	
				15 months
		6 years	11/7/70	
				20 months
		8 years	31/3/72	
				11 months
		9 years	23/2/73	
				12 months
		10 years	24/2/74	
				15 months
		11 years	25/5/75	
				x=14.6 months
B	14/3/69	30 months	28/9/71	
				6 months
		36 months	3/4/72	
				11 months
		47 months	10/2/74	
				8 months
		55 months	30/10/74	
				10 months
		65 months	26/8/75	
				9 months
		74 months	17/5/76	
				$\bar{x}$=8.8 months
C	31/3/72	22 months	21/1/74	
				10 months
		32 months	22/12/74	
				13 months
		45 months	17/1/76	
				$\bar{x}$=11.5 months
D	23/2/73	21 months	27/11/74	stillborn.
E	24/2/74	22 months	7/1/76	end of rec.

The delay between puberty and sexual maturity, and its role in ungulate society as described by Anderson (1978) for nyala, is markedly similar to that of sitatunga. The male forms fewer associations with age and is more solitary and dominant, especially when related to fixed loci.

A female within the home range of a dominant male will attract him during her 2 days of oestrus and allow him to mate with her.

Conception.

Although sitatunga do breed throughout the year, in the Bangweulu, 2 conception peaks are defined (Figure 16). One is in the period immediately following the heaviest rainfall and highest water levels (mid-March - May), and the other peak is in the October - December period marking the onset of the rains. These peaks are derived from observation of the presence of calves throughout the year, from the captured sample, and from the foetal growth velocity extrapolations.

Although these conception and parturition peaks are derived from a small sample of foeti (n = 10) and a small sample (n = 18) of relative age calves captured over a short period in one year (1975), rather than throughout the year, the peaks are supported by studies on bushbuck and nyala (Figures 16, 17 and 18).

The early peak covers the period when the level of water in the sedge marshes begins to drop and the sitatunga retreat to the deeper water and denser thickets of the riverine strip. Conversely, the late peak occurs during an expansion of water onto the sedge marshes with an accompanying spread of sitatunga from the dry season confines of the reed thickets. Both periods are dynamic in nature which may assist solitary sitatunga males to mate with a larger number of females then might be the case in the dry season which bridges the two peaks. An additional cue may be the changing photo-period and temperature changes typical of autumn and spring.

Gestation Period.

Information was collected from a number of zoos (Table 13) regarding the length of gestation. I settled on 7½ months (225 days) as falling within the range of the two congenerics of similar size; nyala, 220 and lesser kudu (*Tragelaphus imberbis*) 222 days.

A comparison of birth weights and gestation periods of seven species of tragelaphines suggests that birth weight and gestation period increase with body size.

Table 13. Gestation periods quoted for sitatunga.

Gestation period	Source of information
225 days	Heinroth (1908)
7 months	P. Gutnecht, Ville de Mulhouse zoo (1975, pers. comm.)
249 days	Anderson (1978)
7-7½ months	A. Dyhrberg, Copenhagen zoo (1975, pers. comm.)
7½-8 months	Jobaert (1957)

The gestation period cited by Anderson (1978) of 249 days does not place the sitatunga within the general size gradation. Instead it places it above that of the nyala, a species which attains a slightly higher weight than sitatunga.

As allometric laws do scale various biochemical and physiological processes (Demment and van Soest, in press) to size in mammals and since there is sufficient evidence available to suggest that parameters such as growth and maximum rates of reproduction are also a function of body size (Western, 1979), I believe 225 days to be the most likely gestation period.

Foetal growth.

Anderson (1978) has compiled a table of foetal growth constants *a*, calculated for most of the tragelaphines, where birth weights and gestation periods are available. The growth constants fall within a narrow range, 0.010 to 0.014, with the sitatunga having a rating of 0.009. As his growth constants for sitatunga are based on a gestation length of 249 days, I have recalculated the growth constants a using a 225 day gestation period. This was calculated as follows:

$$\sqrt[3]{5.99}=(225-\frac{225}{5})$$
$$a=0.0010$$

The birth weights given by Anderson (1978) for sitatunga are retained, as they correspond with the full-term foetus which I collected. The information from zoo birth weights ranging from 1.8 kg - 4.95 kg with an average of 3.31 kg is, I think, unrealistic for feral sitatunga since the average falls below the mean birth weight for bush-buck (Allsopp, 1971) which are smaller than sitatunga. These low values may be a factor of impaired diet or lower growth rates of zoo animals in temperate climes. A sample of 10 foeti were aged and dates of parturition and conception extrapolated (Table 14).

Although a small sample, this does suggest a birth peak from mid-May to the end of July, the period following the cessation of the rains, and a conception peak in the period immediately prior to and during the onset of the rains.

Table 14. Foetal ages estimated by the method of Huggett and Widdas (1951)

Sex	Weight (kg)	Foetal age (days)	Estimated birth	Estimated conception
F	6.0	226	6/12/75	22/4/75
M	1.6	162	25/5/75	10/10/74
M	3.0	189	1/6/75	16/10/74
M	0.475	123	2/8/75	17/12/74
M	1.75	165	11/7/75	26/11/74
M	4.25	206	19/6.75	4/12/74
F	1.0	145	19/7/75	24/10/74
?	0.05	81	12/7/75	27/11/74
?	2.50	180	17/11/75	2/4/75
?	0.50	124	3/5/76	17/9/75

As Allsopp (1971) suggests from the constants _a_ available for various species, foetal velocity may determine breeding seasonality by accommodating growth rates so as to present the neonate to the world during optimum conditions.

Parturition Interval.

Communications from Wroclaw zoo point to a range in parturition interval of 6 to 20 months, with a mean of 11.63 months (Gucwinski, pers. comm.)(Table 11)

Births.

Sitatunga give birth to one calf, though I did come across one record of twinning from the Antwerp zoo (van

Puijenbroek, pers. comm.) Females will give birth until they are at least 11 years (zoo data), confirmed by one 11 year old (relative age) found to be pregnant during the study. Sitatunga do probably conform to the general biology of the nyala however, which are reported by Anderson (1978) to breed until they are 14.

The mean parturition interval for sitatunga, taken from information supplied by European zoos (Table 11), is 11.6 months and for nyala it was reported as 9.9 months (Anderson, 1978).

Sexual Activity.

Sitatunga males are sexually active throughout the year, a fact confirmed by their activity in zoos. Nyala males possess a similar capability (Anderson, 1978).

The duration of oestrus is 1 - 2 days. The cycle is probably similar to that of bongo (*Tragelaphus eurycerus*) (Brownscheidle, 1979) and nyala (Anderson, 1978) of 22 and 10 - 34 days, respectively. In the field, oestrus may be detected in sitatunga by the presence of a male. In nyala the restless behaviour of the female, which may emit a clicking sound, signals oestrus. In zoos it was noted that sitatunga in oestrus had a slight discharge from the vulva, though it was not confirmed in the case of bongo (Brownscheidle, 1979).

Seasonality of Reproduction.

While sitatunga breed throughout the year (Owen, 1970;

Ansell, 1960), an observation further supported by European zoos (Figure 19), there is evidence to suggest that they may respond to environmental cues and drop their young when conditions are favourable.

The information received from European zoos on sitatunga births shows a birth peak in June, an extremely favourable period in Europe, and a secondary peak in January (Figure 19). However, at variance with this data - in particular that of the Antwerp zoo - the Paris zoo shows a peak in January and a trough in June.

In the Bangweulu, a sample of 17 group III animals captured over a few days in study area 3, provided a peak in the early wet season similar to the Saiwa swamp sitatunga in Kenya (Owen, 1970). A further peak in birthrate is suggested by the foetal age extrapolations (Table 14) and by observations in the field of young (Plate 4) and newly born animals. The early rainy season peak occurs when a great deal of vegetative growth takes place, but before the high rainfall peak in early March with the concomitant peak in water levels. The other peak takes place during declining water levels which, for a short time, provides new areas of vegetation while allowing easier movement in the shallower water. However, the general trend is a decline in food resources which may suggest higher mortality of young conceived at this time.

Allsopp (1971), examined bushbuck data in Zambia, a species previously thought to show no evidence of seasonal breeding (Wilson and Child, 1964). Allsopp found distinct parturition periods in December and April (Figure 17). The latter point is also the start of one of the sitatunga peaks. Simpson (1974) also records two parturition peaks in the bushbuck of the Zambesi drainage, while Morris and Hanks (1974) confirm the early rains peak for bushbuck but, due to the nature of their study, were unable to confirm the second peak. The reported bimodal breeding pattern of bushbuck in Kenya (Allsopp, 1971) is disputed by Anderson (1978) on the grounds of the uneven distribution of his sample and the number of non-pregnant females. However, as there is a change in vegetation quality induced by the rains and changing photoperiod, one suspects that bushbuck in Kenya could conform to the general pattern of species which browse having a bimodal reproductive peak. Owen (1970) did observe an increase in sightings of young sitatunga in November, although she could not, by observation alone, draw any conclusions concerning a second peak.

The fact that bimodal peaks of conception are common among African ungulates, especially browsing species, suggests the cause may be related to external or environmental cues. The reaction to decreasing autumnal light and increasing spring light is widely accepted as having considerable influence on the behaviour of animals. Undoubtedly these changes are reinforced by other environmental cues which accompany these fluctuations i.e. rainfall, flooding and

Plate 4. Sitatunga calf in Cyperus digitatus.

vegetation growth. In the case of the sitatunga on the Lukulu estuary, the autumn dates cover the period when waters are in retreat, revealing new areas of vegetation upon which the sitatunga is able to feed. This seasonal uncovering of food resources is also important for lechwe in their annual migration which follows the retreating waters to the Chambeshi drainage line. The drying-up phase in the Lukulu takes place before the onset of winter when both plant growth and the growth of mammals are minimal (Jeffrey and Hanks, 1981; Anderson, 1978).

The vegetation phenology of Africa is influenced primarily by rainfall. In the Bangweulu perimeter it is rainfall and the bimodal movement of water onto and away from the sedge marshes which is probably the ultimate factor governing the amplitude of breeding peaks. The unequal bi-modal reproductive peak of nyala, with its emphasis on an autumnal peak, is suggested by Anderson (1978) to be a function of the effects of gestation length and post-partum oestrous cycles. As both nyala and sitatunga are poly-oestrous and have gestation periods of 7½ months, this does result in some distortion of the peaks and conceptions throughout the year. In addition, the 'lying up' phase of the neonate negates the forces of natural selection which tend to produce a concentrated unimodal breeding season in open-plain species, so that predation of the young will be minimized.

PARASITES AND DISEASE

Ticks collected from sitatunga in November, 1975, were identified as *Rhipicephalus compositus* and *Haemaphysalis aciculifer*. *R. compositus* has been recorded from leopard, lion, zebra (*Equus burchelli*), bushpig (*Potamochoerus porcus*), warthog (*Phacochoerus aethiopicus*), roan antelope (*Hippotragus equinus*), buffalo and cattle while *H. aciculifer* has been recorded from Zambia but its hosts have not been as they are old records (Howard, pers. comm.). In general, the population was remarkably free of endo- and ectoparasites.

Generally, the sampled population was in exceptionally good condition. Two animals were captured which were blind in their right eye (a group C male and a group A female). In addition, a calf (group III) was blind in both eyes. All three were in excellent condition and showed no ill-effects from their disability. This exemplifies the tremendously protective and sustaining role of the habitat in which they live. Examination of their blind eyes showed them all to be milky white.

Capture mortality and injuries.

It was difficult to assess the extent to which captured animals were injured. I believe that there were few injuries due to the cushioning effect of the water and reeds. One adult female was killed accidentally by a male when being transported, while a female calf and adult female died shortly after capture and immobilization, probably from injuries sustained from the airboat.

Predation.

No cases of predation were observed. The principal non-human predators are likely to be python and crocodile, followed in importance by lion, hyena and leopard.

The degree to which sitatunga are preyed upon by man is not possible to quantify. That they are taken in areas lying close to villages is certain. However, much of their habitat is almost impenetrable so that man, as a hunter, can have little effect on their populations, except where habitat has become reduced, though their survival in small patches of marsh on the Lulimala river does not make this certain. Ansell (pers. comm.) believes that people are not significant predators while Hughes (1933), who possibly knew more about sitatunga hunting and the habits of the swamp populace than any man living or dead, recognized the resourcefulness of the people in hunting and trapping sitatunga. Nowhere did he remark or indicate that this effect was, in any way, significant however.

Population Density.

The nature of the sitatunga's habitat makes a census of the animal exceedingly difficult, and in areas of homogeneous papyrus swamp, impossible. Attempts at an aerial census in the Lulimala and the Lukulu estuaries using an aerial transect sampling system were carried out by Grimsdell and Bell (1975). Over a 9 km transect on the Lukulu they estimated 225 sitatunga and over 6 km on the Lulimala they estimated 168 sitatunga. From these estimates they suggested that sitatunga were likely to occur, in suitable habitat, at densities of 10 km^2 and stated that this figure could be much higher. They further reported that there was as least 620 km^2 of prime sitatunga habitat in the southern sector of the basin.

Owen (1970), through long observation of a small riverine swamp, suggested a total of 44 animals over 6 km and extrapolated this to c. 55 km^2.

My own extrapolations based on observations and on the captured sample as well as those animals which eluded capture suggest that the minimum densities of sitatunga range between 10 and 20 km^2 with the possibility that they may range higher. My observation of 9 sitatunga within study area 1, an isolated area of 4 ha, supports this.

MOVEMENTS AND USE OF THE VEGETATION.

In the Bangweulu, as for most of Africa, sitatunga inhabit two fairly distinct habitat types: the first is deep water papyrus marsh, and the second, the mixed communities associated with river systems which are dynamic in nature. In the former, sitatunga live in stable homogeneous communities where water level fluctuations are of relatively low amplitude in comparison to that of the rivers which flood annually and provide a greater interspersion of cover and feed types. In addition, as the papyrus marsh floats on the water, sitatunga are unaffected by fluctuations in the water level unless there is an excessive flood. As the rains do not create more habitat for sitatunga within papyrus marsh it is unlikely that there is any significant movement of the population or even a proportion of the population.

The Lukulu estuary is characterized by permanent river swamp and the seasonally flooded sedge marsh and water meadows. Sitatunga expand their movements into the sedge marsh while it is flooded, only moving out when it dries out in July/August when desication of the vegetation occurs.

a. Study Area 1

The spoor of an adult male was seen to pass from the main body of river marsh some 6 miles distant, and into the Kang'omba marsh (study area 1). This occurred at the beginning of the first rains in November. Similar examples of adult males wandering away from the marsh at the start of the rains were reported by Kingdon (1982) as frequently occurring in Uganda (Lake Victoria). That this movement is triggered by the rains is likely and may serve as a dispersal cue for sub-dominant males.

b. Study Area 2.

In the dry season sitatunga are concentrated in those areas containing permanent water and cover (Figure 5).

In the wet season the animals expand into the sedge marsh where a rapid growth of sedge and grass occurs over a short time. Their return movement is, in turn, governed by the depth of water in the marsh and by the availability of cover. As the subsiding water reveals a further rich quantity of food, they linger for as long as possible until it becomes too dry or the vegetation too desicated to hide and support them. Figure 21 shows the distribution of sitatunga within the study area, a distribution closely related to water depths and an interspersion of cover types (Figures 20 and 4).

c. Study Area 3

This area of sedge marsh floods slightly in advance of the sedge marsh in study area 2. Sitatunga move rapidly into the marsh from the adjoining reed thickets next to the Lukulu river. The uniform depth of water (up to a metre) with its profuse amounts of cover and feed is ideal habitat for sitatunga. They use the area provided they are not hunted in the beating drives so common there and for which sedge marsh is ideally suited, and provided the vegetation is not burned. In October 1975 this area was burned however. The effect of fire was to produce an almost impenetrable covering of *Sesbania microphylla*, a woody plant which is an indicator of underutilization by lechwe. The *Sesbania* growth resulted in only four sitatunga being seen in two days. The only species able to make use of the area after burning were elephant and buffalo. This is at variance with the recommendation that sedge marsh be burned on a rotational basis in order to improve productivity (Verboom, 1982), although his suggestion that papyrus should receive an annual burn treatment in order to increase both quality and quantity of sitatunga food bears consideration.

This area tends to dry rapidly through evapotranspiration so that by July it is dry and little used by sitatunga.

THE FOOD SUPPLY.

The circumscribed habitat of the sitatunga satisfies the total biological requirements of the species, a fact reflected in their sedentary lifestyle, high density and survival even when living close to man. The relationship of the sitatunga with its environment is somewhat paradoxical, in that they exist within a region where less than 10 mm of rain falls within 3 consecutive months, qualifying it as a dought area (Balinsky, 1962); yet in fact occupying a region copiously supplied with water, food and cover. The general result of such a drought is to lower the protein content of the vegetation which in turn limits wild herbivore populations (Bell, 1970). This availability of protein is determined by a number of factors (Grimsdell and Bell, 1975):

a. The standing crop of vegetation, which is the net result of the production versus defoliation regimes. Unlike lechwe, sitatunga are not affected by the annual immersion of the standing crop (water meadows) in water.
b. The protein content of those plant parts and species selected by sitatunga.
c. The position in the vegetative structure of those particular parts which are selected.
d. The digestibility of the vegetation which is consumed; a factor which varies between species.

The sitatunga falls between the categories of grazer and browser being referred to more correctly as a gleaner

(Kingdon, 1982). It has a wide feeding range yet, at the same time, can select plants and plant parts most desirable (Owen, 1970). As a medium sized ruminant it stand mid-way between those species utilizing a high fibre content of food and those using a low fibre content. As Demment and van Soest (1983, in press) suggest, the fibre components of the diet increase with body size at an increasing rate, but although the medium size antelope must eat a higher fibre diet than small herbivores, their reduced metabolic rate/gut capacity ratio allows the evolution of gut structures which are able to delay the food long enough for adequate digestion to occur. Being a ruminant, and protected as it is by the vegetation, it is likely that the sitatunga is allowed to ruminate undisturbed and so is able to make efficient use of the vegetation.

Although rumen samples were collected from fifteen animals these data were not available for this study.

THE WET SEASON FOOD SUPPLY

A notable feature of the rains is the excessive and rapid growth of the vegetation, and the expansion of the sitatunga range in the Lukulu estuary by the rapid growth of sedge marsh where flooding occurs to a depth of 0.66 m. That this sedge has long been recognized as playing an important role in the life of sitatunga is born out by the local Bemba name for sedge marsh, Fibenga Nsobe, "the reed of the sitatunga" (Fanshawe and Mutimushi, 1965). Although no protein assay was made of the vegetation this was an aspect which received the attention of Grimsdell and Bell (1975). Their work focused mainly on the water meadows and intermediate grasslands which are of such crucial importance to the large herds of black lechwe. Crude protein percentages of plant material on the edge of Chikuni island (study area 2) and on the water meadows, was high: grasses (10.2% - 12.8%), dicotyledons (11.3% - 12.4%) and sedges (10.2 - 12.0%). This dropped sharply in the intermediate grassland to 4.8% for grasses, 7.4% for dicotyledons and 7.0% for sedges (Grimsdell and Bell, 1975).

These high protein values for plant material which is seasonally flooded, in comparison to the peripheral and intermediate zones, suggests the importance of the sedge marshes which contain many of the grasses and sedges sampled within the flooding zone. However, the unexpectedly high silica percentages of the water meadow grasses; 26.4% dry weight as opposed to 5.9% for the intermediate grasslands, may affect digestion as well as increase the wear of sitatunga teeth.

Grimsdell and Bell (1975) also made assays of the protein content of Eleocharis sp., the tubular sedge which is associated with Cyperus digitatus. Eleocharis is an important plant component of the seasonally flooded sedge marsh as well as the permanently flooded sedge marsh which characteristically surrounds patches of permanent water.

This plant was found to have a protein content of between 12.8% and 13.6%, which closely resembles the protein values for the water meadow grasses.

PROTEIN CONTENT RELATIVE TO WATER DEPTH

Grass protein content tends to reach a peak between 6 and 12 cm of water which means that in the dry season the grasses immediately behind the retreating waters are high in protein (Grimsdell and Bell, 1975). Depths of up to 31.7 cm still produce readings of 10.6% protein however, which are higher than the values for the intermediate and peripheral grassland.

BEHAVIOUR

ACTIVITY PATTERNS

Owen (1970), carried out observations on sitatunga in the Saiwa swamp in Kenya and found that they were active during the first five and last two hours of daylight, and at night. Kingdon (1982), stated that they are most inactive from about 10 or 11 a.m., to 5 - 5.30 p.m. and that they feed again in the evening followed by a long period of rumination. While I did notice a general slackening of activity during the heat of the day adult animals were seen feeding then on the edge of the water meadow. The night, generally, is a period of high activity born out by the spoor found on the swamp edge in the morning. It is likely that, as for a number of other ungulates, their activity ceases to a great extent late at night and during the early hours of the morning, especially when it is cold.

AGGREGATIONS AND SOCIAL GROUPINGS

A total of 101 sightings of sitatunga groups was made in study area 2 over a period of 2½ years (Figure 21). In study area 1, 18 groups were counted over a period of 8 hours on three consecutive days.

a. Study Area 2.

In this area, 76.3% were single animals, 19.3% two animals and 4.0% three animals (Table 15). The high percentage of single animals may be ascribed to the activity of the airboat in breaking up groups of sitatunga.

b. Study Area 1.

Owen's (1970) findings, where 45.9% were single, 34.8% two animals, 10.6% three animals, 5.0% four animals, 1.7% five animals, 1.4% six animals, 0.3% seven animals and 0.3% nine animals, corresponds more closely with the observations made on the undisturbed population in study area 1 (Table 16) where 50.0% were single, 22.2% two animals, 16.7% three animals and 5.6% four and five animals respectively.

The striking feature of the observations in this area is the dynamic nature of the group, breaking and forming up rapidly as shown in Table 16. The group of 9 sitatunga shows evidence of being a cohesive sub-society, joined or breaking up at will but always joined, if not by sight, by auditory and olfactory modes of communication. The sedentary nature of the sitatunga makes this hypothesis tenable and it is perhaps necessary to redefine what an aggregation is. Sitatunga do tend to show that they aggregate in larger numbers than usual only when in the open. During aerial surveys, the occasional group of 5 to 7 animals was observed but always on the dry ground of levees and termitaria. Meinertzhagen (1916) saw 12 males, 9 females and 5 juveniles from the vantage point of an anthill on Nkose island. In the Ipeta swamp 19 animals were observed but these were clumped in twos and threes and may not have been in sight of one another (Kingdon, 1982).

Anderson (1979) found that nyala tended to gather in larger groups on open ground. Nyala are a species with similar social groupings to sitatunga (Owen, 1970), lesser kudu and bushbuck (Jarman, 1974).

Although group IV males were seen together on three occasions during the period of the study it is possible and most likely, that there were also males of a lower class present.

The relative absence of group I calves is perhaps due to the 'lying up' phase, a common feature of the tragelaphines (Walther, 1964). Immature animals were encountered alone, and as suggested by Kingdon (1982) from the observations of Meinertzhagen (1916) and Owen (1970), they would appear to be more independent than other antelope. However, as introduced earlier, they may only be alone in the human sense or as man perceives them.

c. Study Area 3.

Due to the habitat which consists of tall <u>Cyperus digitatus</u> swamp (sedge) interspersed with small levees covered sparsely with <u>Phragmites communis</u>, there was difficulty in making definite observations of the aggregations of sitatunga in this area. During the early stages of a capture operation it was not unusual to come on two, three or four animals clearly in groups. This tended to occur when approaching one of the levees and suggests that dry areas are the foci for sitatunga aggregations. At first, these animals appeared undecided whether to adopt crypsis as a defense, or, whether to flee. As time progressed, sitatunga would depart in the direction of the river with its large thickets and deeper water, dispersing rapidly. This was not the case with females and young calves which tended to stay together as much as possible.

INFLUENCE OF ENVIRONMENT ON SOCIAL ORGANIZATION

The habitat of the sitatunga is analagous to the carapace of the tortoise in that it provides permanent protection for the animal. An understanding of this specialized environment will allow certain conclusions to be drawn as to the 'real' rather than the 'observed' life history of the animal.

Vegetation Structure.

Although sitatunga habitat varies from the large monotypical papyrus swamp to the diverse communities of rivers and their estuaries, they do have one thing in common: dense and tall vegetation. This cover, either because of water depth or plant density affords the sitatunga protection from predators. Such an environment allows them to maintain constant olfactory, auditory and visual communication with each other. The nature of the habitat may cause observer bias, for one must look past the purely visual aspect of the researcher, to an observation composed of the animal in relation to its environment (i.e. its ecology), rather than just the

Table 15. The observed sex and age structure of different group sizes in study area 2.

Group Size	Adult Male	Adult Female	Subad. Male	Imm. Female	Juv. Male	Calf	No.	%
One		1					39	50.6
			1				3	3.9
	1						24	31.2
				1			5	6.5
					1		6	7.8
							77	100.0
Two		2					4	20.0
		1	1				1	5.0
	1		1				2	10.0
		1			1		7	35.0
	1	1					4	20.0
		1		1			1	5.0
		1			1		1	5.0
							20	100.0
Three		3					2	50.0
	2		1				1	25.0
		2			1		1	25.0
							4	100.0

Single animals : 76.3%
Two animals : 19.3%
Three animals : 4.0%

Table 16. Aggregations of a population of 9 sitatunga in study area 1 observed over three days for 8 hours

Group Size	Adult Male	Adult Female	Subad. Male	Imm. Female	Juv. Male	Calf	No.	%
One					1		1	11.2
				1			1	11.2
			1				1	11.2
		1					3	33.4
	1						1	11.2
							2	22.3
							9	100.0
Two			1		1		1	25.0
	2						1	25.0
	1				1		1	25.0
	1			1			1	25.0
							4	100.00
Three	1		1		1		1	33.3
	2					1	1	33.3
	1			1		1	1	33.3
							3	100.0
Four	2			1		1	1	100.0
Five	3			1		1	1	100.0

Single animals: 50.0%
Two animals : 22.2%
Three animals : 16.7%
Four animals : 5.6%
Five animals : 5.6%

animal 'seen' in its environment. Thus, the information regarding aggregations reported for sitatunga in different areas, both in this study and Owen's (1970) are the "observed" rather than the 'real' aggregations.

The protection afforded by vegetation allows all age groups to be independent. It also allows for sitatunga to be well distributed so as to exert a minimal physical effect on the vegetation. It may also have allowed for small stable societies of sitatunga to evolve, as they are not required to move a great deal since all their requirements are met within a small area. This allows for the maintenance of high densities in habitat which few other animals are able to utilize.

Habitat Modification.

Sitatunga construct resting areas by flattening the vegetation. In papyrus and other tall vegetation they push the stems inwards and flatten them down, producing a dry platform. Owen (1970) observed them trampling in circles, while those I observed merely lay down using 'nests' previously constructed. The neonate is probably left on one of these platforms for the first few weeks after birth.

A feature of sitatunga habitat, particularly in dense reed thickets, are the tunnels which they fashion and keep cleared by constant use. They also make use of the tunnels made by hippo (*Hippopotamus amphibius*). Tunnels enable sitatunga to move rapidly away from predators and allow them access to different parts of their home range. The tunnels may also have the effect of channeling sitatunga activity so that both mutual avoidance of dominant males and reproduction are enhanced. Tunnels, however, also make them susceptible to snaring and trapping.

SOCIAL BEHAVIOUR

Auditory Communication.

Sitatunga were heard roaring on two occasions, a sound which is not unlike the sawing of a leopard but without the return action or inhalation roar (Manning, 1975). Barking, as in other members of the genus Tragelaphus, is carried out mainly by males. Owen (1970) records two sounds made by sitatunga; one, the bark which she likens to a train gathering steam and which she recorded only when sitatunga were alarmed and the second, the squeek/click emitted by feeding animals. I did not hear the latter which is perhaps analagous to the rumblings of elephant while feeding. This clicking is also recorded for bongo (Hamann, 1979), and both bushbuck and nyala (Anderson, 1979). Its communicatory function, especially in sitatunga, may serve to link animals separated by vegetative barriers. Conversely, it may also allow sitatunga 'groups' to feed or lie up separately, while remaining in contact.

There was a tendency for some females and immature animals to bleat on capture. Those experiencing a greater degree of stress emitted loud bawls.

Visual Communication.

a. Pelage Colour and Body Size

Communication is facilitated by the extreme sexual dimorphism of the species. Some adult males and females and immatures could be taken for different species so striking are the colour differences.

The tragelaphines are distinguished by their elaborate broadside displays which assert their physical presence. In males, these displays are made more pronounced by a dorsal ridge of hairs. This is particularly well developed in the nyala, showing the importance of the dominance ritual and lateral display in sire selection (Anderson, 1979). Sitatunga, however, do not possess a dorsal ridge of hair.

The most noteworthy characteristic, apart from the horns of males, is the extreme difference in body size between the sexes. Anderson (1979) states that in nyala "the only function of this dimorphism must be social communication with the aim of obtaining mating rights". The absence of inguinal glands and the unsure status of the pedal glands in nyala lend credence to the view that the highly developed visual display is necessary in that species.

Sitatunga, on the other hand, possess inguinal glands which may serve in agonistic displays or in mating behaviour and which, in view of its habitat, makes lateral displays of the body perhaps less important. This animal has developed instead, both the laying of scent and frontal displays.

The extreme size of adult males and their low numbers relative to adult females suggests that sexual dimorphism allows for differential survival favouring adult females. As predation appears not to be a factor in the regulation of sitatunga, the limits set upon the population would be induced by the limits of vegetation (Peek in Caughley, 1981). These limits would, perforce, be felt by the largest animals in the population possessing the highest energy requirements during the height of the dry season, when the habitat is most restricted and plant growth is minimal.

b. The Nose Chevron

The nose chevron, found in both sexes, is absent entirely from some individuals. When presented by an adult male in the typical lowered head threat posture, the chevron is most conspicuous (Plate 5) resembling, in miniature, the adult horn shape. (Figure 9) When presented in a non-threatening manner (Plate 6), the chevron appears as two flashes but without the horn shape. When an adult male is observed standing in swamp vegetation, the horns blend in with the vegetation. However, the nose chevron is clear, especially if held in an aggressive manner. This posture was noted occasionally while attempting to capture a male that was blind in one eye. It was also noted in those adult males newly released from the airboat and still slightly under the influence of the tranquillizer. Not surprisingly, as Kingdon (1982) notes, females do not present the chevron in the same manner.

Plate 5. The nose chevron of an adult male presented in a 'threat posture'.

Plate 6. The nose chevron of an adult male presented in a 'non threatening" posture.

c. Tail Flashing

Tail flashing was observed on many occasions when approaching sitatunga with the airboat. Although usually performed by adult females, it was also observed in adult males (Plate 2), subadult males and in immature males. Performance of this signalling device usually occurred in the open, and where it did occur, the calf was induced to follow until both disappeared into a thicket. It was also observed when the airboat suddenly came up on a mother and her calf. In this case, the female flashed as she ran off while the calf lay immediately down.

When making this signal the animal did not alter its gait as is usually the case for cursorial mammals. Smythe (1970) questions that the signalling device has intraspecific connotations and suggests that it serves to induce a predator to attack from a distance enabling the prey species to escape. Although it may unwittingly serve this function in sitatunga, no ready explanation is forthcoming for those sitatunga which flash when surprised at close quarters by a predator.

Its primary function would appear to induce the following response. The sitatunga tail, in its normal position, is characterized by a white tip of approximately 6 cm long. Seen from the rear, the only noticeable feature in an unusually drab posterior, is the white tip, which tends to be jerked continuously. Its function therefore, may be to assist the calf when following its mother in thickets. The tail when lifted, reveals a brown patch of hair followed by a large patch of bristly white hair running up to the base of the tail. It is this latter patch which is revealed when escapting from predators. As it is twice as large as the white tip it is clearly visible.

Olfactory Communication.

Sitatunga do not possess facial glands, nor was it possible to substantiate the presence of pedal glands. They do however, have inguinal glands which confirms the findings of Hughes (1933) and Kingdon (1982). These probably serve in laying the individual's scent through its range, enabling animals to both avoid and meet one another.

The commonest form of intraspecific inspection is nose sniffing which suggests that smell is of considerable social importance. This is especially marked in a zoo situation if an animal is a newcomer (Walther, 1964). Mutual licking and grooming is highly developed in the species also indicating that olfactory relationships are reinforced by these actions. Sitatunga females lick the calves' noses when fetching them from the 'lying out' position suggesting that recognition of the mother is reinforced by this action.

Adult males also test the females' urine for the presence of the oestral pheromones which signal the readiness of the female to mate.

REPRODUCTIVE BEHAVIOUR

In study area 1, the adult male (group IV) was observed driving a female with head and neck stretched forward in the typical manner of the tragelaphines (Walther, 1964). Although he did sniff at the base of her tail when she allowed him to approach, I could not confirm that "Flehmen" had occurred. Previous to this, the female had run off a short way on first being aware of the male's approach, but then had allowed herself to be approached and later mounted.

This male was not seen sniffing at the perineal region of females when close to them as reported by Anderson (1979) for nyala, but appeared to ignore them while they were in an obviously anoestral stage.

FEEDING BEHAVIOUR

Sitatunga tend to feed rapidly for long periods, moving slowly along and only very occasionally looking up. They were also observed feeding while lying down, making full use of their long and agile tongues to draw in the vegetation. Their movement tends to be linear in progression, selecting those vegetative components which appear in front of them. As they move, they lift their rear hooves very high and place them slowly down.

In deeper water, they may feed with only their eyes and nose above the surface.

COMFORT BEHAVIOUR

Grooming appears highly developed in the species and in the tragelaphines as a whole, with this being particularly evident in the mother's licking of her infant calf. It has also been reported (Walther, 1964) that other adult females will assist the mother in grooming the calf all over. Individuals groom or scratch themselves, and on one occasion, a female appeared to scratch her side with a piece of sedge stem which protruded from her mouth, though this was possibly accidental.

SPATIAL BEHAVIOUR

The habitat occupied by the sitatunga provides a continual supply of water, green feed and cover, and has allowed for high densities and a sedentary lifestyle. It has also been a strong selective force in evolving the necessary behavioural mechanisms by which the species is able to exist in such constricted circumstances.

Home Range.

Following Jewell (1966), home range can be defined as the area over which an animal normally travels in pursuit of its routine activities.

a. Study Area 1

In the Kang'omba swamp, due to its isolation from other pockets of swamp and the protection afforded by the Game Department in the contiguous village of Chiundaponde, a small population of sitatunga exist in a small (0.04 km^2) home range within an extremely restricted habitat. The only adult male was observed in the exact same patch 2 months later and there were no signs of egress from this area over 4 months.

b. Study Area 2

The study area lying between the island of Chikuni and the river produced some data relating to minimum home range of sitatunga (Table 17) derived from all the observations and capture work (Figure 21).

Table 17. The minimum home ranges of 9 sitatunga in study area 2, between Jan., 1974 and Jan., 1976.

Sex	Minimum Area (km^2)
F	0.48
F	0.03
F	0.17
M	1.28
M	0.48
M	0.07
M	0.26
M	0.06
M	0.02

For adult males (Figure 22) the mean size was 0.36 km^2 with a range of 1.28 - 0.02 km^2 and for adult females (Figure 3)) for which data were available, the mean size was 0.17 km^2

with a range of 0.48 - 0.01 km^2. The activity of the airboat created a certain measure of disturbance and may have created more movement than would normally occur under undisturbed conditions. Owen (1970) found that of 11 recognized individuals recorded over a period of 4 to 14 months none had moved further than c. 500m from the position where they were first sighted. My findings (Figure 22, 23 and 24) confirm this.

Jewell (1966) and Ewer (1968) consider that the importance of a fixed home range lies in the animal's familiarity with the area and its accessibility to resources. It also provides a ready means of escape from predators. Leuthold (1972) considers that there is little evidence to support this supposition. My findings do not contradict the view of Jewell and Ewer. As sitatunga home ranges do overlap the effects may be to give males and females access to each other. It would also be possible for dominant males to avoid each other by the laying of scent. The presence of inguinal glands is likely to assist these processes.

Territoriality.

Territoriality is a pervasive phenomenon, a concept which has created a diverse and often confusing litany of definitions from workers. There is general agreement that a territory is a geographically fixed spatial area. Various definitions and emphases have been placed on behavioural relationships within this space expressed in terms of defense, exclusion and dominance (Owen-Smith, 1977).

In ungulates, it is the adult males which are territorial but, as in the case of the black lechwe (Manning, in prep) usually only a small proportion of the males defend territories and then only during the period of rut. Territorial males, depending on the number of times females come into oestrus, become solitary or are attached to female groups, while sub-dominant males are associated more in all-male groups. Owen-Smith (1977), found that in less sociable species such as the white rhinoceros (Ceratotherium simum), non-territorial males are also solitary, which may account for the reported absence of territoriality in East African rhino (Diceros bicornis) and bushbuck. While Leuthold (1972) considered the sitatunga, together with other tragelaphines, completely non-territorial, Jarman (1974) considered bushbuck to be territorial and gave his opinion that all species in his Class B group which included sitatunga, could be territorial. The adult males, he noted, are infrequently associated, suggesting mutual antagonism, and when they associated, as occurs in bushbuck, there is a perfect gradation in the length of the horns which provides evidence of a linear hierarchy (Kingdon, 1982). Observations on sitatunga tend to confirm this, for adult males were only encountered together three times and on all occasions it was clear that there existed both a gradation of horn length and a stage of development.

As the home ranges and movement patterns of adult males overlap this does not, in itself, negate the possibility that the dominant males exhibit a form of territoriality, as territorial males may penetrate the territories of others provided they exhibit the necessary submissive behaviour of sub-dominant males (Owen-Smith, 1977; Manning in prep.).

The short periods of aggression induced in captive males is suggested by Kingdon (1982), to show that there may be a turnover in dominance. The evidence I received from zoos does not support this view but it may show that sitatunga are to some degree territorial. Communication from Ville de Mulhouse zoo reveals that the adult males are permanently aggressive and do not allow anyone into the enclosure (Gutnecht, pers. comm.). In the Antwerp zoo, a 6-year-old male chased a castrated older animal around an area of approximately 1,000 m^2 (Verlaeckt, pers. comm.). However, in the Whipsnade zoo, there is no evidence of dominance from a herd of 6 males and 4 females, whether or not the females are in oestrus (Manton, pers. comm.). The Regents Park zoo (Unsigned, pers. comm.) reported that the dominant male was aggressive towards other adult males, eg., kudu and beisa oryx (Oryx beisa), within his territory, and this created tension in the whole herd. Young males which entered the dominant male's position engaged in serious combats and the dominant male on asserting his dominance harassed his rivals.

Given the constricted nature of zoo habitat it is not surprising that adult males show intraspecific and interspecific aggression. However, in the wild, sitatunga males exhibit a high degree of aggression as well, with fights between males occasionally resulting in the death of one of the protagonists (F.C. Selous in Lydekker, 1908). Jobaert (1957) witnessed combats between males, and frequently found males which had been killed in combat. Jobaert (1957) also recorded the extreme aggression of male sitatunga toward bushbuck males that approached their area and considered this to be further evidence of the existence of territoriality.

The question which is pertinent here is: What factor or factors contribute to the genetic success of a population confined in habitat but having perennial supplies of food, water and cover? Clearly, the dominance of the fittest males would, to some measure, enhance the survival of the population as a whole. If there is no evidence that survivorship of territorial males is increased as a result of food gains (Owen-Smith, 1977) then territoriality would be an advantage in order to enhance mate selection. As female sitatunga do not have larger home ranges or exhibit greater movement than males, territoriality in sitatunga would be advantageous since mate selection would be greatly enhanced.

Where patches of dry gound occur within sitatunga habitat, as in the Luitikila and Munikashi estuaries north of the Lukulu estuary, they are the foci of sitatunga activity, especially adult males. As no clear evidence is available of two adult males of the same group appearing on the mounds together, this must suggest the existence of an avoiding mechanism related to fixed loci. That these areas are the results of the carefully orchestrated dispersals of termite nymphs and not of the sitatunga's making should not detract from the point that sitatunga do have spatially fixed home ranges and do assert dominance.

When all the resources are available within a restricted area for the dominant male, some form of territoriality can be expected (McBride, 1971). In the case of sitatunga, this may find its expression outside the normal stereotype of territoriality, i.e. land-defense, but rather in an intermediate form in which the maintenance of home range expresses an element of territoriality (Jewell, 1966).

RELATIONSHIP WITH OTHER SPECIES

Due to the nature of the sitatunga's habitat and its cryptic habits, few observations were made of its relationship with other species. Sitatunga were seen feeding near lechwe but never close to them, in the sense of animals intermingling.

On one occasion an otter (Aonyx capensis) passed three sitatunga females causing one of them to follow behind it for a few yeards with her nose held down to the marsh close to the track.

PLAY

Walther (1964) remarked on the 'running games' of the tragelaphines where each animal 'trained' by itself. I observed this behaviour in a calf which ran around by itself for some time in a highly excited manner.

COMPETITION

Interspecific competition for food resources or space is not a factor of importance for sitatunga. Although elephant, buffalo, hippo and lechwe do make some limited use of sitatunga habitat it is usually temporary.

In the case of the large herbivores, their effects may be beneficial, especially where they pass through papyrus, clearing paths as they go and opening up more feeding area to the sitatunga.

Lechwe.

a. Study Area 3.

Lechwe make little use of this area during the flood, but the presence of the plant *Sesbania microphylla* and the deeper water suggests that this is the limit of their eastern range at present population levels.

b. Study Area 2 (Figure 5)

This area is one of the main crossing points for lechwe during their mgration to and from the Chimbwe plain water meadows. The main northerly movement takes place from May to July when lechwe move steadily through the sedge marsh across the line of levees on the western side of the study area and finally across the river. At this time lechwe are always to be seen on the Lubavu levee preparatory to moving across to the Buteka plain. Lechwe are occasionally encountered on Chate levee as well.

The next wave occurs at the beginning of the rains when the males arrive from the north-east in advance of the females, to be followed by the latter once the first territories become established on the water meadows.

Although some overlap of range appears to occur here, lechwe do not linger in the places favoured by sitatunga due to the generally unfavourable water depths.

SITATUNGA/PREDATOR SPACE RELATIONS

Although no instances of quadruped predation, or behavioural effects of predation were observed, the reactions of sitatunga to the presence of the airboat, to myself and assistants were noted.

Sitatunga depend on crypsis for protection when in thick cover, a behaviour noted particularly for adult males and calves. When in the open, they rapidly move towards cover, some with tail flashing. This flight reaction occurs when animals are exposed and approached rapidly by the airboat. It is usually noted in adult females but, on 1 occasion also in a subadult male with an adult female. If the distance between airboat and animal in the open is less than 60 m the adult males tend to adopt crypsis by sinking as low as possible into the vegetation. At times they also begin to slowly creep away. In deeper water, they will sink down with their nose above the surface and their horns laid back parallel to it. Calves tend to adopt crypsis as well, although their mothers ran off.

Sitatunga are not noted for their aggressive nature but when wounded or attacked they may become fierce (Gedge, *in* Lydekker, 1908; Jobaert, 1957). I did note one adult male, blind in one eye, making repeated charges at the approaching airboat.

CONSERVATION OF THE SITATUNGA.

Recommendations for the conservation and management of a species are usually concerned with aspects of maximum sustainable yield (MSY), and the particular methodology of how this is to be attained. Both of these will present insuperable difficulties due to the deficiency of the data with which to set the MSY, and the philosophical biases which determine the modus operandi of a management programme.

As it is not possible to encapsulate the last fact within the management equation, decisions must be made on the data at hand, with the proviso that monitoring and further investigation continue. At all costs, species which are able to be managed must not only be utilized, but must be seen to be utilized. This point concerns the modus operandi and is the central issue of management in Africa about which all conservation issues pivot.

Conservation in Africa is a concept foisted by the West on Africa. The driving force behind the delineation of land as National Parks and Game reserves stems from the belief by the West that the people of Africa were remorselessly killing off the game (Graham, 1972). This idea has been similarly voiced for the North American situation (Williams, 1917). The effect of the preservation/conservation philosophy has been a remarkable structure of National parks and Game reserves. However, it has also paralysed African Governments, resulting in their inability, for fear of world censure, to pursue wildlife utilization programmes which would be of benefit to the rural cohabitants with wildlife, and ultimately, of benefit to wildlife itself.

Where utilization programmes have been attempted they have been large, overfunded projects, run by people and organizations without a clear idea of the objectives and little knowledge of local conditions or the role of the wild animal in the African psyche. Attempts are still being made to enjoin venison and wildlife products in the ranks of other commodities such as oil, sugar, coffee and wheat. This is an act of great folly, for if successful, wildlife would be guided by laws of supply and demand (Parker, pers. comm.), a most unsatisfactory situation and one which would pose great danger to the conservation of this resource.

The way ahead is clear. Whatever we do with wild animals, it must involve the people. Failure to do this will leave the resource open to the exploiters and will further alienate the very people we wish to convert.

SITATUNGA AND MAN

In the Bangweulu sitatunga have long been sought for their meat and soft long-furred skin. The latter was used as swaddling clothes. Unlike the lechwe, whose numbers plummeted due to an increase in both the flooding level and the commercial poaching of the Second World War years, the sitatunga is protected by the general impenetrability of its swamp home, its solitary disposition and its ability to live in areas of deep water.

Sitatunga do not lend themselves easily to classical management because of their inaccessible habitat. They also do not provide data easily regarding their intrinsic rate of increase or what the subsistence level may be which are required to set the MSY. However, this should not deter managers. Subsistence hunting must be fully legalized to gain the support of human cohabitants of the sitatunga.

LAND-USE AND HABITAT MODIFICATION

Zambia's wetland system (54,000 km^2) constitutes one of the most biologically productive life forms in the world, as wetlands may yield a mean net primary production of 2500 grams of dry organic matter per sq. m. per year, as opposed to the 2000 grams produced by a tropical forest (Verboom, 1982). In Zambia, the wetlands are highly productive and fertile, in marked contrast to the leached soils surrounding them. The attention of the agriculturists (dykers and blasters) and hydro-electric planners (Manning and Moss, 1977) area already focused on the wetlands.

In the Lukulu estuary, a canal built by the Water Affairs Department to facilitate transport by canoe from the mainland to the swamp islands, departs from a point just north of study area 2 and cleaves the Buteka plain and the bottleneck between the Lukanga and Mutoni woodland. The effect of this is to draw off water rapidly from the estuary, and so cause an early drying of the Lukulu marsh further down. This marsh is an important nesting area for the shoebill stork (*Balaeniceps rex*) (Manning (b), in prep), and, excellent sitatunga habitat. Although this may not be strongly deleterious to the sitatunga, animals such as the shoebill, which are already restricted in number, may have further pressure exerted upon them.

The proposal to produce hydro-electric power on the Luapula river, with the basin serving as the reservoir, poses extremely grave effects on both wildlife and people, although if the level does not exceed the 1160 m. contour mark, effects on sitatunga should not be deleterious (Manning and Moss, 1977).

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PERSONAL COMMUNICATIONS

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APPENDIX A (Verboom, 1982).

Vegetation types and plant species of the Bangweulu

1. Open water, rivers and lakes (Chambeshi class).

GRASSES & SEDGES	TREES, SHRUBS & HERBS
	Nymphea caerulea
	Nymphoides sp.
	Ottelia mucrinata
	Ottelia sp.
	Potamogeton richardii
	Urticularia inflexa
	Trapa natans
	Pistia stratiotes
	2622 (Verboom specimen number.)

2. River fringes, Vossia belt (Mutole class).

Vossia cuspidata	Aeschynomene fluitens
Echinochloa stagnina	" cristata
Paspalidium geminatum	" elaphroxylon
Oryza barthii	
Scirpus cubensis	

3. Recent ox bows, lake basin and permanent swamp (Luko class).

Cyperus papyrus	Limnophyton obtusifolium
" digitage	Ipomea rubens
Fuirena sp.	Vigna nilotica
Phragmites communis	Thallia welwitschii
Pycreus mundtii	Hibiscus diversifolium
Fymbristylis subaphylla	Mukia sp.
Panicum parifolium	Thelpterus cotta (fern)
	Ficus asperifolia

4. Old ox bows, peat bogs, permanent swamp (Mushitu class).

Typha capensis	Adonstena caffra
Mariscus deciduus	Limnophiton obtusifolium
Scirpus rhodesicus	

5. Lake basin, deep water floodplain. (Chisongo class).

Scirpus brachyceras	Thallia welwitschii
Eleocharis plantaginea	Ipomea aquatica
Pennisetum glaucocladum	
Miscanthidium teretifolium	
Leersia hexandra	
Oryza barthii	
Sacciolepis africana	

6a. Lake basin, deep water floodplain (<u>Nsoke class</u>).

Oryza barthii
Leersia hexandra
Eleocharis dulcis
Sacciolepis africanum
" sp.
Robynsiochloa purpurescens
Echinocloa stagnina
Aeschynomine cristata
Commelina purpurea

6b. Lake basin, shallow water floodplain (<u>Nsoke class</u>).

Leersia hexandra
Oryza barthii
Pycreus mundtii
Sacciolepis africana
" alba
Eleocharis plantaginea
" dulcis
Cyperus radiatus
Rhyncospora holoschoenioides
Aeschynomine cristata
Elodea densa
Felicia barbellata
Hygrophylla sp.
Lindernia oliverana

7. Lake basin, shallow water floodplain, sedge marsh (<u>Mikanshi class</u>).

Cyperus digitata
Mariscus deciduus
Eleocharis articulatus
Scirpus rhodesicus
Sacciolepis alba
Thallia welwitschii
Eriocaulon temsisii
Rhyncospora mauritii

8. Lake basin, shallow water floodplain, water meadow and swale (<u>Luiya class</u>).

Acroceras macrum
Panicum glabrescens
" parvifolium
Sacciolepis typhura
Echinochlea pyramidalis
Entocasia imbricata
Pycreus mundtii
Eulalia geniculata
Paspalum commersoni
Eleocharis dulcis
Cyperus digitatus
Mariscus deciduus
Sesbania microphylla
Crassocephalum picridifolium
Ludwigia leptocarpa
Adonostema caffrum
Polygonum salicipholium
Sphaeranthus chandleri

9. Low terrace, point bars, intermediate grassland (<u>Mayengele class</u>).

Setaria anceps
Themeda triandra
Aeschynomine indica

9. (cont.)

Tristachya rhenanii	As for water meadow
Eragrostis capensis	
Brachiaria nigripedata	
" filifolia	
Allopteropsis semiallata	
Diheteropogon sp.	
Eragrostis lappula	
Loudeta superba	

10. Terrace, lacustrine plain, peripheral grassland (Lweo class).

Loudetia simplex	Aschynomine nyassae
Monocymbium ceresiiforma	
Aristida malicenta	
Eragrostis lappula	
Loudetia superba	
Tristachia rhenanii	
Trachypogon spicatus	
Diheteropogon digrandigglumis	

11. Old terrace, lacustrine plain, peripheral grassland, suffrutex savannah (Mupundu-Mufinsa class).

As above	Parinari capensis
	Syzigium huillense
	Anona nana
	Gardena Sp.

12. Old lake shore, laccustrine plain, bush groups, woodland fringe (Mupundu class).

As above	Parinari sp.
	Combretum sp.
	Uapaca sp.
	Landolphia sp.
	Pyliostigma sp.
	Baphia obovata

13. Recent levees, intermediate grassland (Akambizi class).

Panicum repens	Tephrosia rhodesica
Eragrostis lappula	Dolicus axillaris
Panicum fulgens	Crotolaria ochroleuca
Sporobolus subtilis	Sesbania microphylla
Digitaria abyssinica	Aeschynomine indica
Sacciolepis typhura	Cassia mimosifosia
Tristachyra rhenanii	Indigofera pilosa
Andropogon huillensis	Desmodium salicipolium
Hyparrhenia rufa	Crotolaria glauca
Pennisetum glaucocladum	Eriosema affinii

13. (cont.)

Imperata cylindrica
Andropogon eucomis
Digitaria diagonalis
Eleusine indica
Eragrostis viscosa
" hispida
" aethiopica

Cassia occidentallis
" obtusifolia
Indigofera erecta

14. Old levees, intermediate grassland (Lusanga class)

Panicum repens
Pennisetum glaucocladum
Hyperhenia rufa
" filipendula
Eragrostis lappula
Sporobolus subtilis
Digitaria diagonalis

Tephrosia rhodesia
Dolichos axillaris
Crotelaria ochroleuca
Sesbania sesban
Cassia mimosifolia
Indigofera pilosa
Crotalaria glauca
Eriosema affinii
Cassia occidentalis
Indigofera erecta

15. Upland plateau (Miombo class)

Hyperhenia nyassae
" filipendula
Andropogon gayanus
" schirensis
Tristachya hispida
Digitaria diagonalis
Rhynchelytrum nyassae

Brachystegia spp.
Julbernardia spp.
Afronomum biauriculatum
Smilax spp.
Pteridium aquilinum

APPENDIX B

Some common wildlife species of the Bangweulu

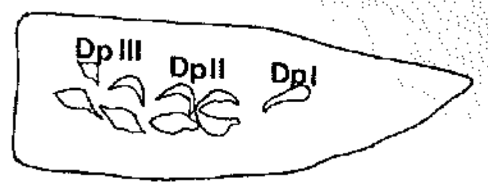
Buffalo	Syncerus caffer
Bushbuck	Tragelaphus scriptus
Crocodile	Crocodylus niloticus
Eland	Taurotragus oryx
Elephant	Loxodonta africana
Hippo	Hippopotamus amphibius
Hyena	Crocuta crocuta
Jackal	Canis adustus
Lechwe (Black)	Kobus leche smithemani
Leopard	Panthera pardus
Lion	Panthera leo
Oribi	Ourebia ourebia
Otter	Aonyx capensis
Puku	Kobus vardoni
Reedbuck	Redunca arindinum
Sitatunga	Tragelaphus spekei
Tsessebe	Damaliscus lunatus

APPENDIX C

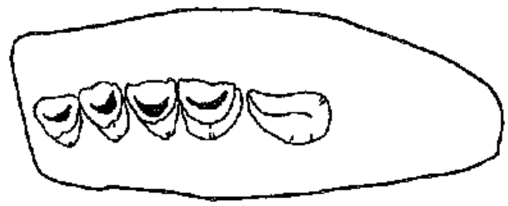
Relative age determination criteria.

Group Relative Age

I FULL TERM

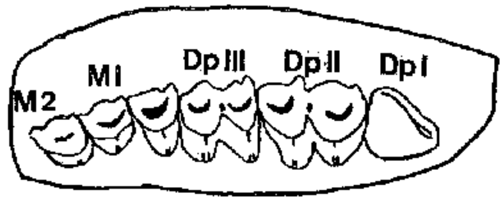


II 2 MONTHS

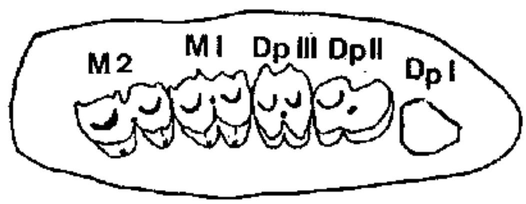


III 4 MONTHS

IV 4-8 MONTHS

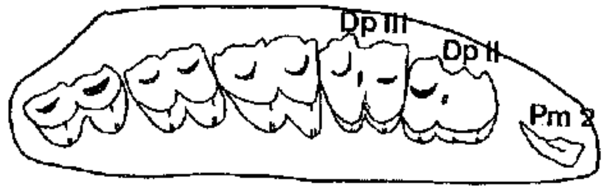


V 8-17 MONTHS

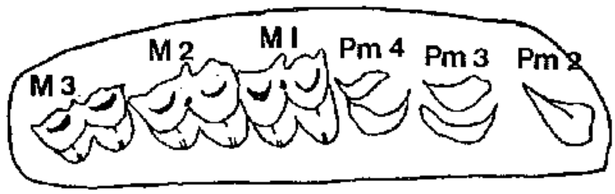


Group Relative Age

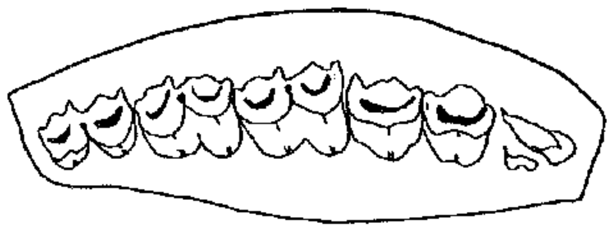
VI 2 YEARS



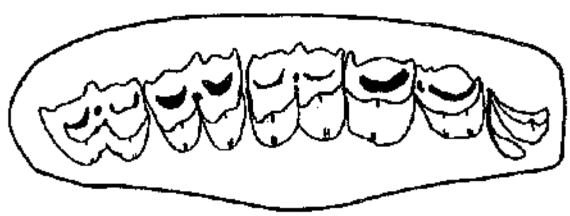
VII ↓



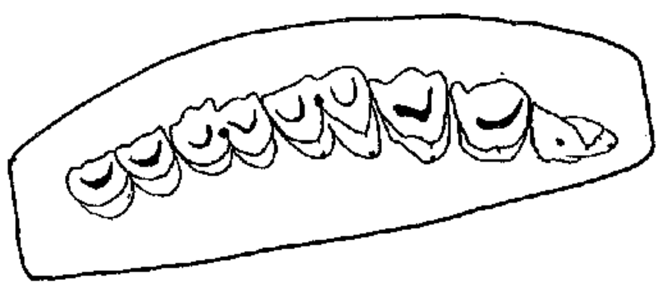
A 2.5 YEARS



B 3.5 YEARS

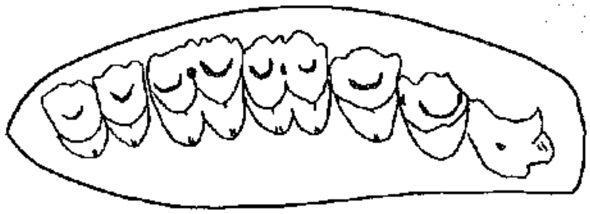


C 4.5 YEARS

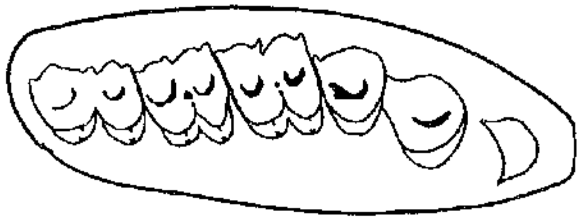


Group Relative Age

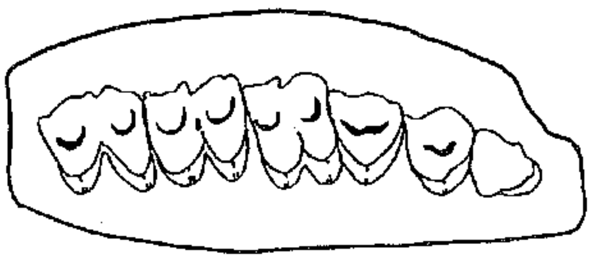
D 5.5 YEARS



E 6.5 YEARS



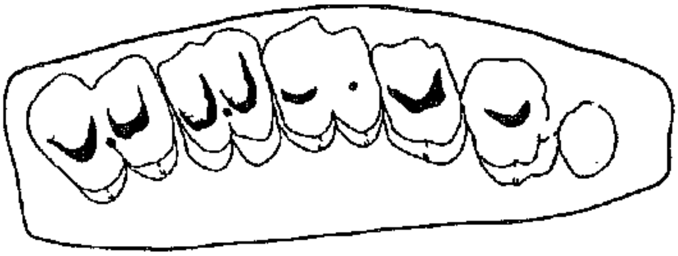
F 7.5 YEARS



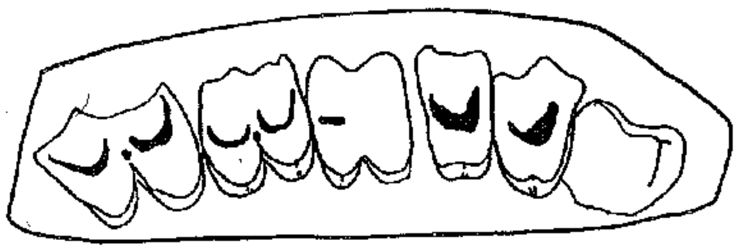
G 8.5 YEARS

Group Relative Age

H 9.5 YEARS



I 10.5 YEARS



J 11.5+ YEARS

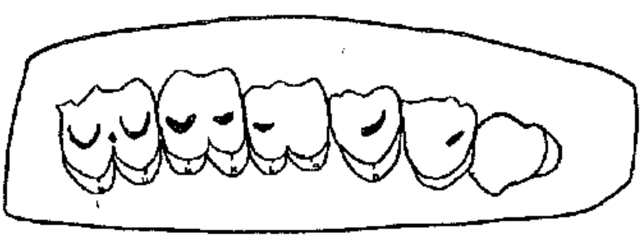


Figure 1. Zambia and the study area.

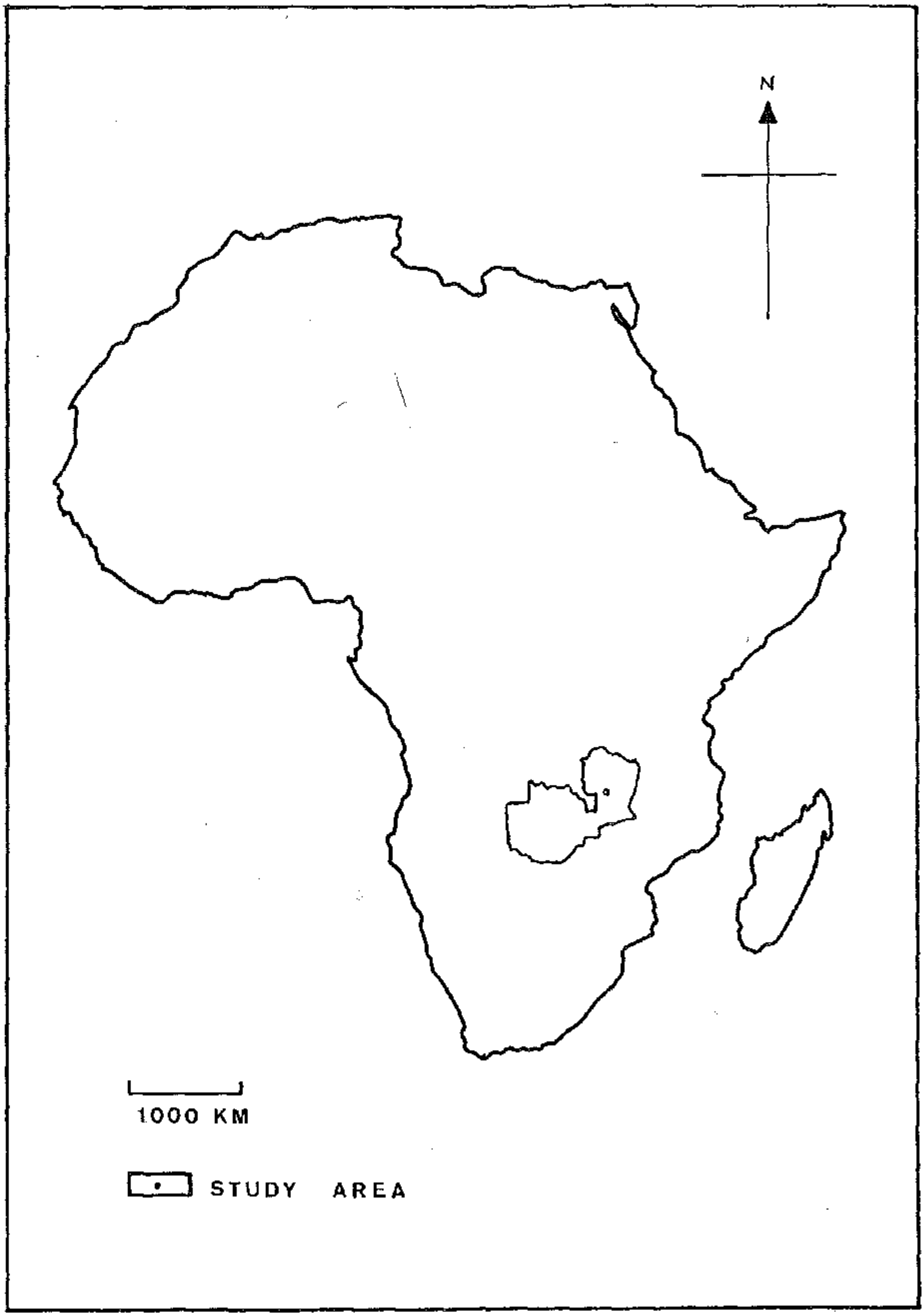


Figure 2. Study areas 1, 2 and 3, South East Bangweulu.

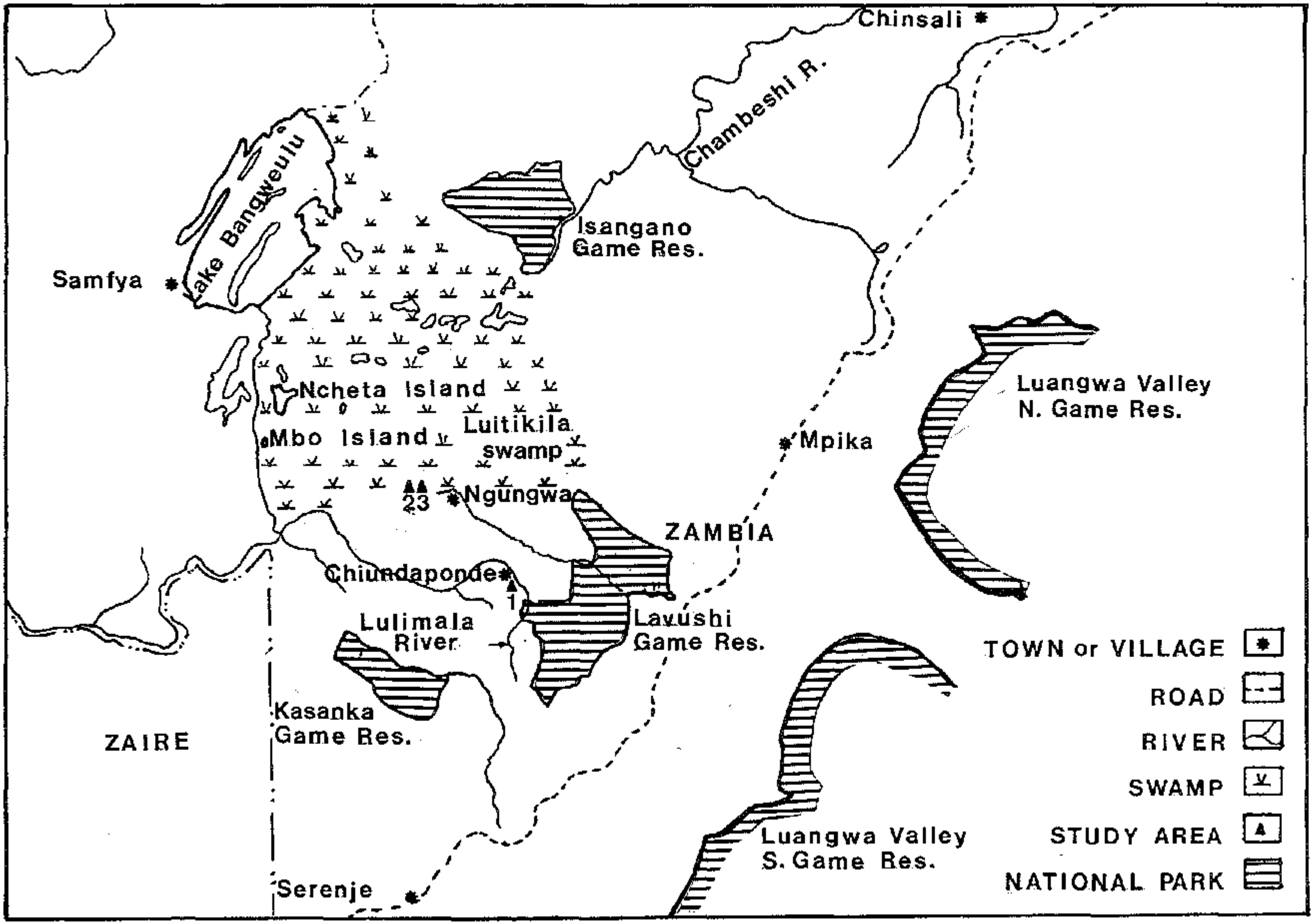


Figure 3.

LUKULU ESTUARY STUDY AREAS NO. 2 & 3

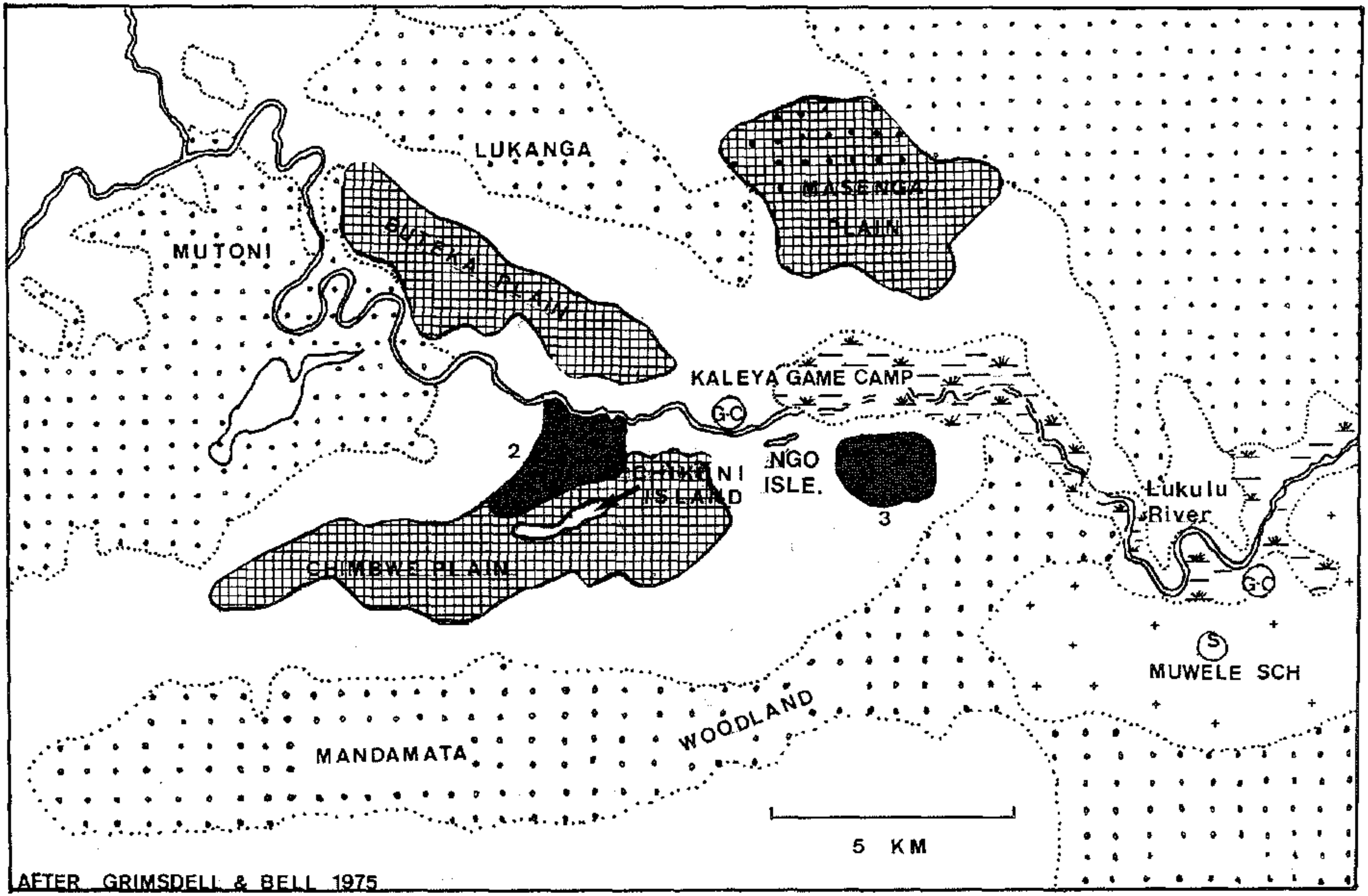


Figure 4.

Vegetation types within study area no.2

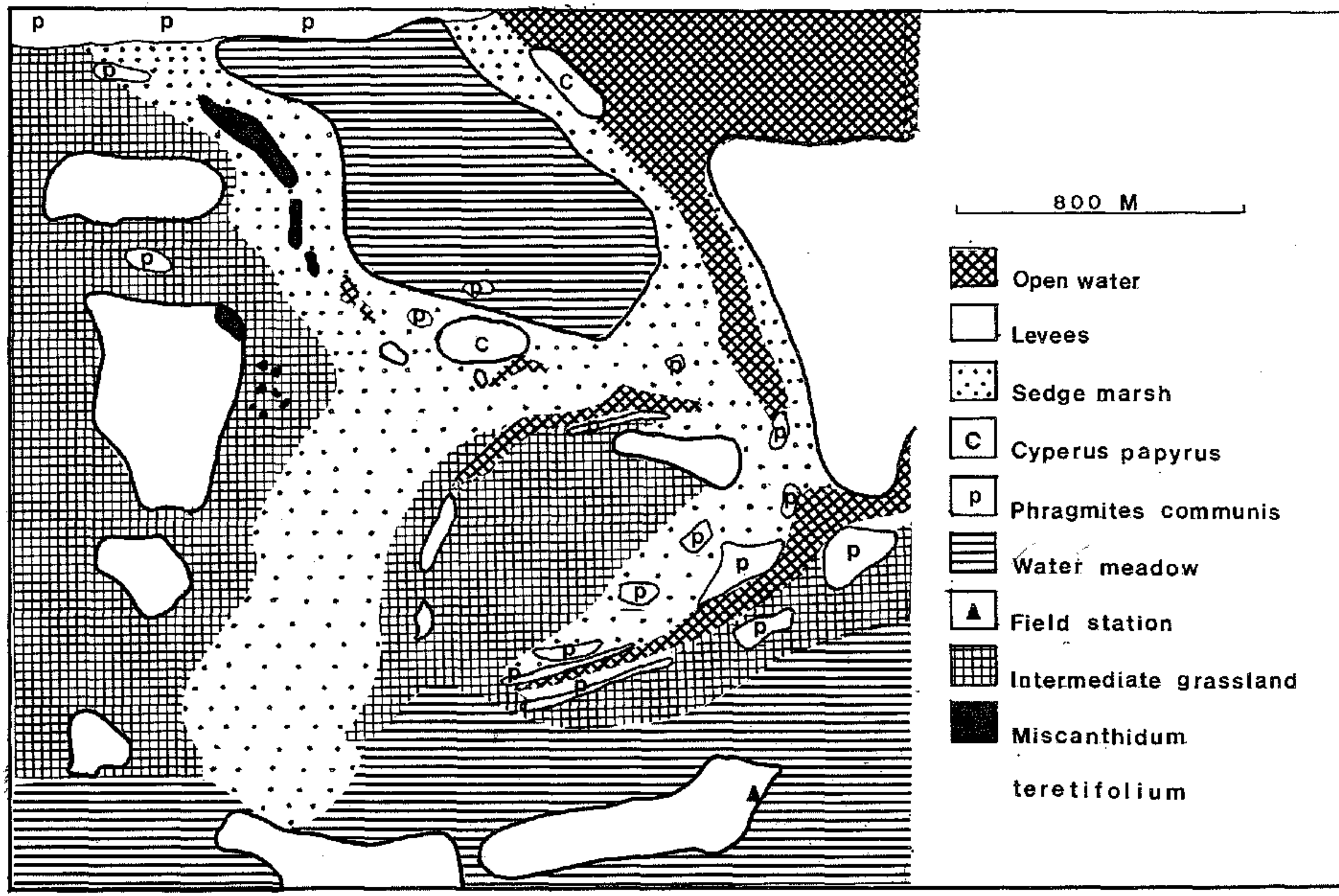


Figure 5.

SEASONAL OCCUPANCE OF STUDY AREA NO. 2 BY LECHWE

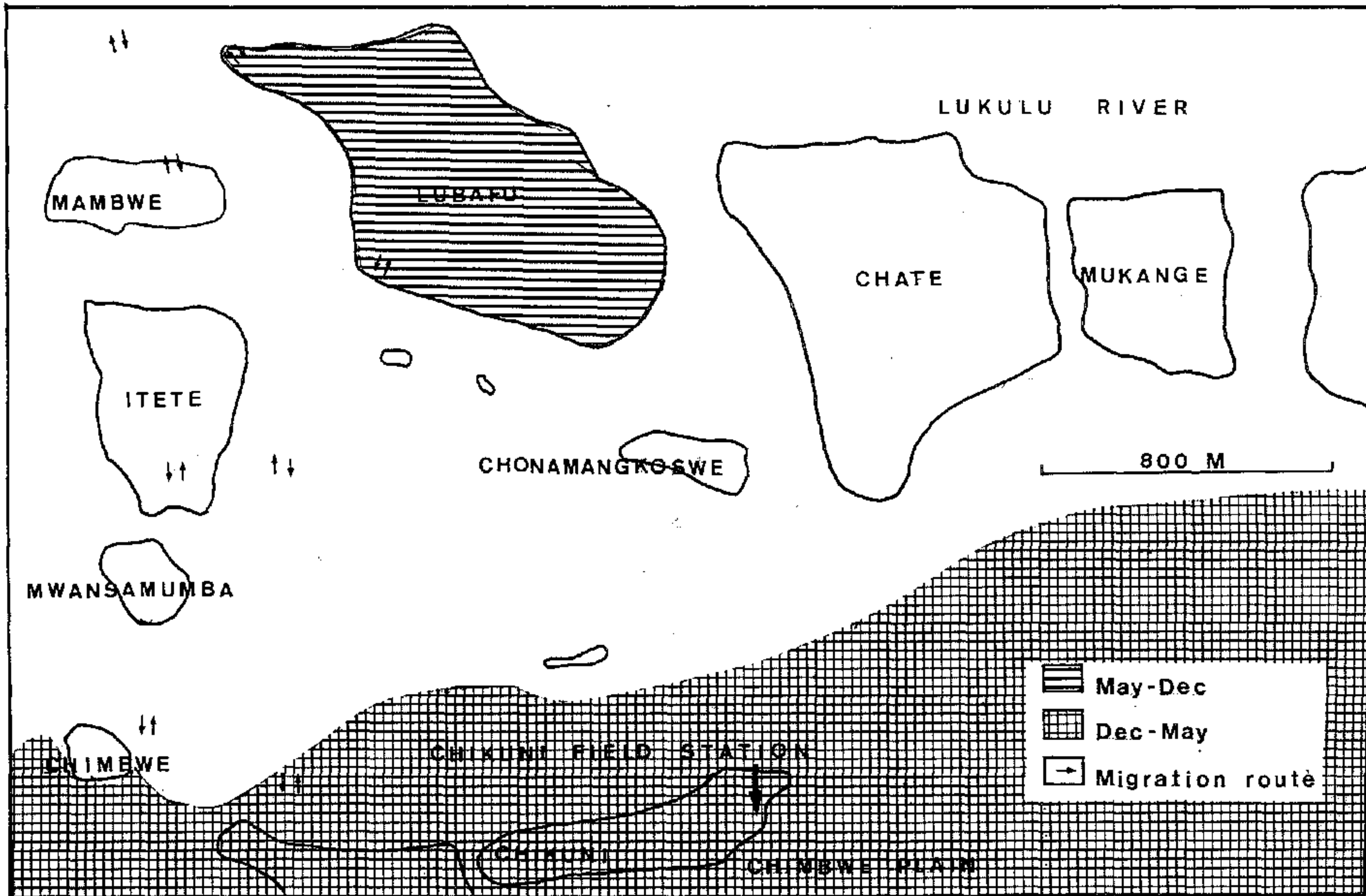


Figure 6 Distribution of sitatunga, Tragelaphus spekei.

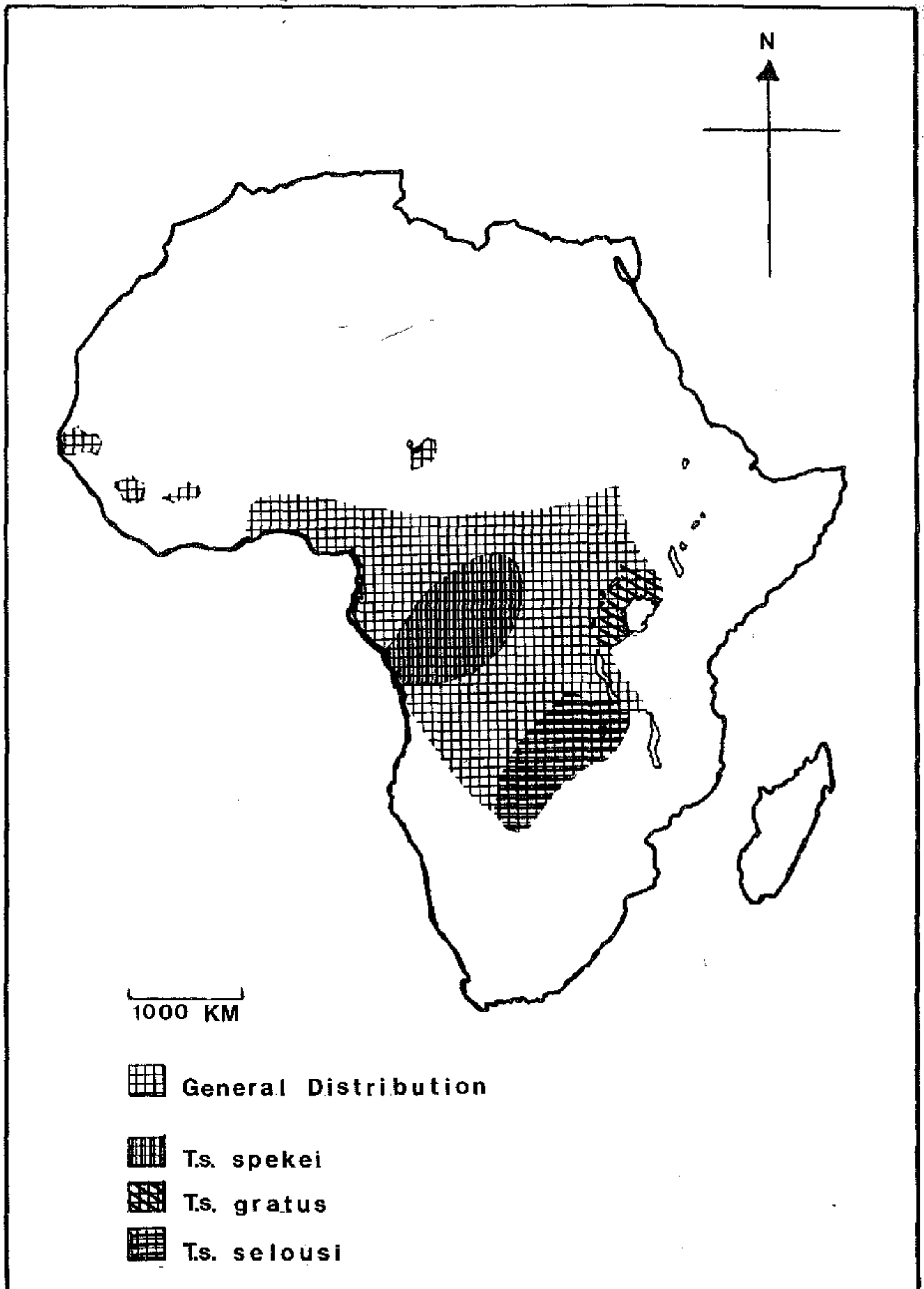


Figure 7.
DISTRIBUTION OF SITATUNGA IN ZAMBIA

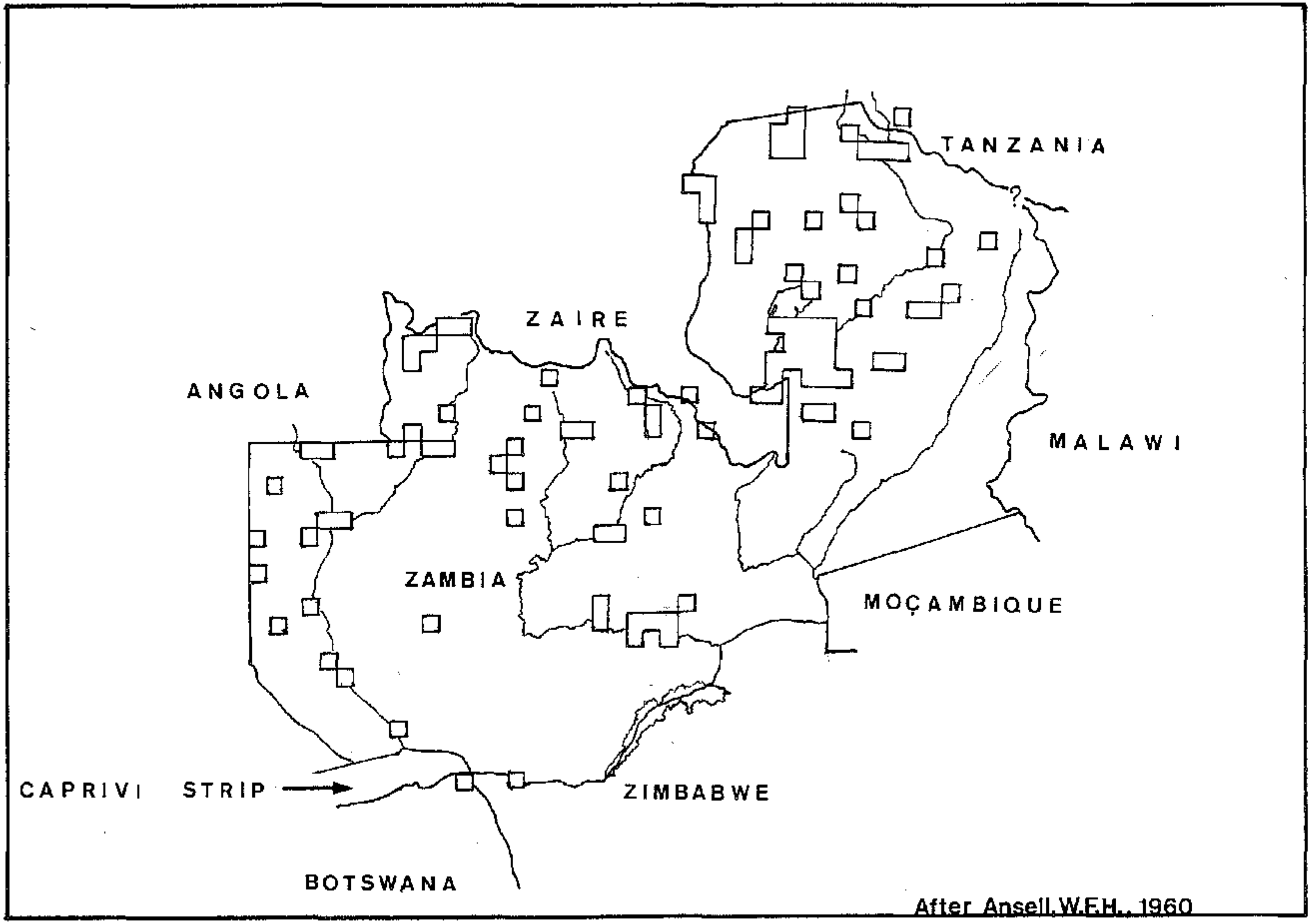


Figure 8A.Horn development in sitatunga.

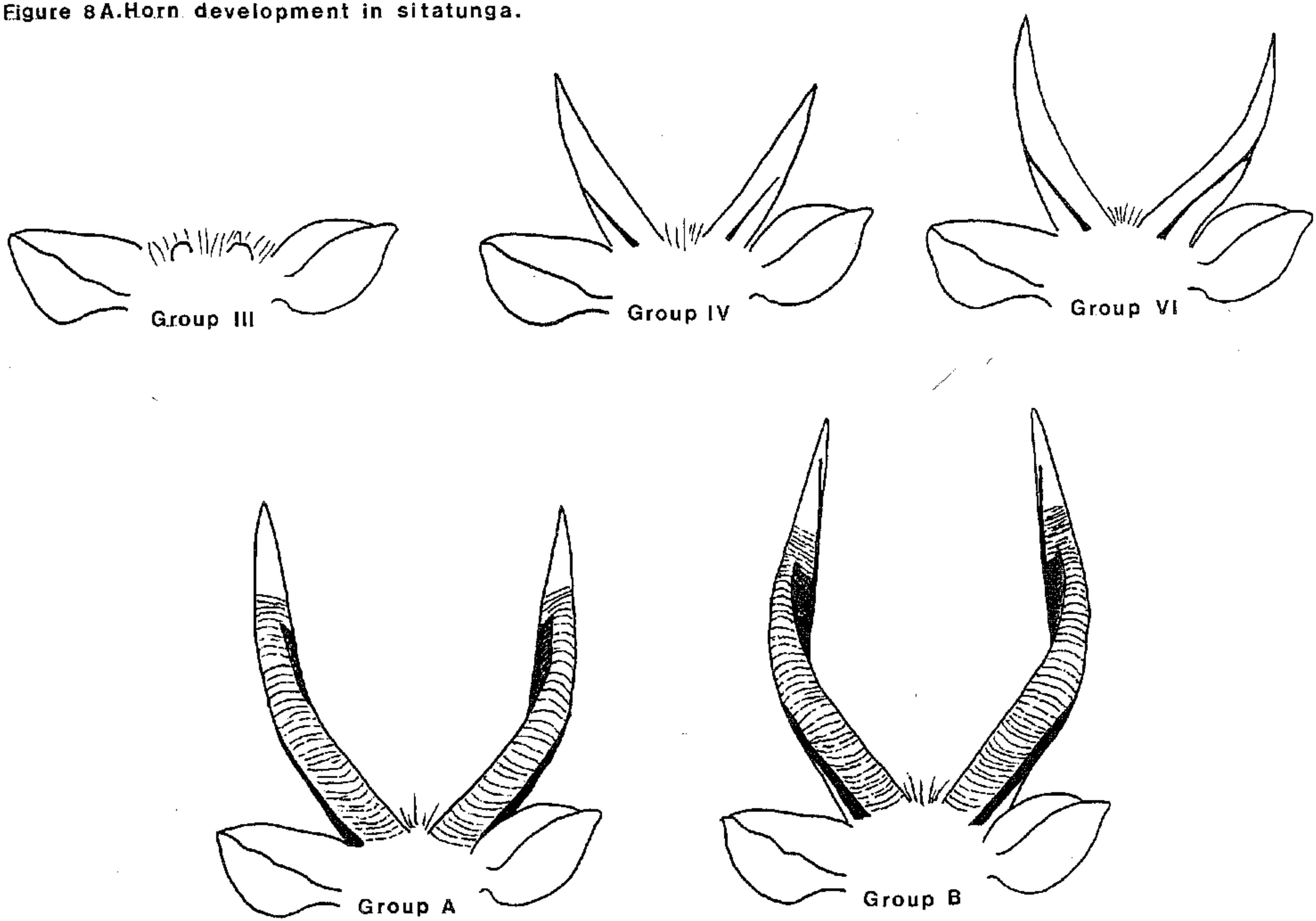


Figure 8B. Horn development in sitatunga.

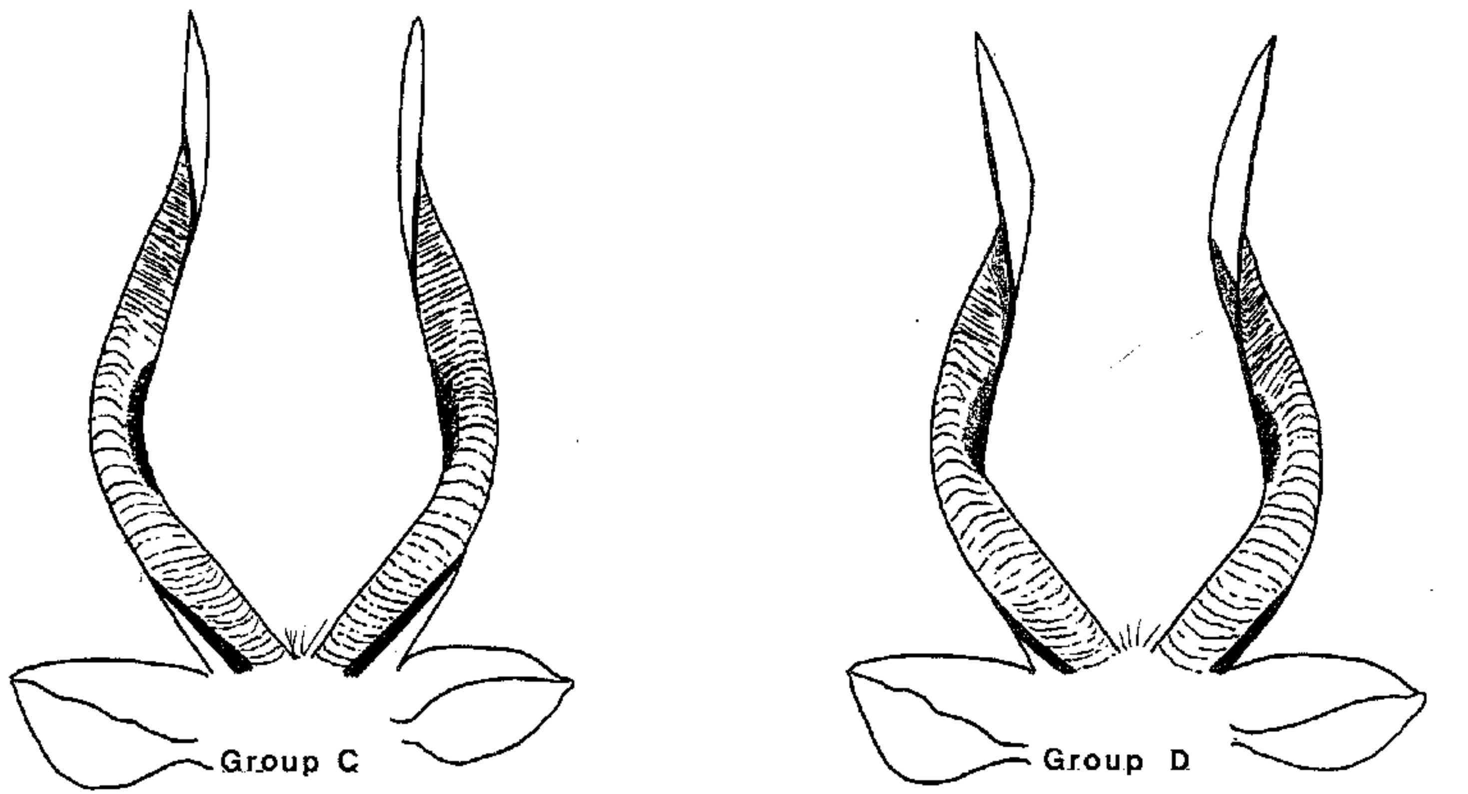


Figure 9. Adult male horn shapes.

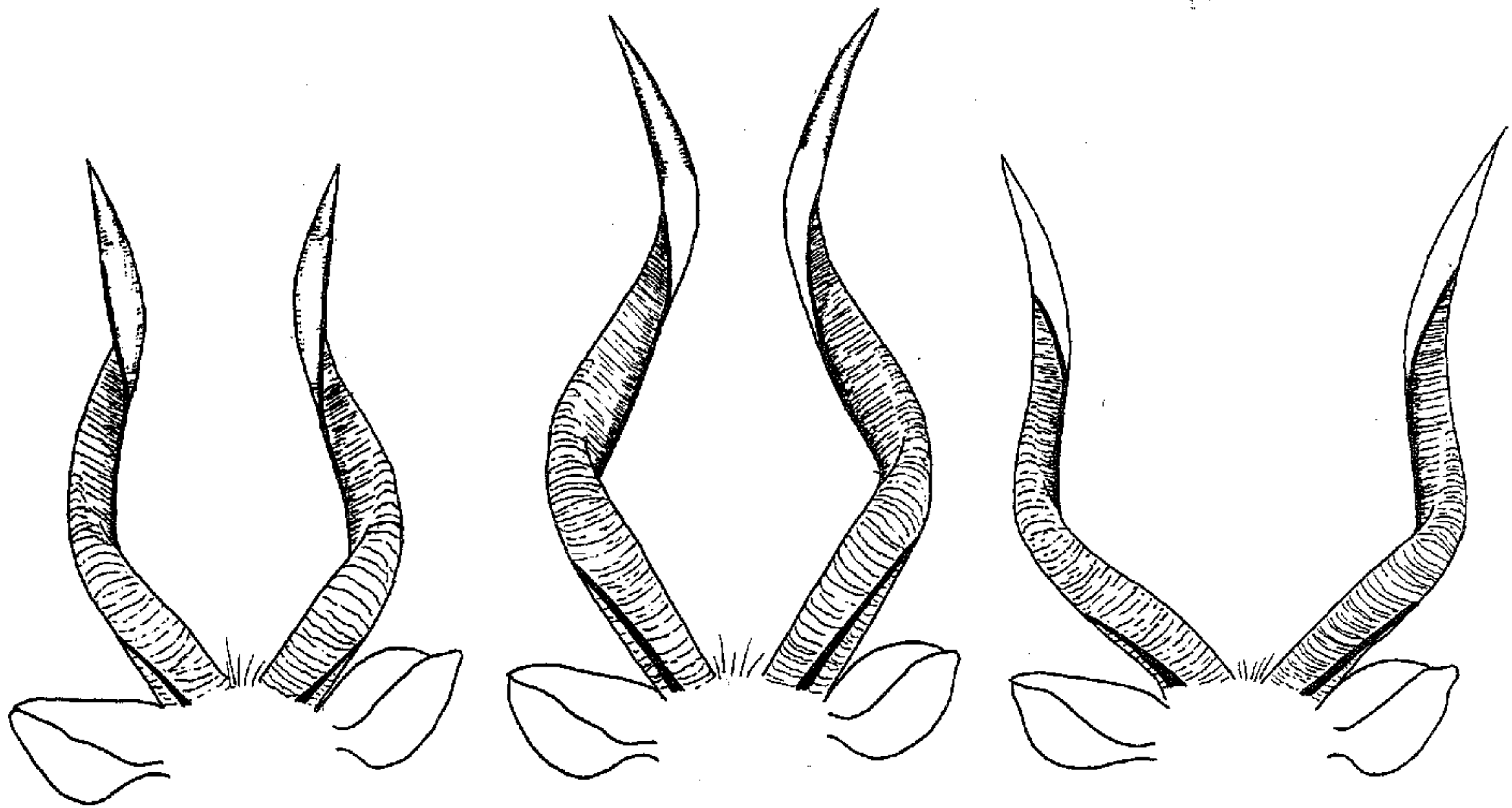


Figure 10. Sex and relative age structure of sample from study area 3. (n = 67)

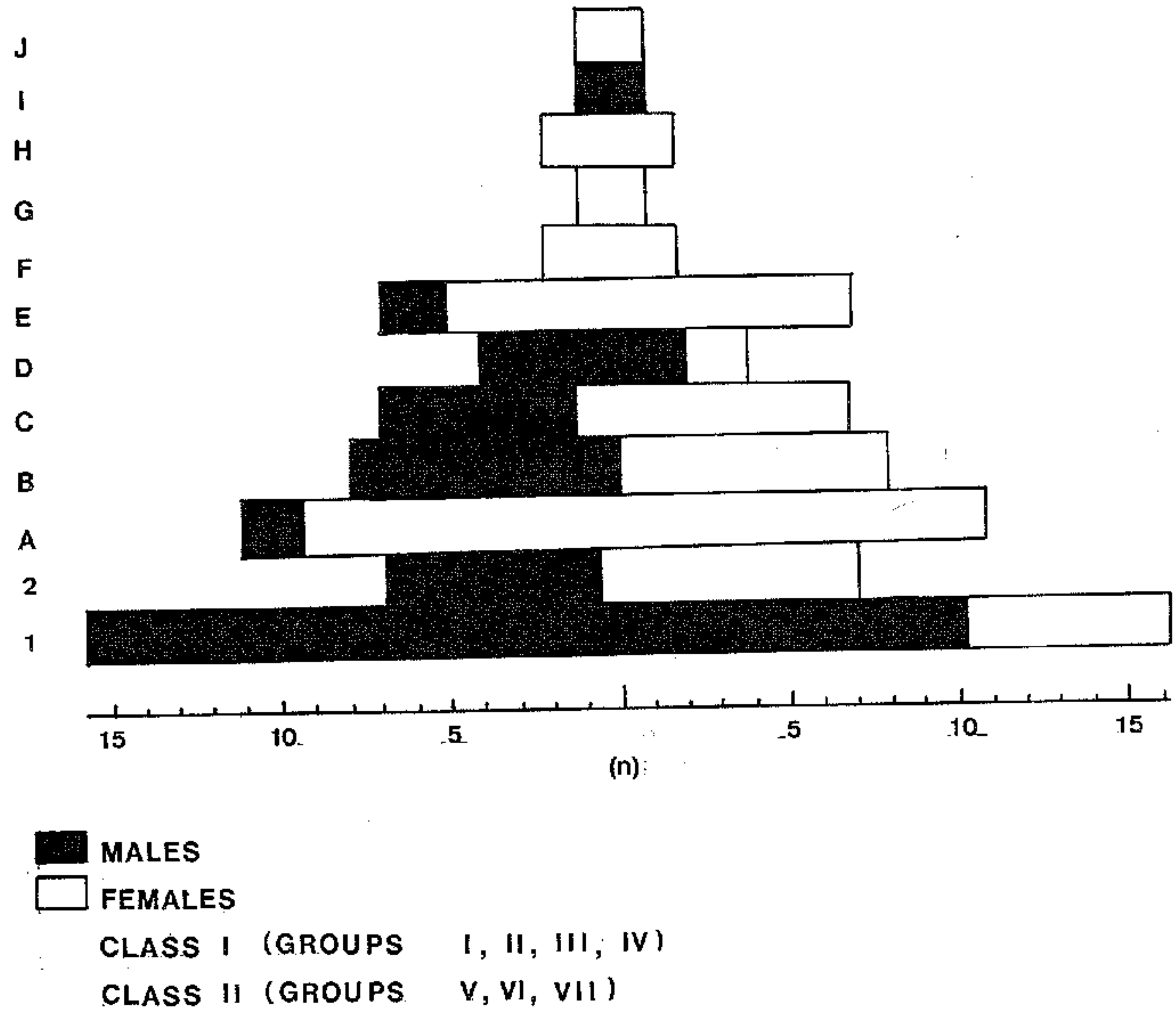
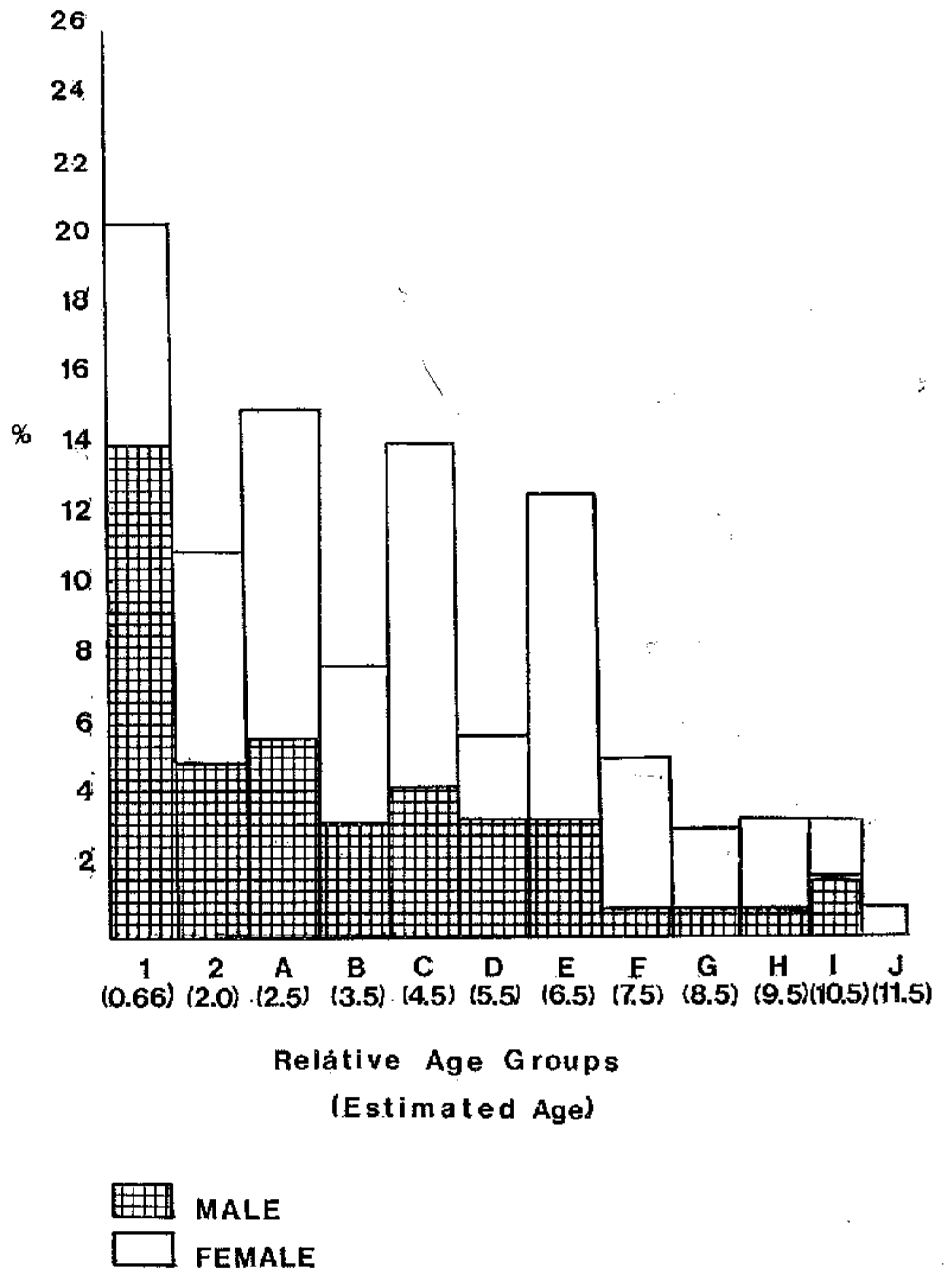


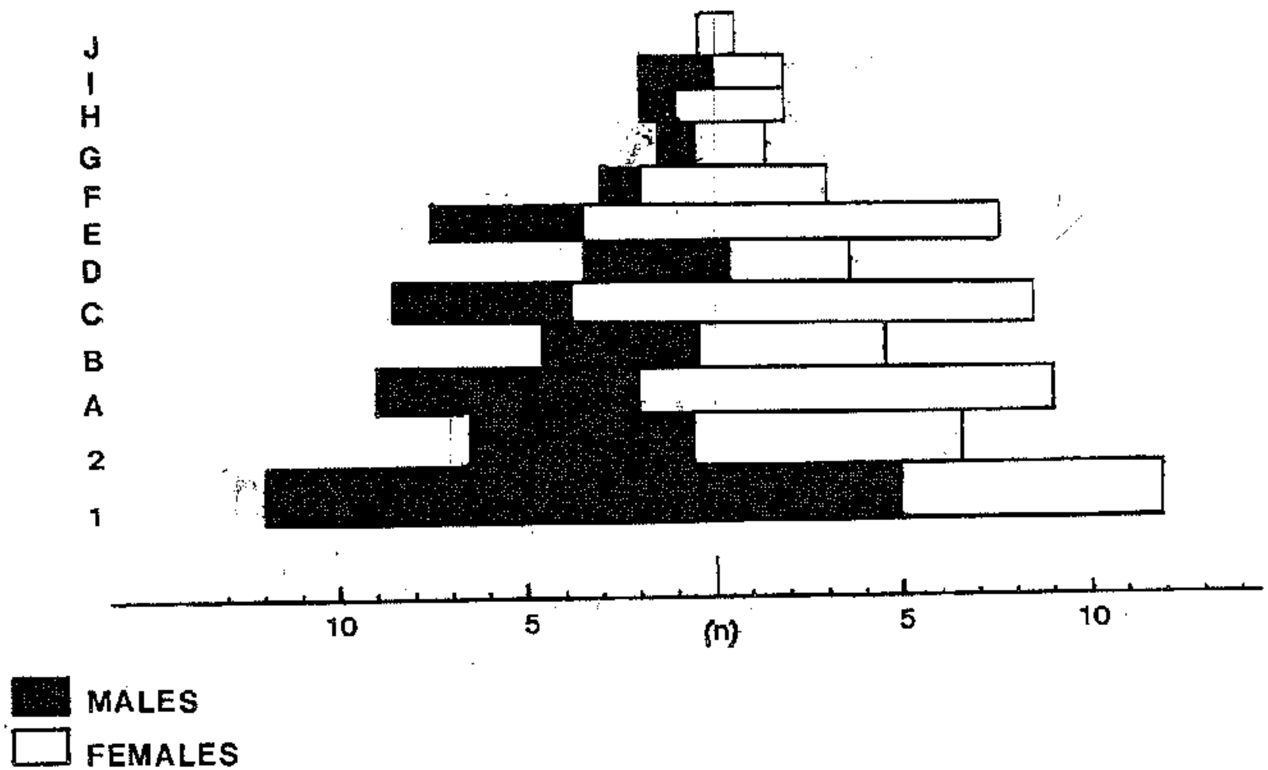
Figure 11. Percentage relative age distribution of total sampled population. (n: 123)



CLASS I (GROUPS I, II, III, IV)

CLASS II (GROUPS V, VI, VII)

Figure 12. Age distribution of the total sample population. (n : 123)



CLASS I (GROUPS I, II, III, IV)

CLASS II (GROUPS V, VI, VII)

Figure 13. Theoretical quadratic growth in live weight curves for male sitatunga. (n:51)

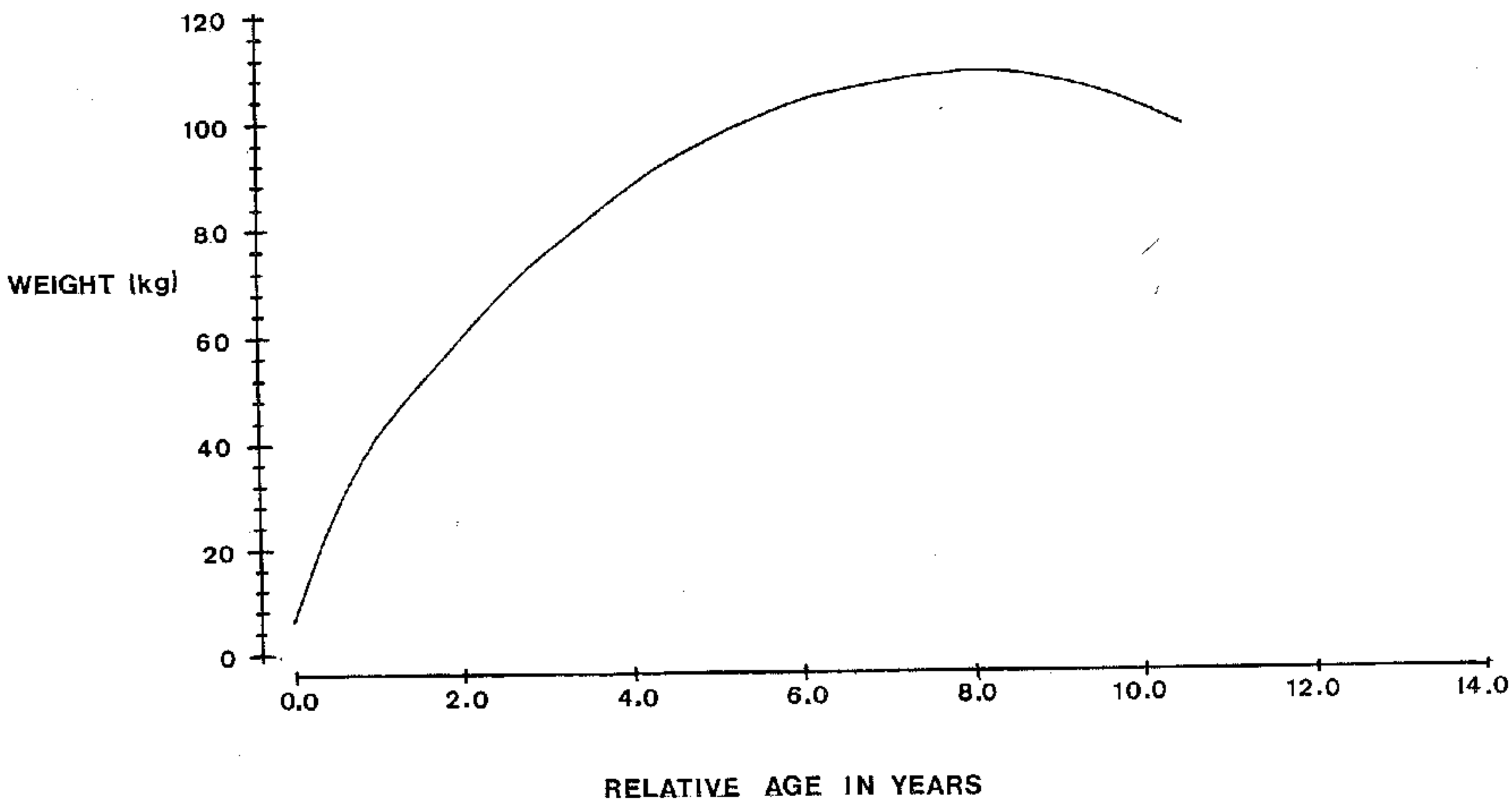


Figure 14. Theoretical quadratic growth in live weight curves for female sitatunga. (n:68)

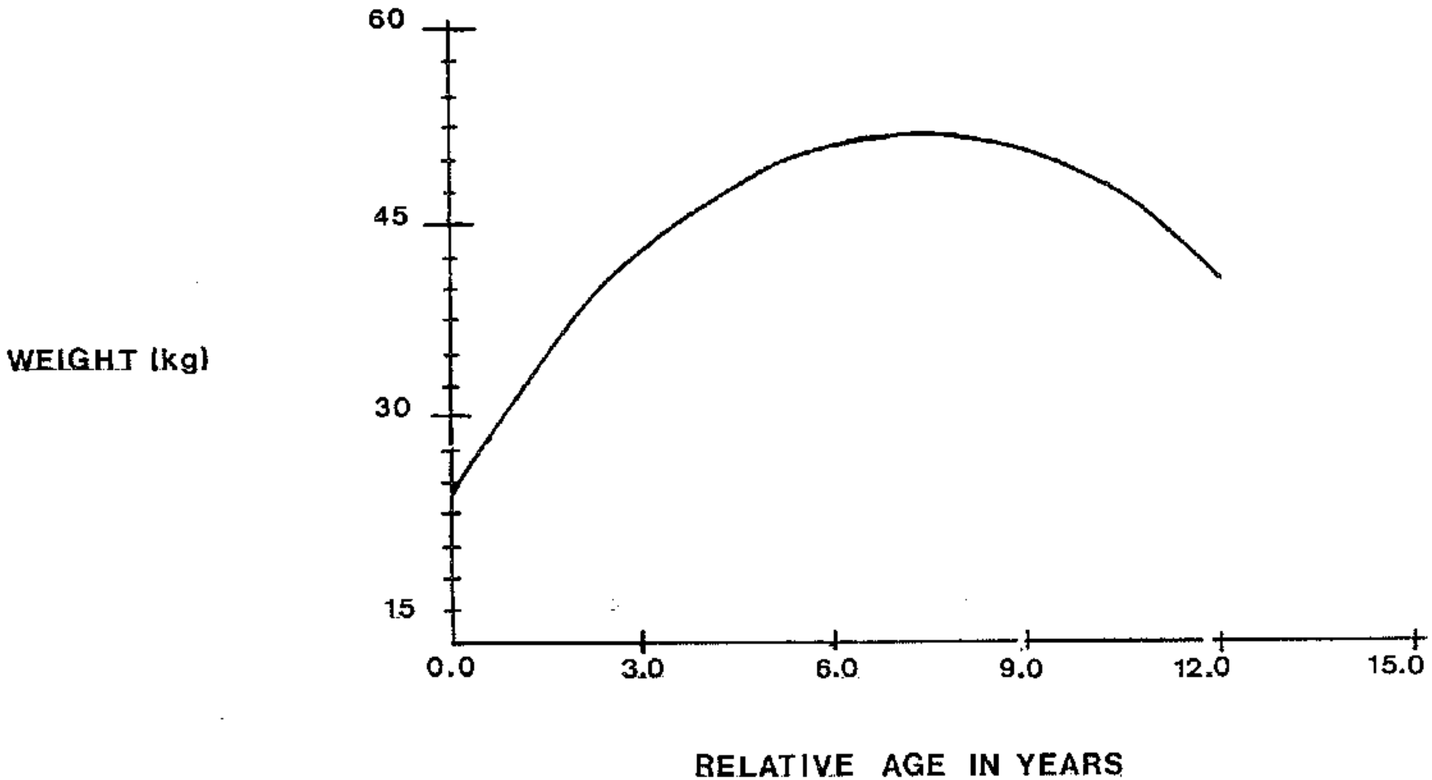


Figure 15. Horn growth of sitatunga related to relative age. (n=5)

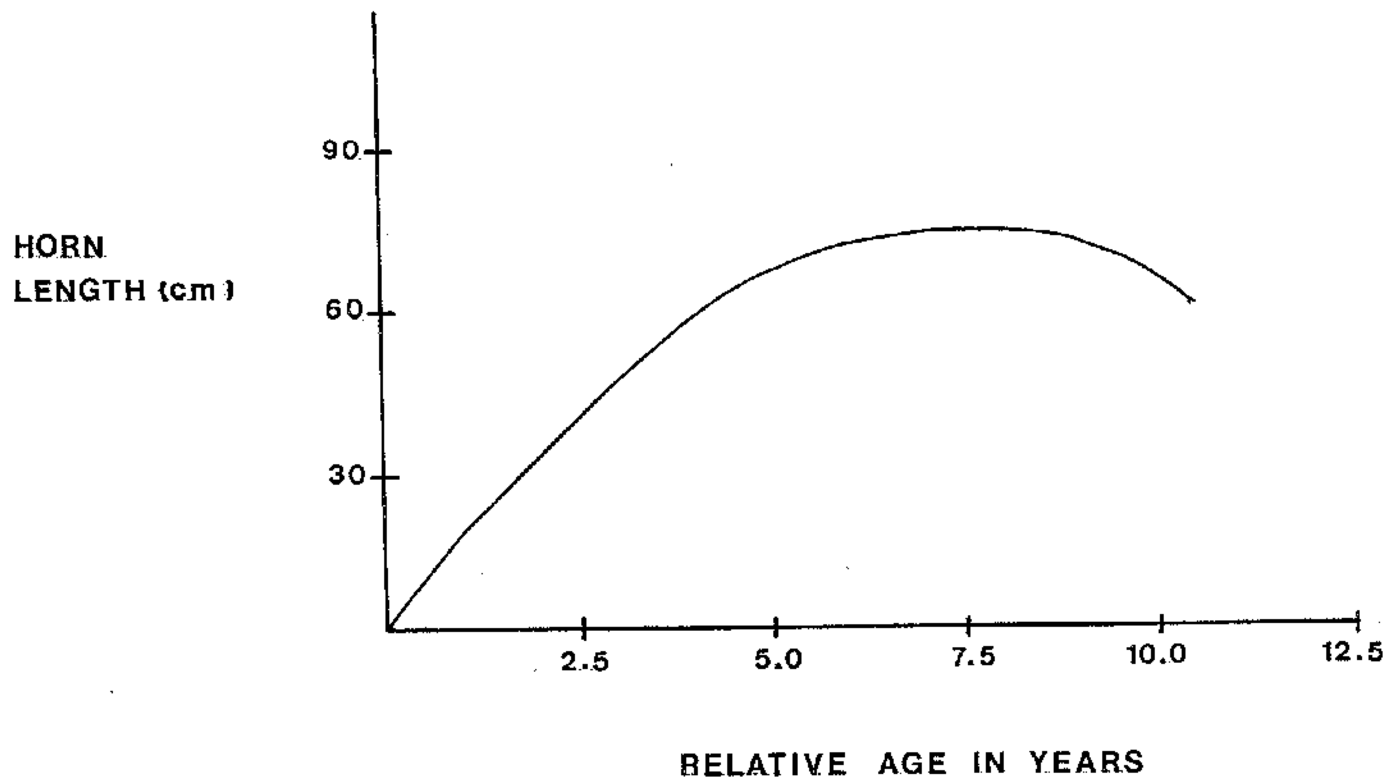


Figure 16. Conception and parturition peaks in the Bangweulu related to rainfall.

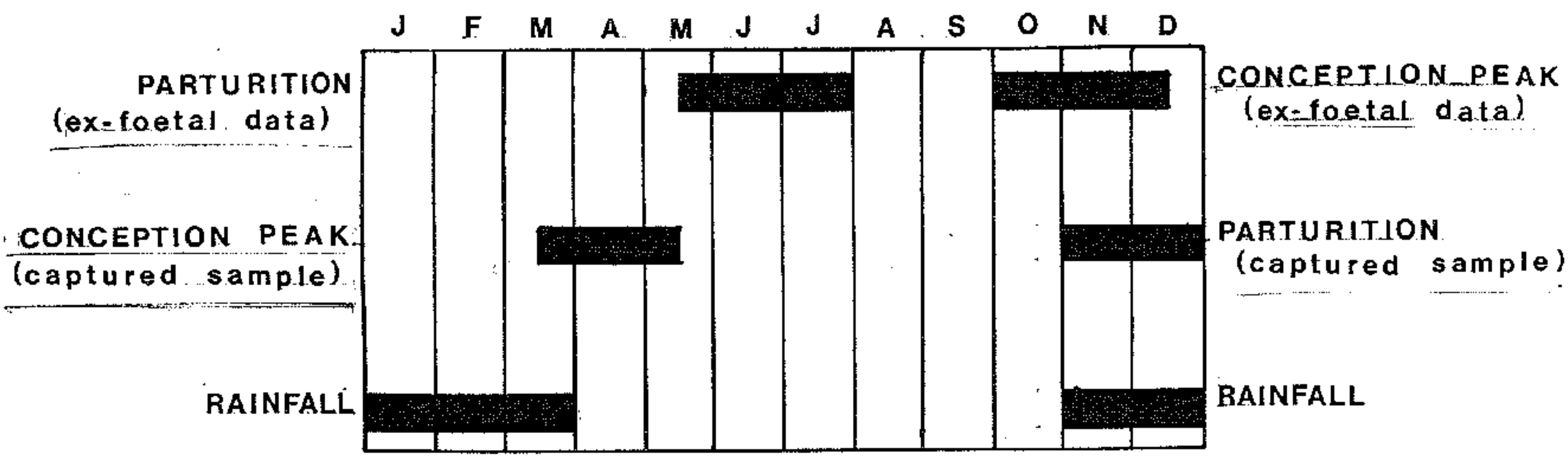


Figure 17. Parturition peaks for sitatunga, two congenerics and for two other species found in the Bangweulu.

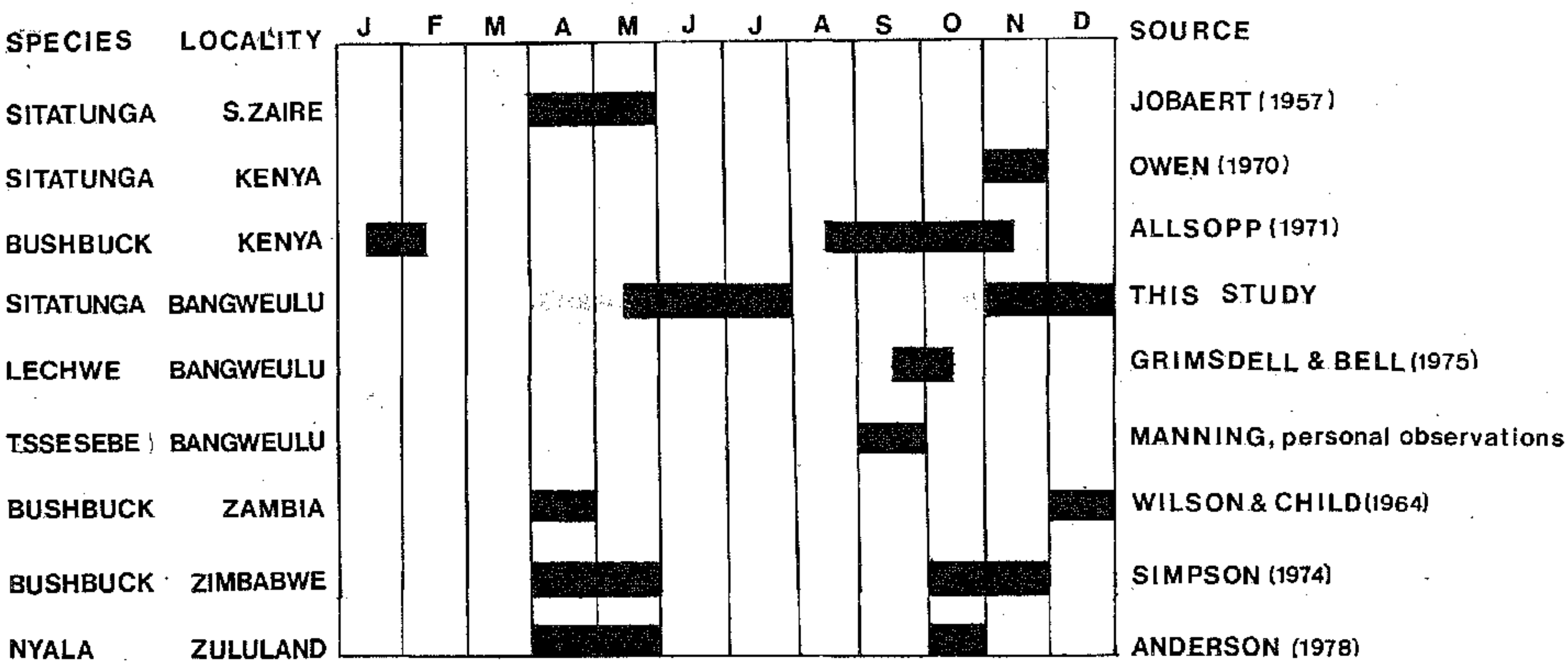


Figure 18. Conception distribution peaks for some nyala, bushbuck and sitatunga populations.

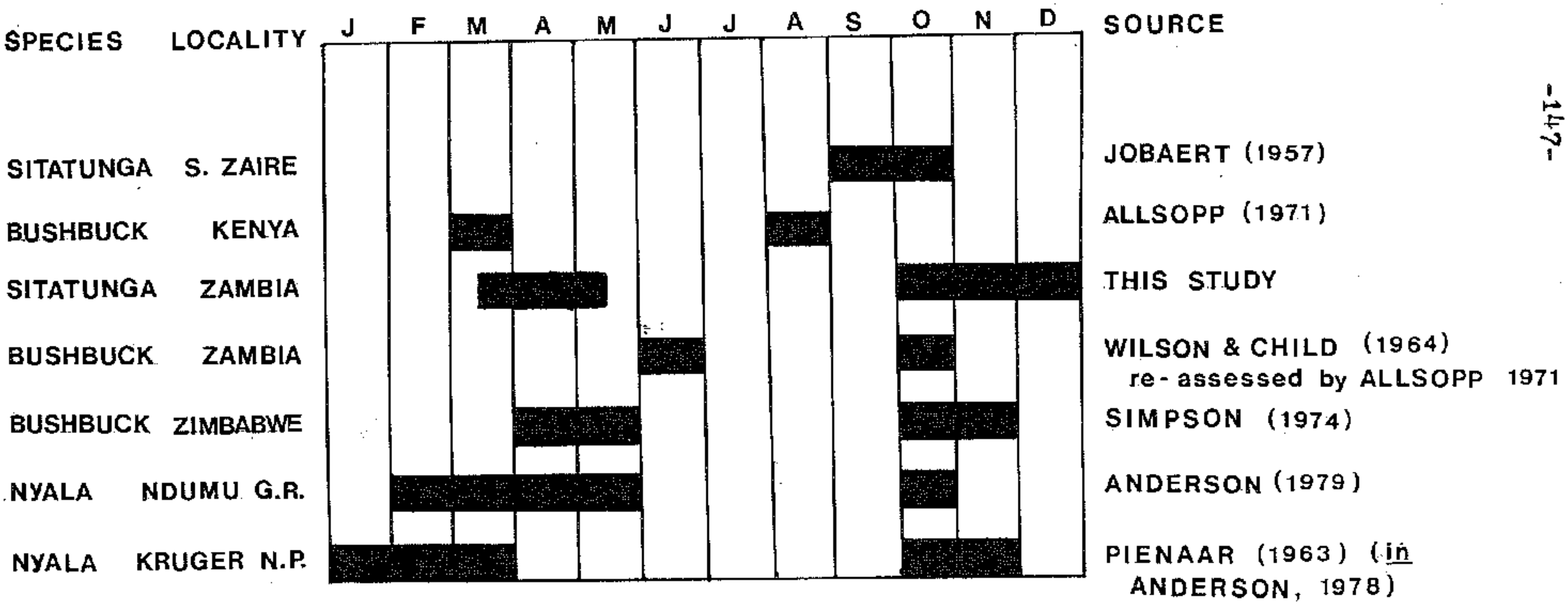


Figure 19. Sitatunga births in four European zoos.

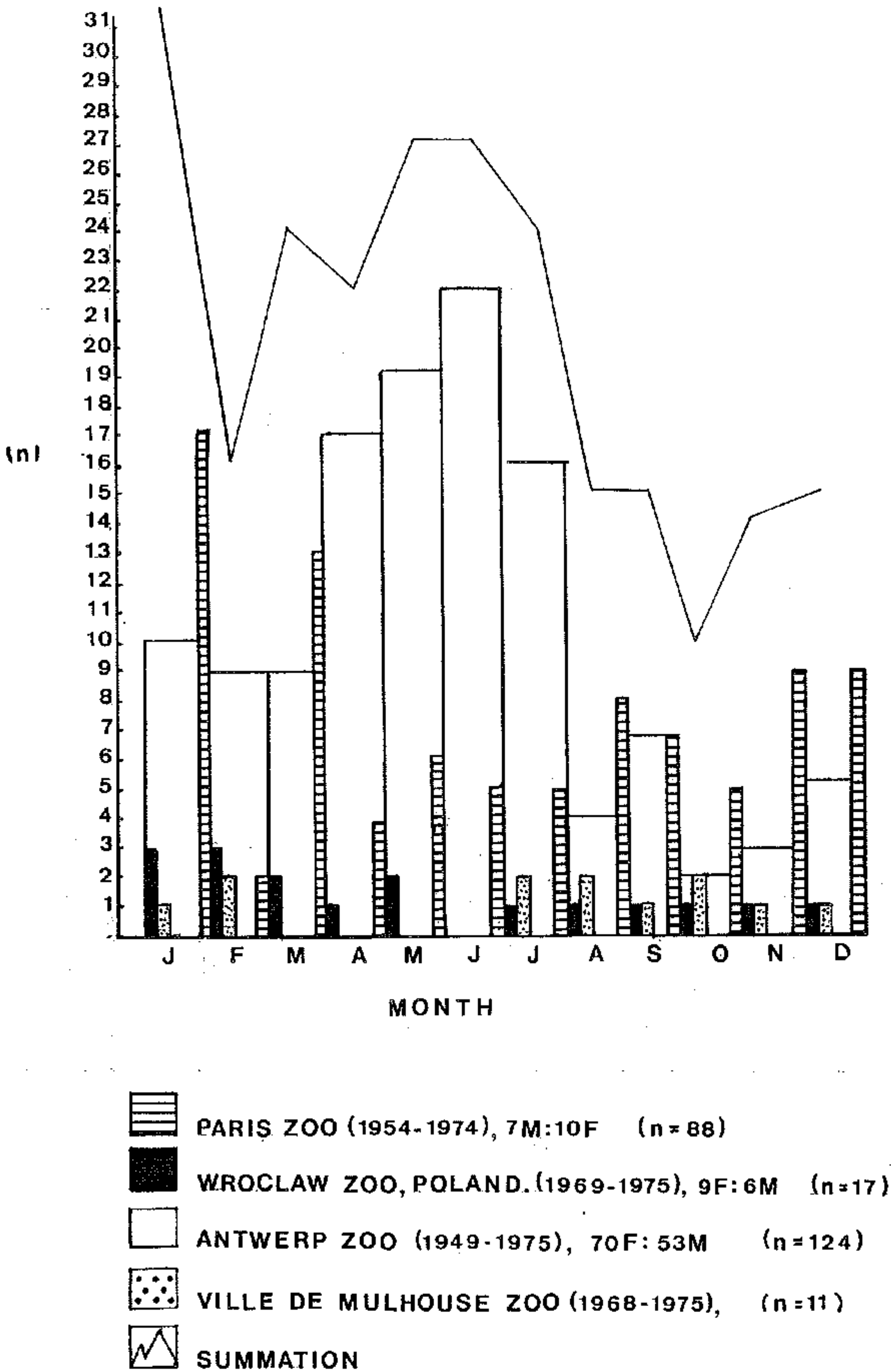


Figure 20.

SEASONAL WATER OCCUPANCE OF STUDY AREA NO. 2

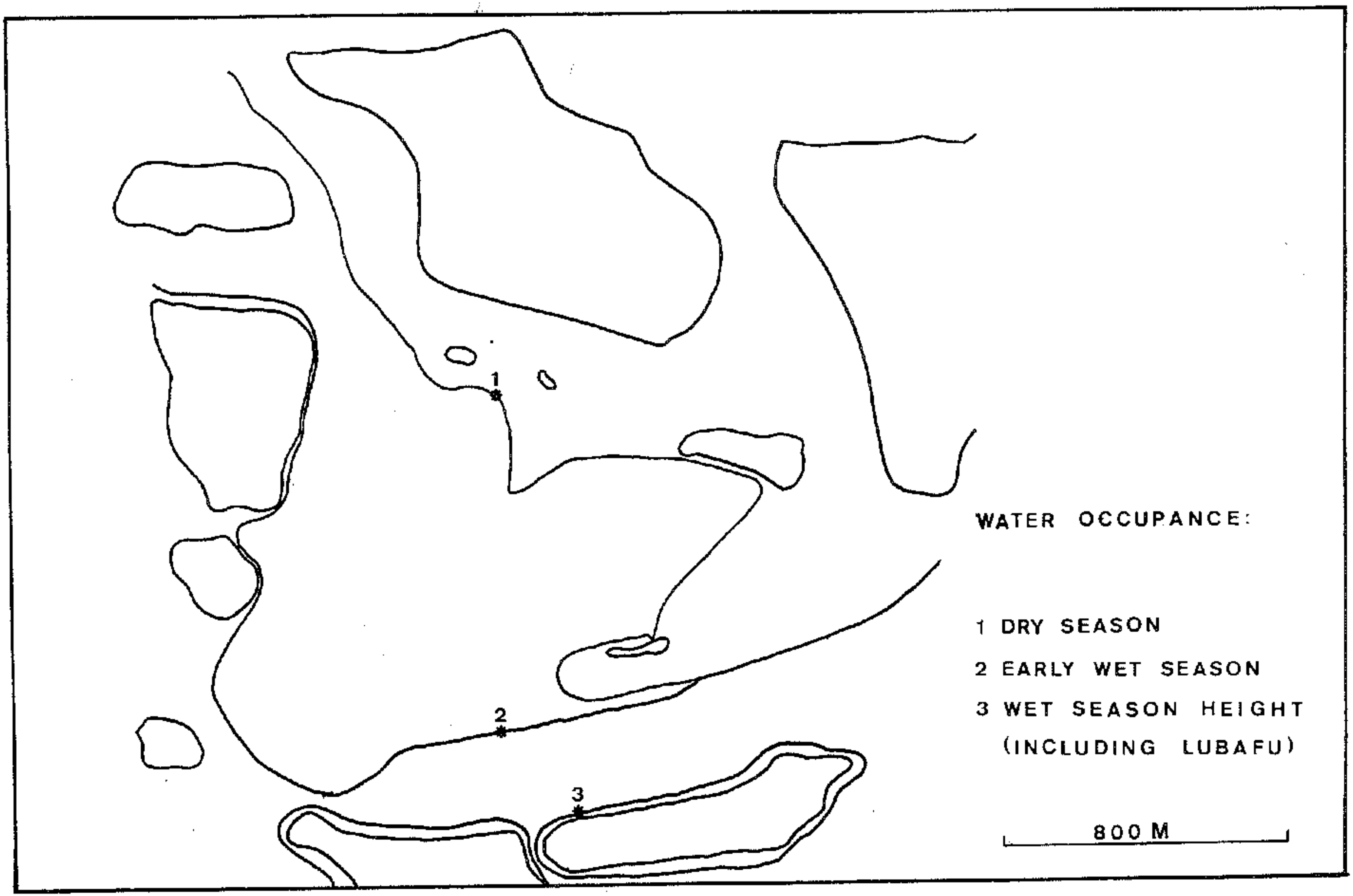


Figure 21.
CAPTURE & OBSERVED POSITIONS OF SITATUNGA IN STUDY AREA NO. 2

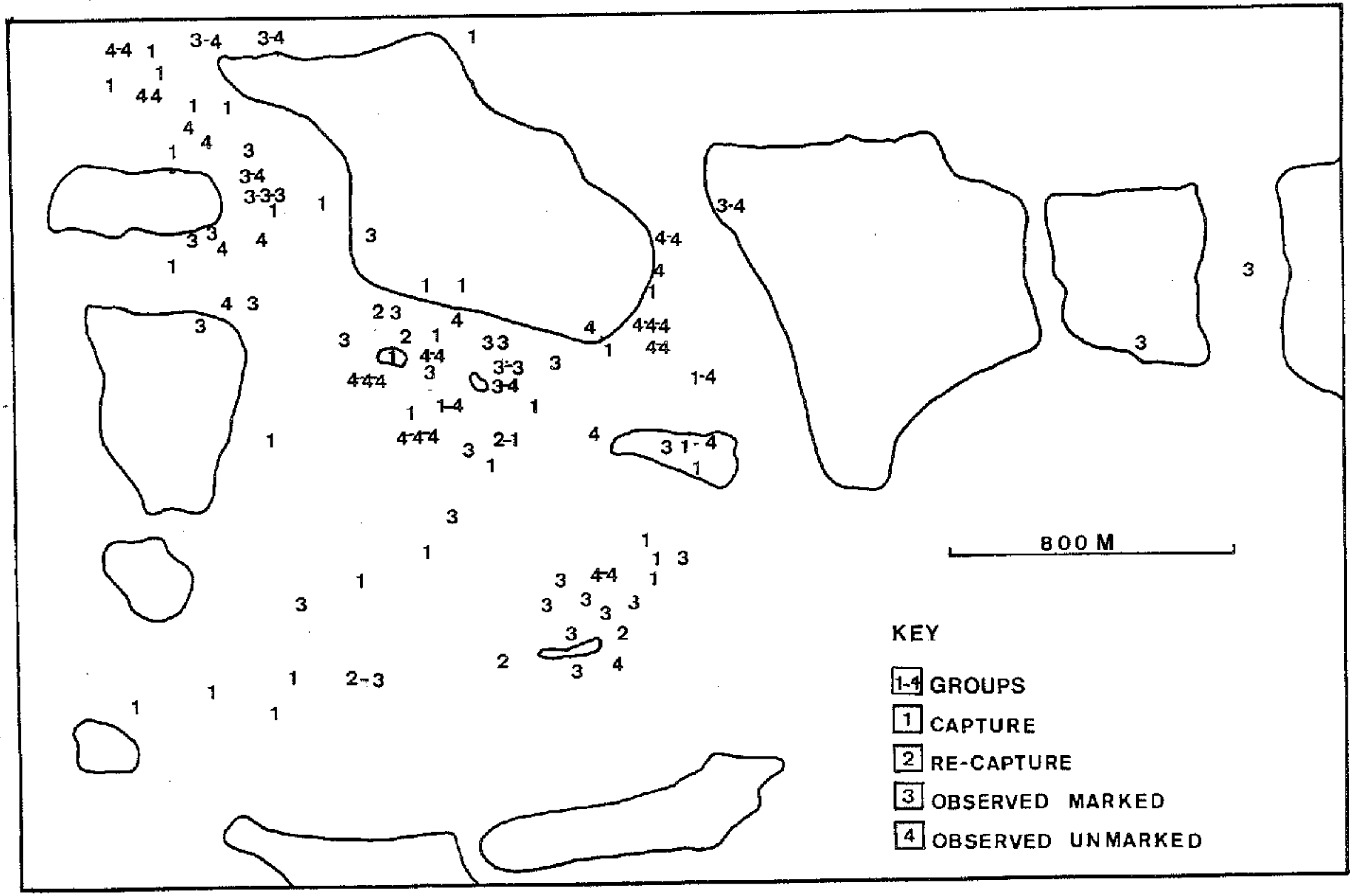


Figure 22.
Study area no.2. Minimum home ranges of six adult males.

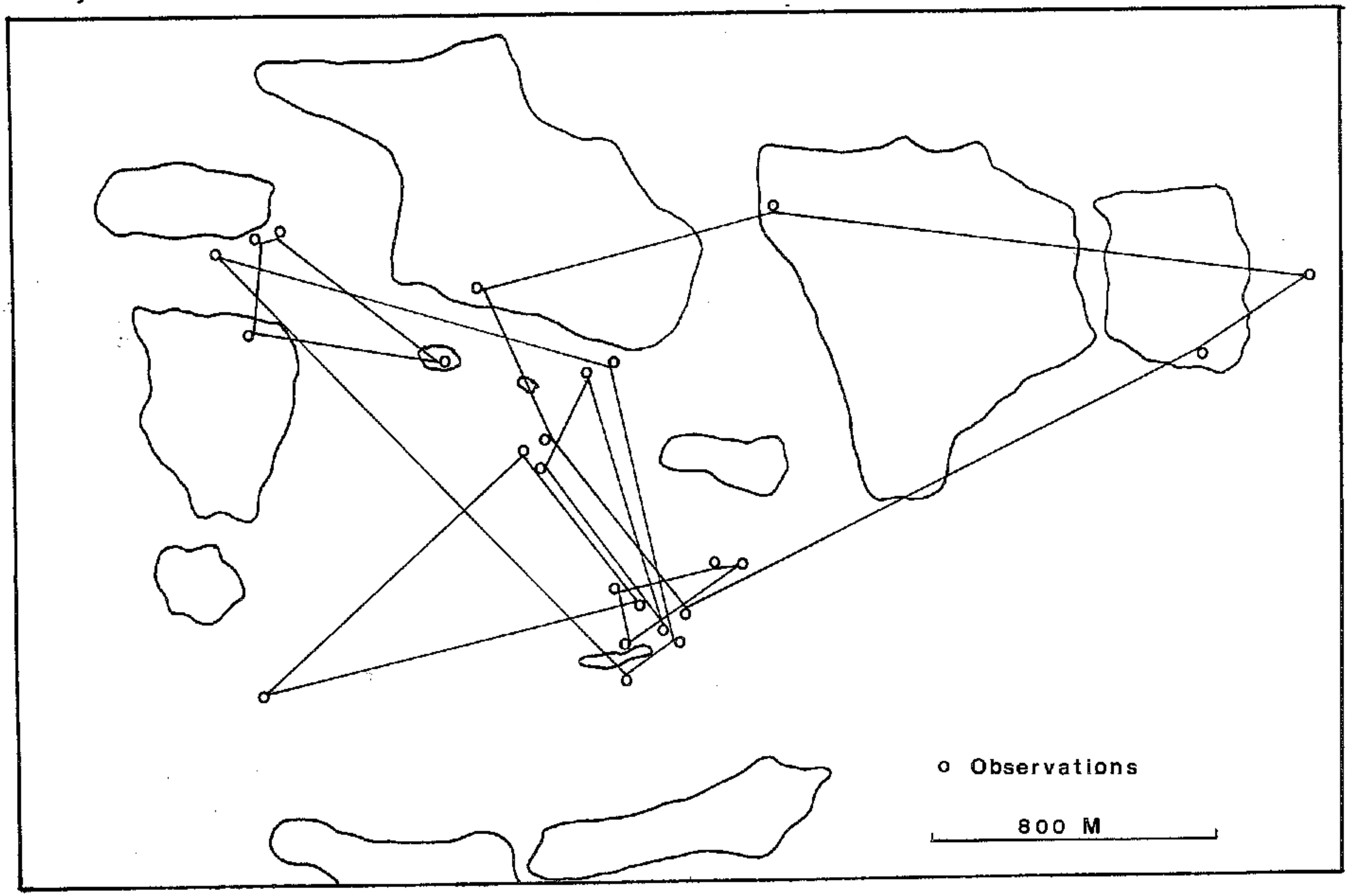


Figure 23.
Study area no. 2. Minimum home range of three adult females.

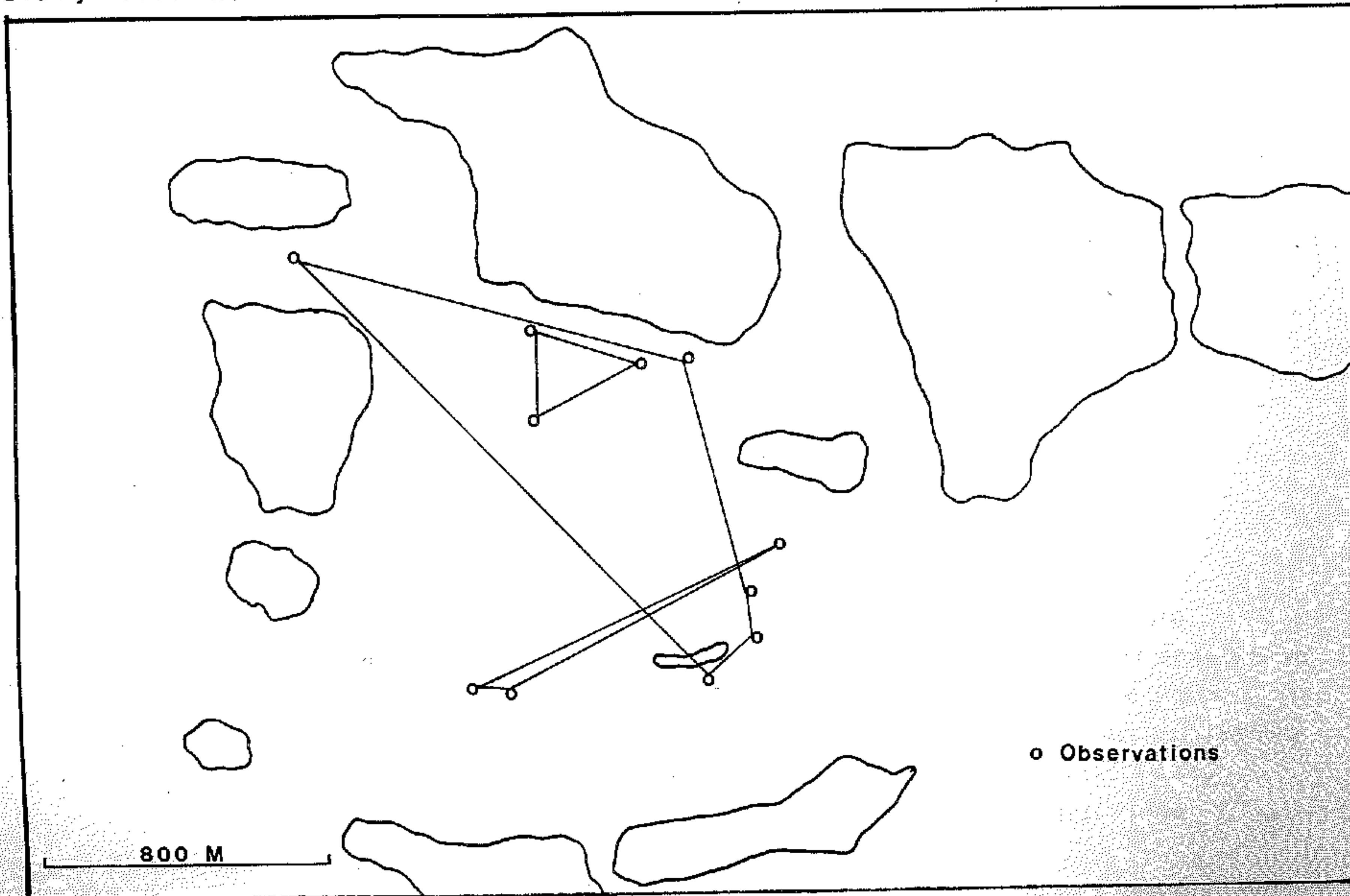


Figure: 24.

Sitatunga marked, & then observed or captured at yearly intervals.